# Arctic Biodiversity Assessment

## Status and trends in Arctic biodiversity

Conservation of Arctic Flora and Fauna

ARCTIC COUNCIL

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**Cover photo:** Muskoxen are hardy animals that had a circumpolar distribution in the Pleistocene, but Holocene climate changes along with heavy hunting may have contributed to its disappearance in the Palearctic and from Alaska and Yukon. In modern times, humans have reintroduced muskoxen to Alaska and the Taymyr Peninsula together with a number of places where the species did not occur in the Holocene. Photo: Lars Holst Hansen.

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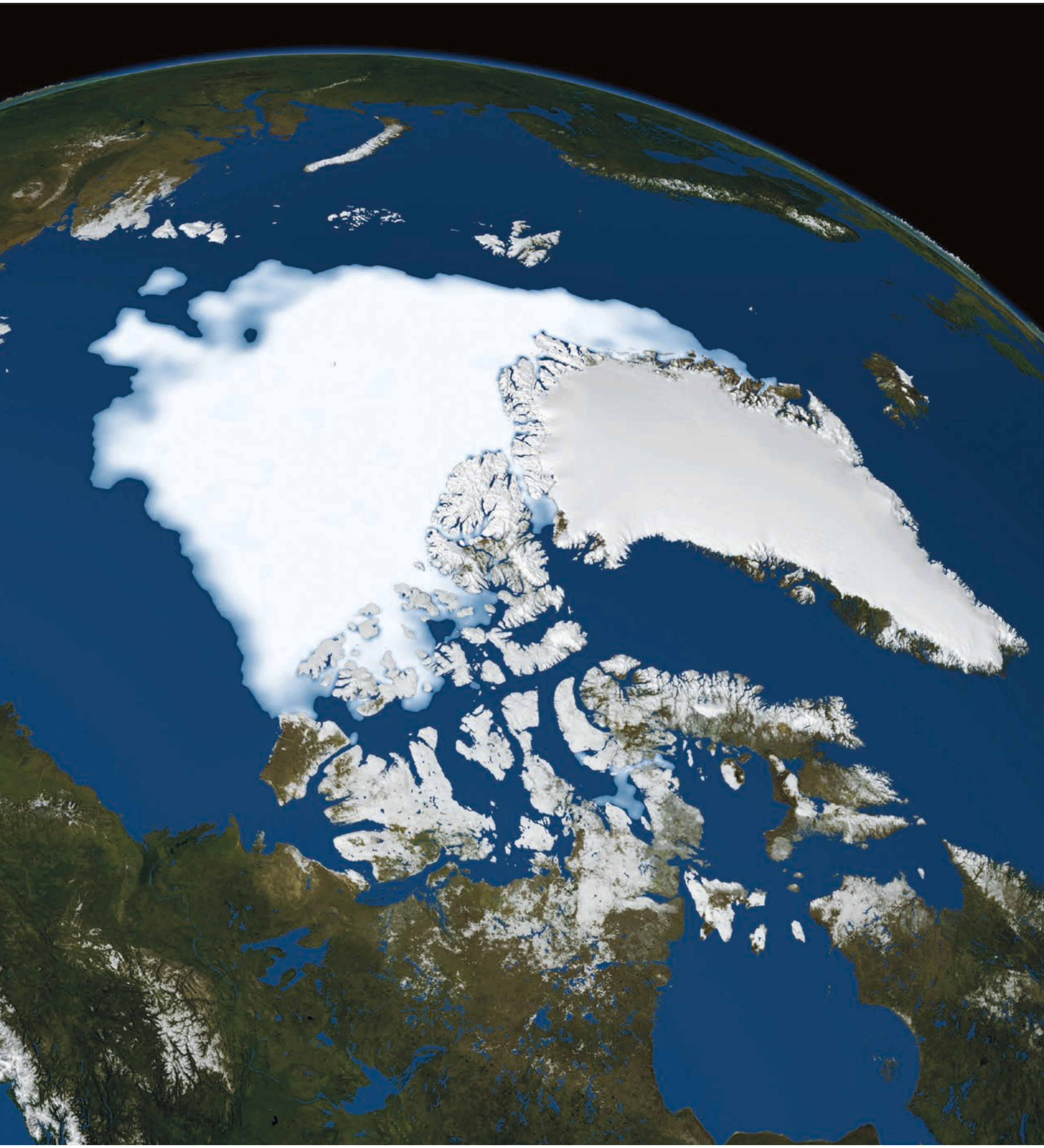

# Preface by CAFF and Steering Committee Chairmen

The eyes of the world are turning northwards. In recent years, interest in the Arctic has increased dramatically within and outside of Arctic countries. This is reflected in the amount of attention given to Arctic biodiversity. While the landscapes and wildlife have been the subject of explorers, scientists, artists and photographers as well as the home of a variety of peoples for a long time, until recently Arctic biodiversity did not feature very prominently in national or international policy work. This, however, is changing, as the unique values of Arctic nature are increasingly discussed at high levels. At the same time, more and more attention has been paid to the interface between science and policy to ensure that policy is built on the best science available.

We are therefore very happy and proud to present the Arctic Biodiversity Assessment (ABA), which has been seven years in the making. It is the result of the contributions from 253 scientists together with holders of traditional knowledge. The chapters in the main document, which you are holding now, have been peer-reviewed by over 100 scientists from all over the Arctic and the rest of the world. We are very grateful for the efforts they have made to ensure the quality of this assessment. We would especially like to thank Chief Scientist Hans Meltofte and the lead authors of the chapters.

In order to communicate the findings presented in this scientific work and to inform policy makers, the board of the Arctic Council's working group on the Conservation of Arctic Flora and Fauna (CAFF) has prepared a summary of the key findings and developed policy recommendations. The key findings and recommendations have been provided in a separate document, which we trust will be useful for all those who make decisions that may affect Arctic biodiversity.

The Arctic is home to a vast array of biodiversity, including many globally significant populations. Included among these are 30% of the world's shorebird species, two thirds of the global numbers of geese, several million reindeer and caribou, and many unique mammals, such as the polar bear. During the short summer breeding season, almost 200 species of birds arrive from almost all parts of the world, connecting the Arctic with the rest of the globe. We therefore hope that the ABA will be consulted frequently within as well as outside of the Arctic.

Biodiversity is life. It is the very foundation of our existence on Earth. In the Arctic, links between biodiversity and traditional ways of life are often seen more clearly than in many other parts of the world. These are examples of ecosystem services, the benefits that we receive from nature. Many ecosystems and ecosystem functions in the Arctic remain largely unstudied and involve little-known organisms, especially microbes. The ABA presents current knowledge also on these processes and organisms and thus provides a base for further work.

But biodiversity is more than a means for humankind to survive. The unique nature of the Arctic is not just an asset for us to use. It is also a source of wonder, enjoyment and inspiration to people living in the Arctic and across the globe. It has intrinsic values that cannot be measured. We sincerely hope that the ABA will not only create the baseline reference for scientific understanding about Arctic biodiversity, but that it also may inspire people to take effective actions on the conservation of Arctic flora and fauna. We hope it gives people reasons to love Arctic nature as much as we do.

Yakutsk, 17 February 2013
Evgeny Syroechkovskiy, Chair of CAFF
Mark Marissink, Chair of the ABA Steering Committee

The king eider is one of the fascinating species endemic to the Arctic.
Photo: Patrick J. Endres.

# Foreword by the Chief Scientist

Until recently, most Arctic biodiversity was relatively unaffected by negative impacts from human activities. Only over-exploitation of certain animal populations posed serious threats, such as the extermination of Steller's sea cow, the great auk, the Eskimo curlew and a number of whale populations in recent centuries, in addition to the contribution that humans may have made to the extermination of terrestrial mega-fauna in prehistoric times.

Human impacts, however, have increased in modern times with increasing human populations in much of the Arctic, modern means of rapid transport, modern hunting and fishing technology, increasing exploration and exploitation of mineral resources, impacts from contaminants and, most importantly, with climate change, which is more pronounced in the Arctic than elsewhere on the globe.

There is no inherited capacity in human nature to safeguard the Earth's biological assets – moral and intellectual strength are needed to achieve conservation and wise use of living resources through cultural and personal ethics and practices. Sustainability is a prerequisite for such balance, but it does not come without restraint and concerted efforts by all stakeholders, supported by mutual social pressure, legislation and law enforcement.

The Arctic is changing rapidly with shorter winters, rapidly melting sea ice, retreating glaciers and expanding sub-Arctic vegetation from the south. If greenhouse gas emissions are not reduced, Arctic biodiversity will be forever changed, and much may disappear completely.

On 18 May 2011, 50 prominent thinkers, among them 15 Nobel Prize winners, issued The Stockholm Memorandum, which among other things states that:

*Science indicates that we are transgressing planetary boundaries that have kept civilization safe for the past 10,000 years. Evidence is growing that human pressures are starting to overwhelm the Earth's buffering capacity. Humans are now the most significant driver of global change, propelling the planet into a new geological epoch, the Anthropocene. We can no longer exclude the possibility that our collective actions will trigger tipping points, risking abrupt and irreversible consequences for human communities and ecological systems. We cannot continue on our current path. The time for procrastination is over. We cannot afford the luxury of denial. We must respond rationally, equipped with scientific evidence.*

Among the many current and projected stressors on Arctic biodiversity addressed in this report is that of invasive species. However, if we want to do something about the many problems facing nature and biodiversity in the Arctic, we need to focus on the impacts of the most globally 'invasive species' of all: *Homo sapiens*.

Hans Meltofte
Copenhagen, 8 February 2013

As opposite to the huge and almost totally ice covered Antarctica, the Arctic is an ocean of pack ice surrounded by a relatively limited fringe of tundra on the adjacent islands and continents. Bowhead whales surfacing amongst melting ice with black guillemots resting on ice. Foxe Basin, Nunavut, Canada, July. Photo: Eric Baccega.

# Introduction

**Authors**

Hans Meltofte, Henry P. Huntington and Tom Barry

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## 1. THE ARCTIC IS CHANGING

The Arctic is home to a diverse array of plants and animals. They are adapted in various ways to a region that is often cold, experiences prolonged daylight in summer and equally lengthy darkness in winter, and includes habitats that range from ice caps to wetlands to deserts, from ponds to rivers to the ocean. Some of the Arctic's species are icons, such as the polar bear, known throughout the world. Some are obscure, with many yet to be discovered. Arctic peoples, too, have adapted to this environment, living off the land and sea in keeping with the cycles of the seasons and the great migrations of birds, mammals and fish. Many birds, for example, spend the summer in the Arctic and are absent in winter, having flown to all corners of the Earth, thus connecting the Arctic with every region of the planet.

Today, Arctic biodiversity is changing, perhaps irreversibly. This introduction summarizes some of the main stressors as described in a series of Arctic Council assessments. Many of these threats have been the subject of intense research and assessment, documenting the impacts of human activity regionally and globally, seeking ways to conserve the biological and cultural wealth of the Arctic in the face of considerable pressures to develop its resources. These assessments have focused primarily on individual drivers of change.

The Arctic Biodiversity Assessment (ABA) focuses on the species and ecosystems characteristic of the Arctic region and draws together information from a variety of sources to discuss the cumulative changes occurring as a result of multiple factors. It draws on the most recent and authoritative scientific publications, supplemented by information from Arctic residents, also known as traditional ecological knowledge (TEK[1]). The chapters of the ABA have been through comprehensive peer reviews by experts in each field to ensure the highest standards of analysis and unbiased interpretation (see list below). The results are therefore a benchmark against which future changes can be measured and monitored.

The purpose of the ABA, as endorsed by the Arctic Council Ministers in Salekhard, Russia, in 2006 is to *Synthesize and assess the status and trends of biological diversity in the Arctic … as a major contribution to international conventions and agreements in regard to biodiversity conservation; providing policymakers with comprehensive information on the status and trends of Arctic biodiversity* (CAFF 2007). The intent is to provide a much needed description of the current state and recent trends in the Arctic's ecosystems and biodiversity, create a baseline for use in global and regional assessments of Arctic biodiversity and a basis to inform and guide future Arctic Council work. The ABA provides up-to-date knowledge, identifies gaps in the data record, describes key mechanisms driving change and presents suggestions for measures to secure Arctic biodiversity. Its focus is on current status and trends in historical time, where available.

## 2. DEFINITION OF THE ARCTIC

For this assessment a more scientific definition of the Arctic was needed than the CAFF boundaries, which are defined as much by political boundaries as by climatic and biological zoning, and therefore vary considerably among the Arctic nations. That such a clear definition is a prerequisite for a meaningful account of Arctic biodiversity can be illustrated by the highly varying numbers of 'Arctic' bird species found in the literature. By including huge tracts of boreal forest and woodland into the Arctic, as politically defined by CAFF, figures of up to "450 Arctic breeding bird species" have been quoted (Zöckler 1998, Trouwborst 2009) as compared with the c. 200 species given in the present report based on a stricter ecological definition (Ganter & Gaston, Chapter 4).

The name Arctic derives from the ancient Greek word *Arktikós*, meaning the land of the North. It relates to *Arktos*, the Great Bear, which is the star constellation close to the Pole Star. There are several definitions of the Arctic. From a geophysical point of view, the Arctic may be defined as the land and sea north of the Arctic Circle, where the sun does not set on the summer solstice and does not rise on the winter solstice. From an ecological point of view, it is more meaningful to use the name for the land north of the tree line, which generally has a mean temperature below c. 10-12 °C for the warmest month, July (Jonasson *et al.* 2000). With this definition, the Arctic land area comprises about 7.1 million km$^2$, or some 4.8% of the land surface of Earth (Fig. 1).

Similarly, the Arctic waters are defined by characteristics of surface water masses, i.e. the extent of cold Arctic water bordering temperate waters including 'gateways' between the two biomes. The Arctic Ocean covers about 10 million km$^2$ (see Michel, Chapter 14 for details).

The vegetated lowland of the Arctic is often named tundra, which originates from the Saami word *tūndar*, meaning treeless plain. In general, the low Arctic has much more lush vegetation than the high Arctic, where large lowland areas may be almost devoid of vegetation, like the Arctic deserts of the northernmost lands in the world.

The sub-Arctic or forest tundra is the northernmost part of the boreal zone, i.e. the area between the timberline and the tree line.[2] Hence, the sub-Arctic is not part of the Arctic, just as the sub-tropics are not part of the

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[1] Traditional ecological knowledge (TEK) has been defined as the knowledge and values which have been acquired through experience, observation, from the land or from spiritual teachings, and handed down from one generation to another.

[2] While the tree line is the limit of often scattered tree growth or forest tundra, the timberline is the limit of harvest of useable timber.

tropics. Like the Arctic, the word *boreal* is derived from Greek: *Boreas* was the god of the cold northern winds and bringer of winter. Related zones are found in mountainous areas outside of the Arctic as sub-alpine, low-alpine and high-alpine biomes.

This assessment follows the Circumpolar Arctic Vegetation Map's (CAVM Team 2003) definition of the Arctic, since this map builds on scientific criteria for Arctic habitats. Furthermore, inclusion of tree-covered sub-Arctic habitats would have expanded the volume of species and ecosystems beyond achievable limits. Yet, different chapters may cover additional bordering areas as needed to provide scientific and ecological completeness. The entire Arctic tundra region (sub-zones A-E on the CAVM) is addressed as comprehensively as possible in terms of species and ecosystem processes and services. Oceanic tundra (e.g. the Aleutian Islands), the sub-Arctic and other adjacent areas are addressed as appropriate in regard to (1) key ecosystem processes and services, (2) species of significance to the Arctic tundra region, (3) influences on the Arctic tundra region, and (4) potential for species movement into the current Arctic tundra region, e.g. due to global change.

For the separation between the high Arctic and the low Arctic, we follow the simplest division which is between sub-zones C and D on the CAVM (Fig. 1). The southern limit of the sub-Arctic is 'loose', since work on a CAFF Circumpolar Boreal Vegetation Map is pending (CAFF 2011). Contrary to the Arctic zones on land, the boundaries at sea are tentative, and on Fig.1 they are indicated only with rough boundaries between the different zones.

**Figure 1.** Map of the top of the northern hemisphere with the high and low Arctic zones delineated according to the Circumpolar Arctic Vegetation Map (CAVM Team 2003), together with a tentative demarcation of the sub-Arctic. Lines indicating similar marine zones are sketched.

## 3. SPECIES AND ECOSYSTEMS INCLUDED

According the Convention on Biological Diversity (CBD), biodiversity is "the variability among living organisms from all sources, including, *inter alia*, terrestrial, marine, and other aquatic ecosystems, and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems." Similarly, ecosystems are defined as "a dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit."

As also stated by the CBD "biological diversity is about more than plants, animals and micro organisms and their ecosystems – it is about people and our need for food security, medicines, fresh air and water, shelter, and a clean and healthy environment in which to live." Hence, in the present report, humans are both considered part of the ecosystems and as outside agents influencing the environment. The main focus, however, remains on status and trends in 'non-human' biodiversity.

This assessment covers all three aspects of biological diversity: species, ecosystems and genetic variation. Chapters 3-11 deal with taxonomic groups, Chapters 12-14 cover major ecosystems, Chapters 15 and 16 deal with two functional groups (parasites and invasive species, respectively), and Chapter 17 addresses genetic diversity. Finally, Chapters 18-20 deal with ecosystem services and other aspects of the human relationship with nature, including linguistic diversity.

Since there is no strict definition of an Arctic species, this assessment includes all species that reproduce in and/or have more than peripheral populations in the Arctic as defined above, i.e. excluding species with accidental or clearly insignificant appearance within the Arctic. Sub-Arctic species and ecosystems are dealt with as outlined above, i.e. where they have direct bearing on the Arctic but not for their own sake. Similarly, ecosystems are included if they have a substantial presence within the Arctic (see e.g. the CAVM).

Regarding distinction between marine, freshwater and terrestrial, in this report the marine includes everything up to the high water mark (i.e. including the intertidal zone). Fens and marshes are considered terrestrial, whereas tarns and ponds are considered freshwater ecosystems together with lakes, rivers and streams.

The organizing principles for the chapters are:

- The species chapters focus on status and trends in distribution, population densities and abundance (population size).
- For some taxa, species lists etc. are given in digital appendixes.
- In the ecosystem chapters, the focus is on status and trends in distribution, composition (habitat and species richness), productivity (e.g. greening), phenology and processes (e.g. grazing and predation).
- Causal explanations of observed changes are provided to the extent that the scientific literature offers analyses or descriptions thereof.
- Similarly, to the extent that the scientific literature holds modeling or other information on future prospects for Arctic biodiversity and ecosystems within the 21st century – including anticipated tipping points and thresholds – these are referred to as well.
- Information from holders of traditional knowledge has been considered in all chapters, in addition to a section on *Indigenous peoples and biodiversity in the Arctic*, which follows this Introduction.
- Cumulative effects are considered where relevant.
- Every effort has been made to avoid bias towards selective reporting of either positive or negative trends.

## 4. STRESSORS OF ARCTIC BIODIVERSITY

Climatically, ecologically, culturally, socially and economically, the Arctic is changing in many ways with implications throughout the region and around the world. In order to set the stage for assessing biodiversity, and to avoid repeating the same descriptions in each chapter, this section summarizes the main findings of major assessments undertaken within the Arctic Council, as these assessments have covered most of the major drivers of change. This section is not intended to be comprehensive, but rather to show the urgency and the timeliness of the ABA. Many changes are rapid and even accelerating, and the various assessments conducted in recent years make possible an examination of the combined effects of multiple stressors.

### 4.1. Climate

The Arctic climate is warming rapidly (ACIA 2005). Summer sea ice extent has diminished greatly in recent years, more of the Greenland ice cap is melting than before, and permafrost is thawing (AMAP 2009a, 2011a, 2011b). All of these changes affect Arctic ecosystems, as described in detail in this ABA. The Arctic Council, in cooperation with the International Arctic Science Committee (IASC), produced in 2005 the *Arctic Climate Impact Assessment* (ACIA), which compiled into one document the information available at that time concerning the changing climate of the Arctic and the resulting effects on the cryosphere, ecosystems and human activities. Since that time, the Arctic Council has contributed to updates concerning various aspects of climate change in the Arctic. This recent information shows that the projections of the ACIA were, if anything, conservative (AMAP 2009a). Newer updates now include biological information, which will allow better monitoring and reporting of the effects of climate change on biodiversity.

### 4.2. Development

The Arctic has abundant petroleum and mineral resources, the development of which has been slowed only by the costs of operating in remote areas with a harsh climate. Nonetheless, oil and gas fields in the Arctic provide a substantial part of the world's supply at present, and many fields have yet to be developed. The Arctic Monitoring and Assessment Programme (AMAP)'s assessment, *Oil and gas activities in the Arctic: effects and potential effects*, describes the petroleum reserves of the Arctic, development to date, likely development in the next two decades, and effects on ecosystems and society (AMAP 2009b). The pace of development will reflect global demand as well as decisions by Arctic governments on the regulation of oil and gas activities and the capture of revenues from them. To date, oil and gas and other developments have had substantial though largely localized impacts on the environment. Further development, particularly the threat of oil spills and the introduction of invasive species in the marine environment, nonetheless poses a risk to much of the Arctic region.

### 4.3. Cultural and social change

Within living memory in many parts of the Arctic, local societies and economies have become ever more connected with the wider world through telecommunications, trade, travel and other influences and interactions. Today, monetary economies, national and regional governmental institutions, formalized educational systems, modern health care and new forms of communications are among the many factors shaping the lives of Arctic residents. While some changes have been highly beneficial, as seen in longer life expectancy and decreased infant mortality, other changes have disrupted traditional ways of life and contributed to environmental degradation. The Sustainable Development Working Group (SDWG) of the Arctic Council published the *Arctic Human Development Report* (AHDR) in 2004, examining a range of issues affecting Arctic peoples. Connection to the environment remains a vital part of the quality of life for many Arctic residents, as well as the foundation for Arctic cultures, but those connections are under threat from many directions (AHDR 2004). The SDWG is currently working on a follow-up to the AHDR.

### 4.4. Transportation

As sea ice retreats, the prospects for shipping in the Arctic increase. The Northern Sea Route across the top of Eurasia has been used by icebreakers and ice-strengthened ships since the 1930s, primarily for transportation within Russia. A regular ice-free summer season would make the route attractive for through-shipping between East Asia and Europe, cutting thousands of kilometers off current routes. Recent summers have seen a few cargo ships making this voyage. The Northwest Passage through the Canadian Arctic Archipelago also offers the prospect of shorter shipping routes and improved access to the region's resources, though not expected to become a transit shipping route for some time. The Protection of the Arctic Marine Environment (PAME) Working Group of the Arctic Council completed the *Arctic Marine Shipping Assessment* (AMSA) in 2009, evaluating the prospects for future shipping activity as well as resulting environmental, economic and social impacts (AMSA 2009). Much of the outcome for shipping depends on the governance regimes that are established in both territorial and international waters by the Arctic states and the global demand for Arctic resources. Increased shipping is also likely to increase Arctic resource development through improved access and lower costs. Local transportation has also improved over recent decades, with the widespread use of motorboats and mechanized snow travel (snowmobiles), as well as regular air service to many parts of the Arctic providing easier access to goods and services from the south.

### 4.5. Contaminants

Persistent organic pollutants (POPs) and heavy metals accumulate in Arctic ecosystems, despite being produced and released at far higher rates in temperate and tropical regions. Contaminants can be transported to the Arctic via ocean currents, large rivers and the atmosphere. In a cold climate, some of these substances tend to settle from the air onto land or into water and then stay there. Other substances, like mercury, have a more complex chemical cycle. These contaminants can accumulate in organisms at the bottom of the food web, and the concentrations of many of these substances magnify as they move from one trophic level to the next. Species at the top of the food web, such as seals and polar bear as well as humans who eat Arctic species, can be exposed to high levels of these contaminants, posing health risks in some instances. AMAP has conducted several assessments of contaminants in the Arctic (AMAP 1998, 2004, 2009c, 2011c). One result of this information was strong scientific and political motivation for the Stockholm Convention on POPs, a global agreement signed in 2001 that explicitly acknowledged concern for Arctic peoples and ecosystems. The biological and ecological impacts of contaminants remain subjects of research in the Arctic, particularly as climate change may alter contaminant transport and uptake (AMAP 2011c, UNEP/AMAP 2011).

## 5. THE ARCTIC COUNCIL

The Ottawa Declaration of 1996 formally established the Arctic Council as a high-level, consensus-based, intergovernmental forum to provide a means for promoting cooperation, coordination and interaction among the Arctic states, with the involvement of the Arctic indigenous communities and other Arctic inhabitants on common Arctic issues, in particular issues of sustainable development and environmental protection in the Arctic. The Arctic Council is comprised of eight Arctic states[3] and

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[3] Canada, Denmark – including Greenland and the Faroe Islands – Finland, Iceland, Norway, the Russian Federation, Sweden and the United States of America.

six Permanent Participants[4] that represent the Indigenous Peoples of the circumpolar north. The Arctic Council is unique among intergovernmental forums in that both Arctic states and Permanent Participants have a seat at the same table. Several observer states[5], intergovernmental and inter-parliamentary organizations[6] and non-government organizations[7] also make valuable contributions to the Council's work.

The Arctic Council members have recognized that their shared ecosystems with unique flora and fauna are fragile and threatened from a number of causes, and that changes in Arctic biodiversity have global repercussions (AEPS 1991). The Conservation of Arctic Flora and Fauna (CAFF) working group was established in 1991 under the Arctic Environmental Protection Strategy (AEPS, a precursor to the Arctic Council) in order to encourage the conservation of Arctic flora and fauna, their diversity and their habitats. CAFF was subsequently incorporated within the Arctic Council.[8]

CAFF's mandate is to address the conservation of Arctic biodiversity and to communicate the findings to the governments and residents of the Arctic, helping to promote practices which ensure the sustainability of the Arctic's resources. CAFF serves as a vehicle for cooperation on species and habitat management and utilization, to share information on management techniques and regulatory regimes, and to facilitate more knowledgeable decision-making. It provides a mechanism for developing common responses to issues of importance for the Arctic ecosystems such as development and economic pressures, conservation opportunities and political commitments. The objectives assigned to CAFF are (CAFF 1995):

- to collaborate for more effective research, sustainable utilization and conservation,
- to cooperate to conserve Arctic flora and fauna, their diversity and their habitats,
- to protect the Arctic ecosystem from human-caused threats,
- to seek to develop more effective laws, regulations and practices for flora, fauna and habitat management, utilization and conservation,
- to work in cooperation with the Indigenous Peoples of the Arctic,
- to consult and cooperate with appropriate international organizations and seek to develop other forms of cooperation,
- to regularly compile and disseminate information on Arctic conservation, and
- to contribute to environmental impact assessments of proposed activities.

Achieving success in conserving Arctic natural environments, while allowing for economic development, depends on obtaining and applying comprehensive baseline data regarding status and trends of Arctic biodiversity, habitats and ecosystem health. This need to identify and fill knowledge gaps on various aspects of Arctic biodiversity and monitoring was identified in the Arctic Council's Strategy for the Conservation of Arctic Biodiversity (CAFF 1997) and reinforced by the Arctic Flora and Fauna report (CAFF 2002) and the Arctic Climate Impact Assessment (ACIA 2005), which recommended that long-term Arctic biodiversity monitoring be expanded and enhanced.

CAFF responded with the implementation of the Circumpolar Biodiversity Monitoring Program (CBMP). The CBMP is an international network of scientists, government agencies, indigenous organizations and conservation groups working to harmonize and integrate efforts to monitor the Arctic's living resources. Following the establishment of the CBMP, it was agreed that it was necessary to provide policy makers and conservation managers with a synthesis of the best available scientific and traditional ecological knowledge (TEK) on Arctic biodiversity. The ABA will serve as a baseline upon which the CBMP will build, providing up-to-date status and trends information to support ongoing decision-making and future assessments of the Arctic's biodiversity.

To take stock of the current state of biodiversity in the Arctic, the ABA was endorsed by the Arctic Council in 2006 (Salekhard Declaration). The ABA has been an inclusive process which has harnessed the efforts of 253 scientists from 15 countries including both Arctic and non-Arctic states. Co-lead authors for each chapter were appointed from North America and Eurasia in order to seek a balanced approach. TEK was recognized as an important contribution to provide 'eye-witness' observations on the status and trends in Arctic biodiversity, and

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[4] Aleut International Association, Arctic Athabaskan Council, Gwich'in Council International, Inuit Circumpolar Council, Russian Association of Indigenous Peoples of the North and the Saami Council.

[5] France, Germany, The Netherlands, Poland, Spain, United Kingdom, People's Republic of China, Italian Republic, Japan, Republic of Korea, Republic of Singapore, Republic of India.

[6] International Federation of Red Cross & Red Crescent Societies, International Union for the Conservation of Nature, Nordic Council of Ministers, Nordic Environment Finance Corporation, North Atlantic Marine Mammal Commission, Standing Committee of the Parliamentarians of the Arctic Region, United Nations Economic Commission for Europe, United Nations Development Program, United Nations Environment Program GRID Arendal.

[7] Advisory Committee on Protection of the Seas, Arctic Circumpolar Gateway, Association of World Reindeer Herders, Circumpolar Conservation Union, International Arctic Science Committee, International Arctic Social Sciences Association, International Union for Circumpolar Health, International Work Group for Indigenous Affairs, Northern Forum, University of the Arctic, World Wide Fund for Nature – Global Arctic Program.

[8] CAFF is one of six Working Groups within the Arctic Council; other working groups include Arctic Contaminants Action Programme (ACAP), Arctic Monitoring and Assessment Programme (AMAP), Emergency Prevention, Preparedness and Response (EPPR), Protection of the Arctic Marine Environment (PAME) and the Sustainable Development Working Group (SDWG).

a process was put in place to allow for the incorporation of TEK within the ABA. TEK coordinators were appointed for Eurasia and North America and compiled TEK material to inform the ABA.

The first deliverable from the ABA process was *Arctic Biodiversity Trends: Selected Indicators of Change* (CAFF 2010), which presented a preliminary assessment of status and trends in Arctic biodiversity and was based on a suite of 22 indicators developed by the CBMP. The 2010 report was the Arctic Council's contribution to the United Nations International Year of Biodiversity in 2010 and its contribution to the CBD's 3rd Global Biodiversity Outlook to measure progress towards the 2010 Biodiversity Targets (CBD 2010a). The CBD COP11 welcomed the report and noted its key findings. Changes in Arctic biodiversity can have global implications (CAFF 2010), and it is critical to ensure that information on such changes is linked into international agreements and legal frameworks. The CBD has recognized the importance of Arctic biodiversity in a global context, and highlighted the need for continued collaboration between the CBD and CAFF to contribute to the conservation and sustainable use of the Arctic's living resources (CBD 2010b), in particular with regards to monitoring and assessing status and trends, and stressors to Arctic Biodiversity. CAFF was requested to provide information on status and trends in Arctic biodiversity to inform the next Global Biodiversity outlook report.

The ABA has benefited from the broad range of research efforts generated by the International Polar Year (IPY) 2007-2008. It contributes to the legacy of IPY by providing a means of integrating and allowing IPY research to reach a wider audience.

A key challenge for conservation in the Arctic and globally is to shorten the gap between data collection and policy response. CAFF has recognized this challenge and in recent years has worked towards developing a solution. This approach has focused on not just developing traditional assessments but also addressing the collection, processing and analysis of data on a continuous basis. Indeed, the ABA provides a baseline of current knowledge, closely linked to the development of the CBMP as the engine for ongoing work, including the production of regular and more flexible assessments and analyses.

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- Ministry of Housing, Nature and Environment, Greenland
- Icelandic Institute of Natural History
- Directorate of Nature Management, Norway
- Russian Federation Ministry of Natural Resources
- Swedish Environmental Protection Agency
- United States Department of the Interior, Fish and Wildlife Service

### CAFF Permanent Participant Organizations

- Aleut International Association (AIA)
- Arctic Athabaskan Council (AAC)
- Gwich'in Council International (GCI)
- Inuit Circumpolar Council (ICC)
- Russian Association of Indigenous Peoples of the North
- Saami Council

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## LIST OF ACRONYMS

| | |
|---|---|
| ABA | Arctic Biodiversity Assessment |
| ACAP | Arctic Contaminants Action Program Working Group |
| ACIA | Arctic Climate Impact Assessment |
| AEPS | Arctic Environmental Protection Strategy |
| AHDR | Arctic Human Development Report |
| AMAP | Arctic Monitoring and Assessment Programme Working Group |
| AMSA | Arctic Marine Shipping Assessment |
| CAFF | Conservation of Arctic Flora and Fauna Working Group |
| CAVM | Circumpolar Arctic Vegetation Map |
| CBD | Convention on Biological Diversity |
| CBMP | Circumpolar Biodiversity Monitoring Program |
| CBVM | Circumpolar Boreal Vegetation Map |
| EPPR | Emergency Prevention, Preparedness, and Response Working Group |
| IASC | International Arctic Science Committee |
| PAME | Protection of the Arctic Marine Environment Working Group |
| POPs | Persistent organic pollutants |
| SDWG | Sustainable Development Working Group |
| TEK | Traditional Ecological Knowledge |
| UNEP | United Nations Environment Programme |

# Indigenous peoples and biodiversity in the Arctic

*Tero Mustonen and Violet Ford*

The late Yukaghir-Chukchi reindeer herder Grigorii Velvin was a well-known storyteller and keeper of his people's culture. He lived in the Lower Kolyma region of Republic of Sakha-Yakutia, Russia. In 2005 he related the following oral history regarding the Yukaghir relationship with bears:

> *About relatives, about my family. Mother of my grandmother, grandmother of my mother. They were Yukaghir. There used to be people from Alai. Especially from my mother's side, they were Yukaghir from Alai. They were considered to be 'proper' Yukaghir. Mother of my grandmother told the story that our ancestor is the bear. One of the ladies got married… She got lost and met a bear. The bear took her as his bride. When the bear would leave its den, it would close the opening with a big rock so that the woman would not leave the den. Once however she managed to escape. She ran to her relatives and said: "He will come after me for sure, please butcher and sacrifice a white reindeer as an offering." Her people followed her orders, made the offering at a campsite and went away themselves. It is told that the bear took the reindeer and left the area. In a way they made a bargain. And thus she was able to escape. She gave birth to a child and that is how our family got started. This family has this oral history. Therefore the Yukaghir here, our tundra Yukaghir, do not touch the bear. It is our ancestor. This is a legend that the mother of my grandmother told. I have heard it. My grandmother told it to my mother and my mother passed it on to me.*
>
> (Mustonen 2009).

This story indicates the deep and multifaceted relationships that the Arctic's Indigenous peoples have with northern ecosystems and species. The Arctic is a *homeland* for the many nations that have existed there for millennia. Arctic biodiversity supports Arctic Indigenous peoples as they maintain and develop their societies, cultures and ways of life. An example illustrating the way in which people renew their connection to the sea can be seen in the ritual of the *Nuataaqmiut* Inupiaq hunters of Northwest Alaska. When they have caught a beluga whale they place a piece of its skin on a pole by the sea shore to indicate to other belugas swimming by that the hunters are treating the body of their dead relative properly and are enabling its spirit to return to the sea (Burch 1998).

Indigenous peoples' perceptions of biodiversity and the challenges it faces globally are based on their dependence on the environment, their values and their belief systems. Varied as these values and belief systems are, the special relevance of Indigenous peoples' views on the protection of biodiversity have been recognized by the international community and clearly set forth in diverse instruments, most prominently, perhaps, in the United Nations Convention on Biological Diversity (CBD).

The CBD, in article 8 on 'In-situ Conservation', specifies the duty of the national parties to the convention to "respect, preserve and maintain knowledge, innovations and practices of Indigenous and local communities embodying traditional lifestyles relevant for the conservation and sustainable use of biological diversity and promote their wider application with the approval and involvement of the holders of such knowledge, innovations and practices and encourage the equitable sharing of the benefits arising from the utilization of such knowledge, innovations and practices".

To the degree that stipulations such as this are implemented, they greatly facilitate Arctic's Indigenous peoples' contributions to the protection of Arctic biodiversity and will provide more opportunities for traditional knowledge to inform the policy making process.

When discussing Arctic biodiversity and Indigenous peoples, we need to appreciate that Indigenous environmental governance regimes have existed and to certain extent still exist in the Arctic. The Saami *siida* family and clan territories (Mustonen & Mustonen 2011, Mustonen 2012), the Northwest Alaskan Inupiaq territoriality (Burch 1998) and the regional governance based on seasonal cycles of the Yukaghir peoples in the Kolyma region of Siberian Russia (Mustonen 2009) are examples of such regimes.

These are *spiritual-cultural systems of reciprocity*, with the characteristics of the surrounding ecosystems dictating the way the relationship between an animal and a hunter is being understood across the community and the region. There is a social dimension to hunting, a spiritual dimension and a direct relationship with the land. What Arctic Indigenous peoples bring to this relationship is associated with their wellbeing, culture and spirituality. Moreover, customary laws were, and to some extent still are, understood and applied with reference to beliefs and values concerned with managing and sustaining biodiversity. These laws prescribe how and when to utilize Arctic ecosystem services.

According to traditional beliefs of the *Amitturmiut* Inuit in Nunavut, if a camp is occupied for too long, the land becomes hot and dangerous. People have to move away to other areas to give the land a chance to cool (Bennet & Rowley 2004):

> *A land could only be occupied for three years. No one can live on this land beyond the three years. … That was the way they lived, always moving to another [place], never occupying one land beyond three winters. … The land itself was prevented from 'rotting' by this. Should one choose to occupy the land beyond three years, then they are bound to face peril, which might include dearth, therefore they had to follow this rule.*

These are not perfect systems of sustainability. They are vulnerable and fragile and dependent upon the conditions of the surrounding environment. It is important to highlight that although cases of overharvest are known, these systems usually operate within the carrying capacity of a particular ecosystem. However one should be careful not to uncritically impose an explanation from the outside as to *why* overhar-

Fish has been an important resource for all Arctic people through millennia. Photo: Carsten Egevang: Arctic char *Salvelinus alpinus*.

vest has happened, and instead carefully examine a range of features of and reasons for a particular event, especially through utilizing the oral histories of the people themselves (Burch 1998).

Another important realization is that the cultural notions of cosmology, time, space and scale of Indigenous peoples in many cases differ markedly from the linear concepts typically applied to time and space by mainstream society. Having their *own knowledge and terminologies*, indigenous peoples conceive ecosystems and species altogether differently.

In short, Arctic biodiversity has been and continues to be managed and sustained by Arctic Indigenous peoples through their *traditional knowledge*. Traditional knowledge is used to observe, evaluate and form views about a particular situation on the land. This knowledge reflects perceptions and wisdom that has been passed on to new generations right up to the present day. However, steps need to be taken to ensure that traditional knowledge is renewed and passed on to the generations to come.

The imposition of 'western' ways of living, introduced diseases and health regimes, formalized school-based education, Christianity, and the criss-crossing of traditional homelands by modern infrastructure have reduced the capacity of Arctic Indigenous communities to maintain their customary ways of understanding and interacting with their environment. The past century has seen the rise of modern conservation practices in tandem with increasing industrial uses of the land, often with no appreciation for traditional modes of life in the region.

The past teaches that it is essential to maintain and support Indigenous management regimes to revitalize language and knowledge systems that organize sustainable practices such as nomadic reindeer herding in Siberia, and to explore best practices of co-management in order to sustain Indigenous ways of life and the biodiversity with which they have long co-existed. Indigenous peoples' views are now recognized as part of the formal environmental decision-making process. Therefore, it is time to initiate a respectful and all-encompassing dialogue between mainstream societies and Indigenous peoples on *how* to manage and preserve the Arctic for future generations.

However, the time has also come to recognize that rights to full consultation and the principle of free, prior and informed consent so often invoked as pivotal Indigenous rights actually are meaningless in themselves. The right to consultation and the consent principle make sense only as related to fundamental human rights of Indigenous peoples: the right to self-determination, to culture, to property and to use of land and waters, to name a few. Although not directly a part of this assessment, the question of these fundamental rights still needs to be addressed in order to determine the role of Indigenous peoples with regards to the future of Arctic biodiversity.

The Arctic Biodiversity Assessment is an important step in the right direction. Now, humankind needs to continue towards regional and local implementation of the messages contained in this report to make sure we act together, with due diligence, for the good of the Arctic today and tomorrow.

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Climate change is already causing earlier snow melt, which initially may benefit many Arctic organisms. But in the longer term it will make it possible for more competitive southern species to 'take over' what are currently Arctic habitats. Photo: Erik Thomsen.

*Chapter 1*

# Synthesis: Implications for Conservation

**Authors**

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## Contents

> » **Nowadays all of the tundra is on the move now. Many forest animals are coming to tundra now. Moose is moving towards the tundra proper nowadays.**
>
> Alexey Nikolayevich Kemlil, a Chukchi reindeer herder from Turvaurgin in northeastern Sakha-Yakutia, Siberia; T. Mustonen in litt.

> » **I too, have noticed changes to the climate in our area. It has progressed with frightening speed especially the last few years. In Iqaluktutiaq, the landscape has changed. The land is now a stranger, it seems, based on our accumulated knowledge. The seasons have shifted, the ice is thinner and weaker, and the streams, creeks and rivers have changed their characteristics.**
>
> Analok, Cambridge Bay, Victoria Island, Nunavut; Elders Conference on Climate Change 2001.

# SUMMARY

Arctic biodiversity – the multitude of species and ecosystems in the land north of the tree line together with the Arctic Ocean and adjacent seas – is an irreplaceable cultural, aesthetic, scientific, ecological, economic and spiritual asset. For Arctic peoples, biodiversity has been the very basis for their ways of life through millennia, and is still a vital part of their material and spiritual existence. Arctic fisheries and tourism are also of particularly high value for the rest of the world, and so are the millions of Arctic birds and mammals migrating to virtually all parts of the globe during winter.

The Arctic is home to more than 21,000 species of often highly cold-adapted mammals, birds, fish, invertebrates, plants and fungi (including lichens) – together with large numbers of undescribed endoparasites and microbes. These include charismatic and iconic species such as polar bears *Ursus maritimus*, narwhals *Monodon monoceros*, walrus *Odobenus rosmarus*, caribou/reindeer *Rangifer tarandus*, muskoxen *Ovibos moschatus*, Arctic fox *Vulpes lagopus*, ivory gull *Pagophila eburnea* and snowy owls *Bubo scandiaca* together with marine and terrestrial ecosystems such as vast areas of lowland tundra, wetlands, mountains, extensive shallow ocean shelves, millennia-old ice shelves and huge seabird cliffs.

The functional significance of different groups of organisms in maintaining the integrity, structure, services and health of Arctic ecosystems, however, is generally greatest among those we understand least. Microorganisms are key elements of Arctic ecosystems, yet they have been little studied.

Anthropogenically driven climate change is by far the most serious threat to biodiversity in the Arctic, and there is an immediate need to implement actions to reduce this stressor. Due to a range of feedback mechanisms, the 2 °C upper limit of human-induced warming, chosen by world leaders, is projected to result in an air temperature increase of between 2.8 and 7.8 °C in the Arctic, likely resulting in severe disruptions to Arctic biodiversity.

Climate change is the most likely explanation for shifts already visible in several parts of the Arctic, as documented by both scientists and Arctic residents. These include northward range expansions of many species and changes in ecosystems likely resulting from habitat warming and/or drying of the substrate associated with warming and earlier snow melt, together with development of new oceanic current patterns.

Future global warming will result in further northward shifts in the distribution of a great many species. This will include boreal species and ecosystems encroaching on areas currently characterized as the low Arctic, and low Arctic species and ecosystems encroaching on areas currently characterized as the high Arctic.

Northward movement of boreal species may increase the number of species found in the Arctic, but this does not represent a net gain in global biodiversity. The additions will primarily be species that are already common in southern habitats, some of which may outcompete or displace unique assemblages of Arctic species with the risk of severe range reductions and possible extinctions.

Terrestrial habitats in the Arctic are bounded to the north by marine ecosystems. Therefore, northward ecosystem shifts are expected to reduce the overall geographic extent of terrestrial Arctic habitats – in particular for high Arctic habitats. Arctic terrestrial ecosystems may disappear in many places, or only survive in alpine or island 'refugia'.

Arctic freshwater ecosystems are undergoing rapid change in response to the influence of both environmental and anthropogenic stressors. The distribution and number of lakes, ponds, wetlands and riverine networks are being altered with significant implications to the structure, function and diversity of associated biological communities.

Also in the marine Arctic, climate-induced effects on species and ecosystems, associated with a decrease in sea ice extent and duration, are already being observed. Of key concern is the rapid loss of multi-year ice in the central Arctic basins and changes in sea ice dynamics on the extensive Arctic shelves, which affect the biodiversity and productivity of marine ecosystems.

A secondary effect of increased $CO_2$ in the atmosphere is ocean acidification resulting from increased dissolved $CO_2$. Since the solubility of $CO_2$ is higher in cold than warm waters, Arctic marine ecosystems are especially prone to acidification, and there are already signs of such changes in the Arctic Ocean. This is an important threat to calcareous organisms, and thereby may have cascading impacts on marine ecosystems including potential impacts on biodiversity and fisheries.

Until the second half of the 20th century, overharvest was the primary threat to a number of Arctic mammals, birds and fishes. A wide variety of conservation and management actions have helped alleviate this pressure in many areas to such an extent that many populations are recovering, although pressures on others persist.

Since the middle of the 20th century, a variety of contaminants have bioaccumulated in several Arctic predator species to levels that threaten the health and fecundity of both animals and humans. However, due to concerted global action to reduce the release of contaminants, there are, as yet, few demonstrated effects on Arctic species at the population level. Lack of data may mask such impacts, however. New contaminants, and changing fluxes of others, continue to be introduced to Arctic ecosystems and related food webs with unknown ecosystem effects.

Arctic habitats are among the least anthropologically disturbed on Earth, and huge tracts of almost pristine tundra, mountain, freshwater and marine habitats still exist. While climate change is the most geographically extensive and potentially harmful anthropogenic impacts at present, regionally ocean bottom trawling, non-renewable resource development and other intensive forms of land use pose serious challenges to Arctic biodiversity.

Pollution from oil spills at sites of oil and gas development and from oil transport is a serious local level threat particularly in coastal and marine ecosystems. A major oil spill in ice-filled waters would be disastrous to marine mammals, birds and other biota, because containing and cleaning up oil spills in broken ice is very difficult, particularly under problematic weather, light and ice conditions.

Many Arctic species spend much of the year outside the Arctic; e.g. Arctic waterbirds are highly dependent on a network of staging and wintering areas in wetlands in many parts of the world. These habitats are experiencing severe development pressure and in some cases overharvest, particularly in East Asia, but also in other parts of the world.

At present, few human-introduced alien species, including pathogens and disease vectors, are spreading unchecked and putting Arctic species under pressure. However, the pathways by which invasive species spread, such as shipping and resource development corridors are rapidly expanding and may dramatically increase the rate of introduction. Many potentially disruptive alien species are also found in sub-Arctic regions and will probably spread northwards along with other species in a warming climate.

There is an enormous deficit in our knowledge of species richness in many groups of organisms, and monitoring in the Arctic is lagging far behind that in other regions of the world. Even for the better-studied Arctic species and ecosystems we have insufficient data on trends in distribution, abundance and phenology and too few natural history specimens for retrospective and baseline analyses. Also the functioning of Arctic ecosystems is insufficiently understood making it difficult to implement ecosystem-based monitoring and management. Hence, there is a critical lack of essential data and scientific understanding necessary to improve the planning and implementation of biodiversity conservation or monitoring strategies in the Arctic.

The multitude of changes in Arctic biodiversity – driven by climate and other anthropogenic stressors – will have profound effects on the living conditions of peoples in the Arctic, including the diversity of indigenous languages, cultures and the range of services that humans derive from Arctic biodiversity. While the ecosystem changes may provide new opportunities, they will also require considerable adaptation and adjustment.

## 1.1. INTRODUCTION

The Arctic holds some of the most extreme habitats on Earth, with species and peoples that have adapted through biological and cultural evolution to its unique conditions. A homeland to some, and a harsh if not hostile environment to others, the Arctic is home to iconic animals such as polar bears *Ursus maritimus*, narwhals *Monodon monoceros*, caribou/reindeer *Rangifer tarandus*, muskoxen *Ovibos moschatus*, Arctic fox *Vulpes lagopus*, ivory gull *Pagophila eburnea* and snowy owls *Bubo scandiaca*, as well as numerous microbes and invertebrates capable of living in extreme cold, and large intact landscapes and seascapes with little or no obvious sign of direct degradation from human activity. In addition to flora and fauna, the Arctic is known for the knowledge and ingenuity of Arctic peoples, who thanks to great adaptability have thrived amid ice, snow and winter darkness.

The purpose of this Arctic Biodiversity Assessment (ABA) is to synthesize and assess the status and trends of biodiversity in the Arctic and provide a first and much-needed description of the state of biodiversity in the Arctic (see Section 2 in Meltofte *et al.*, Introduction for this assessment's definition of the Arctic). It creates a baseline for global and regional assessments of Arctic biodiversity, and is a basis for informing and guiding future Arctic Council work. It provides up-to-date knowledge, identifies data and knowledge gaps, describes key mechanisms driving change and presents science-based suggestions for action to address major pressures.

The ABA identifies current status together with historical trends in abundance and distribution where available, and includes projections of future change informed by scientific literature. It draws on a vast number of scientific publications, supplemented by 'eye witness' observations from indigenous peoples in the context of Traditional Ecological Knowledge (TEK). The ABA has been through comprehensive peer review to ensure the highest standard of analysis and unbiased interpretation. The results are a benchmark against which to help measure and understand the significance of future change, without which the scope and gravity of future changes will be less clearly identifiable, undermining our ability to reduce harm.

Change in the Arctic comes in many forms and from a variety of sources. Several of these stressors have been the subject of intense research and assessments documenting the effects and impacts of human activity regionally and globally, and seeking ways to conserve the biological and cultural wealth of the Arctic in the face of considerable pressures to develop its resources. These assessments have focused primarily on effects and impacts from a range of present and future stressors, such as global warming (ACIA 2005, AMAP 2009a, AMAP 2011a), oil and gas activities (AMAP 2009b), social change (AHDR 2004), marine shipping (AMSA 2009) and environmental contaminants (AMAP 1998, 2004, 2010, 2011b). The ABA, in contrast, looks not at the stressors but at the biodiversity being stressed.

## Box 1.1. Arctic Biodiversity Trends 2010: selected indicators of change

The *Arctic Biodiversity Trends 2010: selected indicators of change* report was the first product produced from the Arctic Biodiversity Assessment. Released in 2010, it was Arctic Council's response to the United Nations International Year of Biodiversity in 2010. At the same time it was a contribution to the Convention on Biological Diversity (CBD)'s 3rd Global Biodiversity Outlook to measure progress towards the CBD's target "to achieve, by 2010, a significant reduction of the current rate of biodiversity loss at the global, regional, and national levels as a contribution to poverty alleviation and to the benefit of all life on Earth."

The report presented a broad spectrum of changes in Arctic ecosystems and biodiversity and provided a snapshot of the trends being observed in Arctic biodiversity today. It highlighted the potentially significant consequences of changes taking place in the Arctic and provided evidence that some anticipated impacts on Arctic biodiversity were already occurring.

The report was based on a suite of 22 indicators developed by the Circumpolar Biodiversity Monitoring Program (CBMP) to cover major species groups with wide distributions across Arctic ecosystems. These indicators include those closely associated with biodiversity use by indigenous and local communities, as well as those with relevance to decision-makers.

## Box 1.2. International conventions on biodiversity issues and the Arctic

Six international conventions focus on biodiversity issues: the Convention on Biological Diversity, the Convention on Conservation of Migratory Species, the Convention on International Trade in Endangered Species of Wild Fauna and Flora, the International Treaty on Plant Genetic Resources for Food and Agriculture, the Ramsar Convention on Wetlands, and the World Heritage Convention. While each of these conventions has distinct and specific aims and commitments, they share common goals of biodiversity conservation and sustainable use.

All Arctic Council countries work through one or several of these conventions to develop and implement national and international policies for the conservation and sustainable use of biodiversity. Collectively, these conventions aim to ensure the conservation and sustainable use of migratory species, areas of natural heritage, wetlands, plant genetic resources and the protection of endangered species. These conventions are complementary to the Arctic Council's efforts to address the conservation of Arctic biodiversity and to promote practices that ensure the sustainability of the Arctic's living resources.

In relation to the United Nations Convention on Biological Diversity (CBD), a Resolution of Cooperation between CAFF and the CBD, signed in 2010, encourages the two organizations to provide and use information and opportunities to promote the importance of Arctic biodiver-

The ABA consists of four components: (1) *Arctic Biodiversity Trends 2010 – Selected Indicators of Change*, which provided a preliminary snapshot of status and trends of Arctic biodiversity (Box 1.1), (2) the present full scientific assessment of Arctic biodiversity, (3) *Cycles of life: indigenous observations of change* (under development) and (4) *Arctic Biodiversity Assessment: Summary for Policy Makers.*

A key challenge for conservation in the Arctic is to shorten the gap between data collection and policy response. The Arctic Council has recognized this challenge and in recent years, through the working group for Conservation of Flora and Fauna (CAFF), has worked towards developing a solution. This approach has focused on not just developing a classical assessment but also addressing the collection, processing and analysis of data on a continuous basis. The ABA is not just a one-time, static assessment, but rather provides a baseline of current knowledge, closely linked to the development of the Circumpolar Biodiversity Monitoring Program (CBMP) as the engine for ongoing work, including the production of regular and more flexible regional and circumpolar assessments and analyses.

Conservation action based on the findings of the ABA will not happen in a vacuum. All Arctic Council states have made commitments that, directly or indirectly, help protect biodiversity and ecosystems through a number of conventions as well as bi- and multi-lateral agreements, including the Convention on Biological Diversity (CBD), United Nations (UN) Framework Convention on Climate Change (UNFCCC), Convention to Combat Desertification (CCD), Bonn Convention (Convention on the Conservation of Migratory Species of Wild Animals; CMS), Ramsar Convention on Wetlands of International Importance, UN Educational, Scientific and Cultural Organization (UNESCO), World Heritage Convention (WHC) and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Each Arctic Council country is a Party to at least one of these conventions and has, thereby, made commitments that have the effect of protecting and restoring biodiversity (Box 1.2).

This synthesis chapter draws on the evidence, findings and suggested actions presented in the peer-reviewed technical chapters of the ABA. It provides an overview of their primary findings and the extensive cross-sectosity. This has led to many opportunities to provide Arctic-specific information into CBD processes (CAFF 2012), and will directly contribute to the achievement of the Strategic Plan for Biodiversity 2011-2020 adopted by CBD Parties in 2010.

The Strategic Plan for Biodiversity 2011-2020 is comprised of a shared vision, a mission, strategic goals and 20 ambitious yet achievable targets, collectively known as the Aichi Targets. The mission calls for effective and urgent action to halt the loss of biodiversity in order to ensure that, by 2020, ecosystems are resilient and continue to provide essential services, thereby securing the planet's variety of life, and contributing to human well-being, including the eradication of poverty.

The 2013 Arctic Biodiversity Assessment will provide data and information on the status and trends of biological diversity in the Arctic to the Fourth Global Biodiversity Outlook and will also contribute to the achievement of the Strategic Plan for Biodiversity 2011-2020 and the Aichi Targets. The Aichi Targets of direct relevance to the findings of the Arctic Biodiversity Assessment are:

- **Target 5**
  By 2020, the rate of loss of all natural habitats, including forests, is at least halved and where feasible brought close to zero, and degradation and fragmentation is significantly reduced.
- **Target 6**
  By 2020 all fish and invertebrate stocks and aquatic plants are managed and harvested sustainably, legally and applying ecosystem based approaches, so that overfishing is avoided, recovery plans and measures are in place for all depleted species, fisheries have no significant adverse impacts on threatened species and vulnerable ecosystems and the impacts of fisheries on stocks, species and ecosystems are within safe ecological limits.
- **Target 9**
  By 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment.
- **Target 10**
  By 2015, the multiple anthropogenic pressures on coral reefs, and other vulnerable ecosystems impacted by climate change or ocean acidification are minimized, so as to maintain their integrity and functioning.
- **Target 11**
  By 2020, at least 17 per cent of terrestrial and inland water, and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes.
- **Target 12**
  By 2020, the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained.
- **Target 14**
  By 2020, ecosystems that provide essential services, including services related to water, and contribute to health, livelihoods and well-being, are restored and safeguarded, taking into account the needs of women, indigenous and local communities, and the poor and vulnerable.

ral scientific literature, and presents suggestions for priority actions on conservation and research. It starts with a description of the characteristics of Arctic biodiversity, outlines the interactions between humans and Arctic wildlife through millennia, provides a brief summary of the conclusions of each chapter and then discusses challenges facing biodiversity by describing stressors from both within and outside the Arctic.

## 1.2. CHARACTERISTICS OF ARCTIC BIODIVERSITY

The Arctic is made up of the world's smallest ocean surrounded by a relatively narrow fringe of island and continental tundra (Box 1.3). Extreme seasonality and permafrost, together with an abundance of freshwater habitats ranging from shallow tundra ponds fed by small streams to large deep lakes and rivers, determine the hydrology, biodiversity and general features of the Arctic's terrestrial ecosystems. Seasonal and permanent sea ice are the defining features of the Arctic's marine ecosystems.

The Arctic tundra, freshwaters and seas support more than 21,000 species of plants, fungi and animals – even when endoparasites[1] and microorganisms are excluded, of which thousands of species may remain undescribed. Although they are less rich in species than other biomes on Earth (see for example, vascular plant richness in Fig. 1.1), Arctic terrestrial and marine ecosystems provide room for a range of highly adapted and particularly cold-resistant species, as well as species that fill multiple ecological niches.

Species richness is unevenly distributed over the Arctic and varies both with latitude and longitude and Pleistocene glacial history. It is also to some extent taxon specific. In most organism groups, species richness declines from the low to high Arctic. Areas that were unglaciated during the last ice age possess higher richness of vascular plants, bryophytes, diadromous and freshwater fishes and terrestrial mammals (Reid *et al.*, Chapter 3, Christiansen & Reist, Chapter 6, Daniëls *et al.*, Chapter 9). The area around the Bering Strait and eastern Siberia is particularly rich in species (e.g. plants, terrestrial invertebrates,

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[1] A parasite that lives within another organism.

## Box 1.3. Two very different polar areas

The Antarctic continent has been isolated from the rest of the world's land masses for about 23 million years (Trewby 2002), and together with an almost total ice cover for 15 million years this has left the Antarctic with a very sparse terrestrial fauna and flora. While the Antarctic continent is huge and almost totally ice covered, the Arctic is made up of the world's smallest ocean surrounded by a relatively narrow zone of island and continental tundra at the edge of the two large northern continents. This means that the Arctic has a rich terrestrial fauna and flora derived from the Eurasian and North American continents and including many species that were widespread at lower latitudes during the Pleistocene. Indeed, about 14,000 terrestrial Arctic species are known to science – even when endoparasites and microorganisms are excluded. The periodic advances and retreats of Arctic continental ice sheets during the Pleistocene caused many local extinctions, but also created intermittent dispersal barriers and population bottlenecks, accelerating divergent evolution of some taxa (see Christiansen & Reist, Chapter 6 and Josefson & Mokievsky, Chapter 8).

One of the results of this is that the Arctic – in contrast to the Antarctic – is inhabited by a variety of terrestrial mammalian predators. The absence of this faunal element from the Antarctic allowed millions of flightless penguins to breed on the continental land mass – a behavior which would be precluded in the Arctic by the presence of Arctic foxes, wolves and polar bears. Not even massive harvest by humans during the last century altered the apparently genetically fixed confidence of much of the Antarctic fauna, so that one can approach the animals almost to within touching range. The presence of land predators in the Arctic meant that the 'northern penguin', the flightless great auk *Piguinus impennis* only lived at the margins of the Arctic, on islands where polar bears, wolves, Arctic foxes and humans were absent – until European mariners reached their breeding grounds a few centuries ago and drove them to extinction.

While the Arctic is very much richer in terrestrial biodiversity than the Antarctic, this is not so for marine life. With c. 7,600 marine species, the Arctic has similar species richness to the Antarctic, even though the species composition of the marine phytoplankton and sea-ice algal communities is different between the two polar regions. The open southern ocean that has encircled the Antarctic for millions of years has allowed many Antarctic marine taxa to disperse around

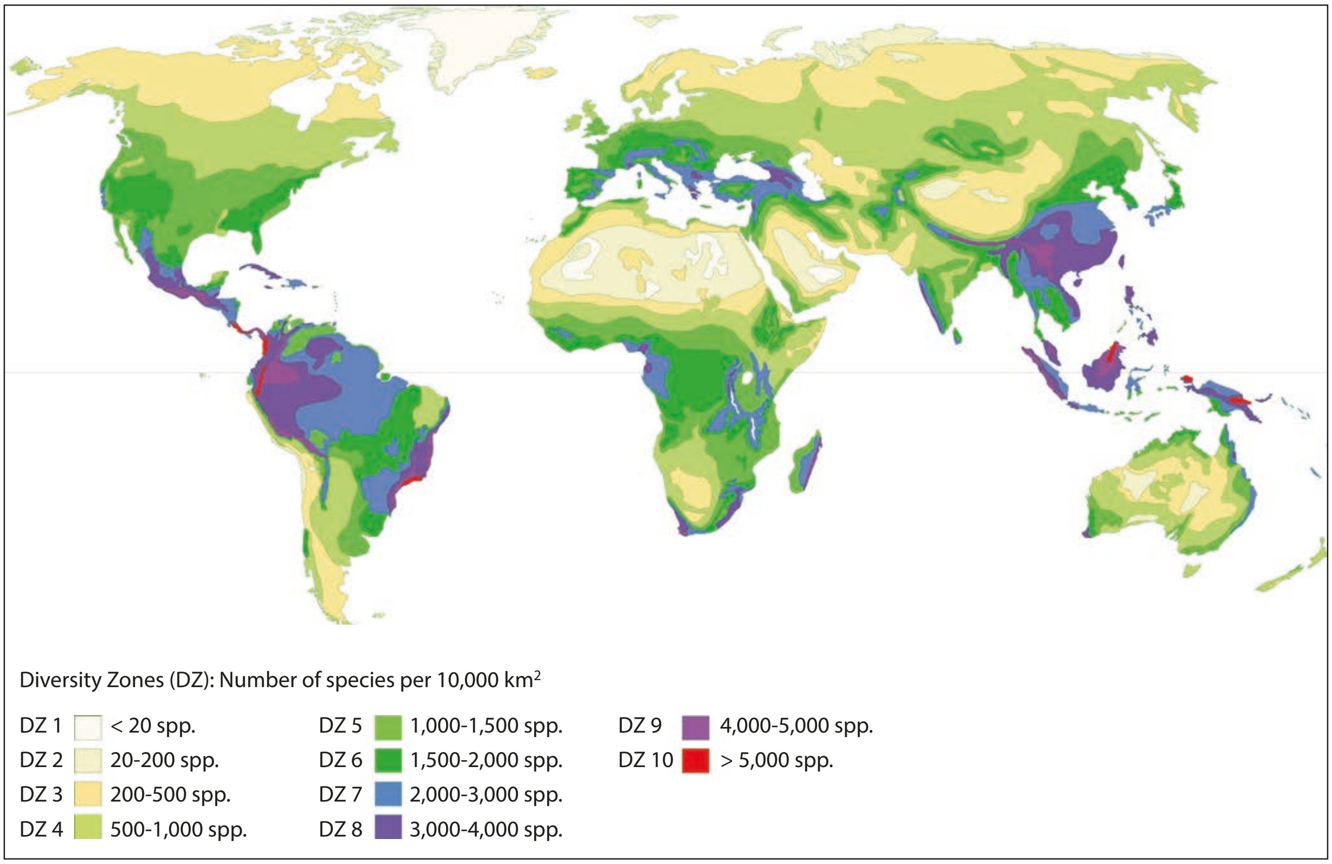

**Figure 1.1.** World species richness in vascular plants (from Settele *et al.* 2010; printed with permission from Pensoft Publishers). See also Fig. 2.1 in Payer *et al.*, Chapter 2.

the entire continent. Given the greater extent of the ice-free southern ocean, compared with Arctic waters, it is not surprising that the total numbers of marine organisms living in Antarctic waters exceed those of similar Arctic species. For example, the most numerous seal species in the world is the Antarctic crabeater seal *Lobodon carcinophaga* with an estimated population in the region of 50 to 80 million individuals (Shirihai 2008); while at least 24 Antarctic and sub-Antarctic seabird species number more than 1 million individuals, 'only' about 13 Arctic and sub-Arctic seabirds reach this level (cf. Cramp 1983-1989, Williams 1995, Brooke 2004, Shirihai 2008, Ganter & Gaston, Chapter 4). In contrast to Antarctica, Arctic marine waters are separated into Pacific and Atlantic zones, each with its own evolutionary history, so that many Arctic genera are represented by different species in the two ocean basins. In addition, marine food webs differ between the two polar regions (Smetacek & Nicol 2005). Taken together, ecosystem structure, sea extent and the presence of humans and mammalian predators in the Arctic have resulted in great differences in structure, composition and functioning between both marine and terrestrial ecosystems in the Arctic and Antarctic regions.

shorebirds and mammals), probably due to the existence of unglaciated refugia during the Quarternary in combination with isolation east and west of the strait and on islands during interglacial periods with elevated sea levels (Payer *et al.,* Chapter 2, Reid *et al.*, Chapter 3, Ganter & Gaston, Chapter 4, Hodkinson, Chapter 7, Daniëls *et al.*, Chapter 9, Ims and Ehrich, Chapter 12). Marine fish have very high richness in the Bering Sea, but much lower richness on the Arctic side of the Bering Strait sill (Christiansen & Reist, Chapter 6). While Iceland and Greenland have particularly low diversity of freshwater fish and terrestrial mammals, Greenland is rich in lichens (Dahlberg & Bültmann, Chapter 10). Marine benthic invertebrates show highest species richness in the Barents/Kara Sea area, although some of those latter patterns partly may result from more intensive sampling in these areas (Josefson & Mokievsky, Chapter 8).

Although the relationship between diversity and productivity remains unclear (e.g. Currie *et al.* 2004), zones of high productivity often support higher diversity of species. Deltas and estuaries of large Arctic rivers are among such areas of high local productivity due to riverine nutrient inputs, mixing zones and upwellings from deep marine waters. These areas contain high fish biodiversity, consisting of mixtures of wholly freshwater species inside the deltas, diadromous species moving between fresh and marine waters, and nearshore marine species tolerant of waters of widely varying salinities (Christiansen & Reist, Chapter 6).

### 1.2.1. Terrestrial ecosystems

The terrestrial Arctic makes up about 5% of the Earth terrestrial surface. Most of it is within relatively short distance from icy coasts that make up one fifth of the total coastline of the world. Compared with most other biomes on Earth, the terrestrial Arctic is generally low in species diversity, which is explained by a number of properties, such as its relatively young age, low solar energy input, extreme climatic variability and decreasing biome area with increasing latitude (Payer *et al.*, Chapter 2). The high Arctic has particularly low vascular plant diversity compared with lower latitudes in the Arctic (Daniëls *et al.*, Chapter 9). But at a small scale, species diversity can be very high. In sample-plots of 25 square meters, for example, almost 100 species of vascular plants, bryophytes and lichens can grow together (Vonlanthen *et al.* 2008) with an unknown number of other fungi, algae and microbes, which is as high as in the richest grasslands of temperate and subtropical regions (Daniëls *et al.*, Chapter 9, Dahlberg & Bültmann, Chapter 10). Together with the absence of woody plants and sedges (*Carex* spp.), this makes this marginal northern rim of the Arctic a unique ecosystem of the world (e.g. Matveyeva 1998, Vonlanthen *et al.* 2008, Ims & Ehrich, Chapter 12).

Terrestrial Arctic ecosystems are characterized by a short productive summer season, but also by large regional differences including markedly steep environmental gradients. For example on the Taimyr Peninsula in Siberia only 500 km separate the relatively lush sub-Arctic and the high Arctic 'desert' (CAVM Team 2003, Callaghan 2005). The defining features of the terrestrial Arctic are cool summers (see Section 2 in Meltofte *et al.*, Introduction) and short growing seasons resulting in low primary productivity and reduced biomass in comparison with southerly latitudes. Adaptations include slow growth and long life cycles in plants and fungi, small fungal sporocarps and small average body sizes in invertebrates (Callaghan 2005, Dahlberg & Bültmann, Chapter 10). Another prominent feature of much of the Arctic is extreme seasonality with ground-level differences of up to about 80 °C between winter minimum and summer maximum temperatures and with strong spatial north-south and coast-inland gradients. Arctic organisms are well adapted to this seasonality either by their ability to migrate during winter, or through characteristics making them suited to the cold and snow (Callaghan *et al.* 2004a). These include short extremities, winter whiteness, insulation through fur, feathers and fat, freeze tolerance, endogenous antifreeze compounds, hibernation and the ability to survive desiccation and oxygen deficiency, together with behavior exploiting the insulative properties of snow. Similarly, sessile organisms such as plants have developed a variety of individual strategies to economize or reduce loss in biomass and to persist through adverse conditions, such as asexual reproduction, small and compact growth, furry or wax-like coatings, positive photosynthesis balance at low temperature and survival at extremely low temperatures and levels of water content during winter dormancy.

Arctic terrestrial biodiversity has had to adapt to the high variability of the Arctic climate both in the form of inter-annual variability (including extreme events) and more regular (short or long-term) climatic fluctuations (see Walsh *et al.* 2011). This variability can drive, and may regionally synchronize, fluctuations in wildlife populations (e.g. Vibe 1967, Krupnik 1993, Hansen *et al.* 2013). Inter-annual variability in weather includes extraordinarily severe winters, highly varying amounts of snow, spells of winter rain and thaw (ice crust formation on land; see Rennert *et al.* 2009), variable timing in spring snow melt and sea ice break up, and poor summer weather including periods of strong winds and snowfall. There is increasing evidence that such events occur in cyclical patterns governed by geophysical phenomena such as the Arctic, North Atlantic and Pacific Decadal Oscillations (see Hurrell *et al.* 2003). Moreover, the internally driven (endogenous) multi-annual, high-amplitude cycles in animal and plant biomass driven by trophic interaction in tundra food webs, contribute to the temporal variability of biodiversity (Ims & Fuglei 2005, Ims & Ehrich, Chapter 12). There is rarely a 'normal' year in the Arctic.

### 1.2.2. Freshwater ecosystems

The Arctic landscape is characterized by a wide range of types and sizes of freshwater systems including flowing systems (rivers and streams) and many types of standing water systems (lakes, ponds) (ACIA 2005, Wrona *et al.* 2006, Vincent *et al.* 2008). High seasonality and in many cases ephemerality characterize all systems (Pielou 1994). A unique combination of climatic, geological and biophysical features, related cold-regions processes and the interactions among them produce a diverse range of environmental conditions that shape Arctic freshwater ecosystems and distinguish them from those found at lower latitudes.

Although freshwater ecosystems are abundant in the Arctic, they do not generally support the levels of biodiversity found in more southerly regions. The regional numbers of freshwater species typically decrease sharply poleward, although the differences among regions in the Arctic can be considerable. Fish species diversity is generally low at both regional and local scales in high latitudes, although considerable diversity of the fishes exists below the species level (Reist *et al.* 2006). Although Arctic freshwater systems generally display less biological diversity than temperate or tropical systems, they contain a diversity of organisms that display specialized adaptation strategies to cope with the extreme environmental conditions they face. Examples of adaptations include life-history strategies incorporating diapause and resting stages, unique physiological mechanisms to store energy (i.e. lipids) and nutrients, an ability to grow and reproduce quickly under short growing seasons, and extended life spans relative to more temperate species (Wrona *et al.* 2005).

### 1.2.3. Marine ecosystems

Arctic marine ecosystems differ from other marine ecosystems on the planet. Dominated by large areas of seasonally-formed sea ice over extensive shelves and a large central area of perennial (multi-year) pack ice – at least until recent times – the Arctic Ocean is characterized by seasonal extremes in solar irradiance, ice cover and associated atmospheric exchanges, temperature and, on the shelves, riverine inflow. The seasonality in environmental conditions and the physiography of the Arctic Ocean, together with its connection to the Atlantic and Pacific Oceans through the 'Arctic gateways', are key elements structuring its diversity of species and ecosystems.

The Arctic Ocean is stratified because the large freshwater inflow from rivers and seasonal sea-ice melt makes the upper layer of the ocean less salty than other oceans. The surface stratification is important in that it can limit nutrient supply from nutrient-rich deep waters to the upper water column, where primary production takes place when there is sufficient light in spring/summer. During winter, the absence of light limits photosynthetically driven primary production, which will resume upon the return of the sun, and is, therefore, dependent on latitude. When sufficient light is available in or under the ice, or at ice edges and in open water areas (e.g. in polynyas and ice-free waters in the Barents Sea), short and highly productive phytoplankton or ice algal blooms develop, delivering of energy and materials to zooplankton and other trophic levels that also display a high seasonality in feeding, reproduction and migration patterns.

In the marine Arctic, the central Arctic basins are typically (in the presence of multi-year ice) regions of low productivity. However, some of the most productive marine ecosystems on Earth are found in the outer Arctic seas (e.g. Barents, Chukchi and Bering Seas) and in polynyas, i.e. recurrent areas of open water amid sea ice. Many species of invertebrates, fish, seabirds and marine mammals occur in large aggregations at such particularly productive sites. Interestingly, Arctic sea ice can host productive microbial communities, and the deep waters of the Arctic Ocean also have unique hot vent communities adapted to very high temperatures, highlighting the range of extremes found in Arctic marine ecosystems.

### 1.2.4. Arctic species and food webs

On a global scale, Arctic terrestrial ecosystems are relatively young, having developed mainly during the last three million years (Payer *et al.*, Chapter 2, Ims & Ehrich, Chapter 12). The early Quaternary Arctic flora included species that evolved from high-latitude forest vegetation by adapting to colder conditions, plus others that immigrated from alpine habitats in temperate regions of Asia and North America. During the Quaternary Period, Arctic ecosystems have been profoundly molded by climatic history, including more than 20 cycles of glacial advance and retreat, along with associated changes in sea-ice cover. In many areas, these

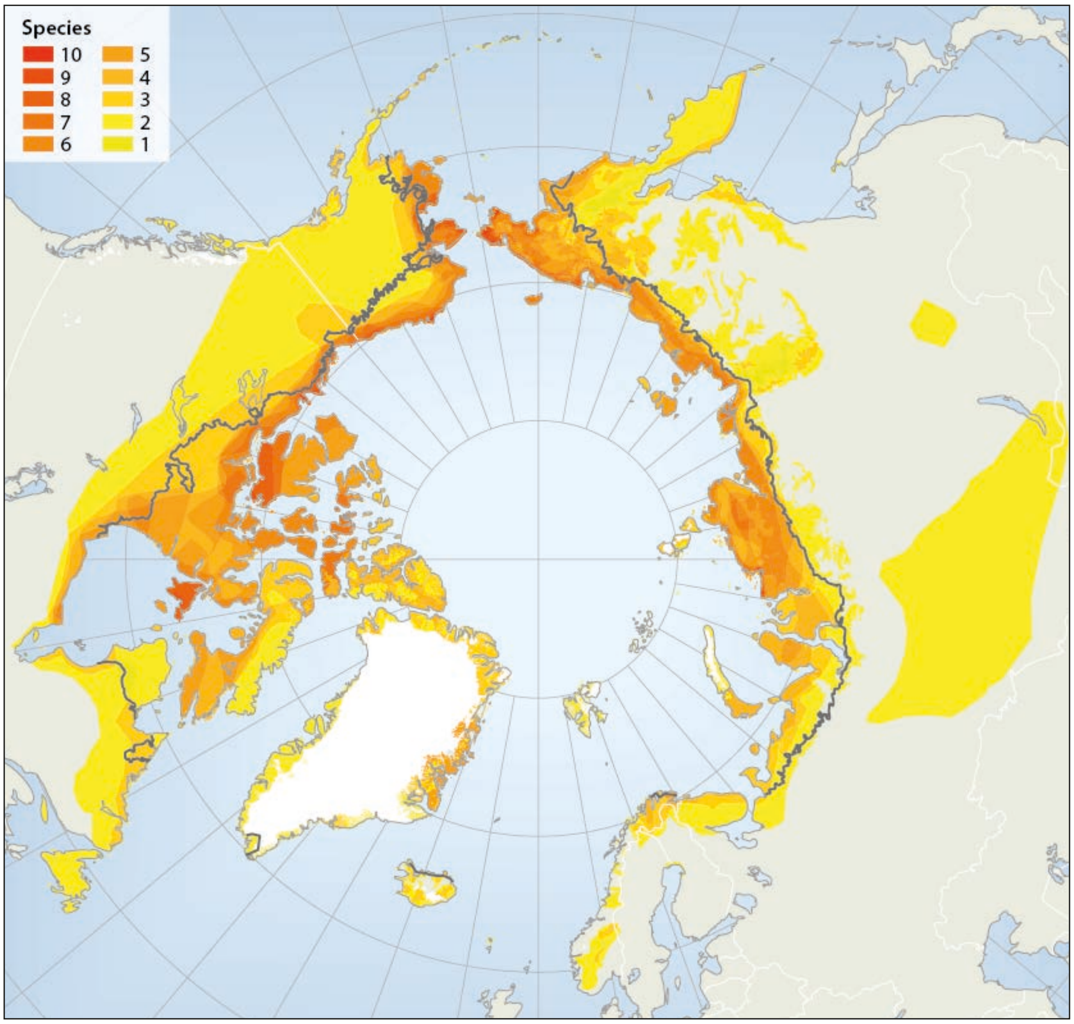

**Figure 1.2.** Circumpolar *Calidris* sandpiper species richness. The dark grey line denotes the border between the Arctic and the sub-Arctic. Adapted from Zöckler (1998).

broad-scale changes displaced, then readmitted, biological communities. Consequently, many Arctic species are well adapted to climate variability and extremes, but poorly adapted for secondary ecological stressors such as increased competition, parasites and diseases (Callaghan *et al.* 2004a).

Many Arctic animal, fungal and plant species are widely distributed within the circumpolar region, with a significant proportion having circumpolar distributions. Endemic species, for which ranges are restricted to a limited geographic region such as the Arctic or parts of the Arctic, are found in many groups of Arctic animals, plants and fungi. However, because of the shifting conditions, local-scale adaptation and speciation is rare outside Beringia, leading to low numbers of local endemics. Among invertebrates, endemic species range from single cell testate amoebae to the higher arthropods such as spiders, mites, springtails and beetles (Hodkinson, Chapter 7). Among marine invertebrates, the moss animals (bryozoans), being sessile and generally characterized by restricted dispersal ability, show a relatively high degree of endemism (Josefson & Mokievsky, Chapter 8). Some helminth parasites also have restricted geographic distributions coinciding with their avian, mammalian and piscine hosts (Hoberg & Kutz, Chapter 15). Among vascular plants, endemic species include more than one hundred narrow-range species especially in Beringia and even some planktonic cold-adapted algae (Daniëls *et al.*, Chapter 9). Among fungi, there are many endemic or restricted range lichens, especially from Svalbard, Greenland, Novaya Zemlya, eastern Chukotka and Ellesmere Island. Most of these are rock-dwelling microlichens confined to the high Arctic (Dahlberg & Bültmann, Chapter 10). Among terrestrial insects, several beetle species are endemic to the Beringia region of NE Siberia. Several species of char *Salvelinus* spp., several whitefishes *Coregonus* spp. and a few other freshwater and marine fishes are endemic or near endemic to the Arctic (Christiansen & Reist, Chapter 6). In birds, the loons/divers Gaviidae and the auks Alcidae are mainly found in the Arctic and sub-Arctic, while the eiders *Somateria* spp. and *Polysticta*, gulls (Laridae) and *Calidris* sandpipers reach their highest diversity there (Fig. 1.2; Ganter & Gaston, Chapter 4). Also among mammals, a number of highly adapted species are found almost exclusively in the Arctic (Reid *et al.*, Chapter 3).

Among flying birds, few of the Arctic species can be classified as restricted range species, i.e. species with a total historical breeding range of less than 50,000 km$^2$ (BirdLife International 2012). However, among other groups, several species exhibit more limited distributions. Some Arctic endemics are confined to one or a few locations, such as longfin char *Salvethymus svetovidovi* and small-mouthed char *Salvelinus elgyticus*, which are found only in Lake El'gygytgyn, a three million-year-old meteorite crater lake in central Chukotka (Christiansen & Reist, Chapter 6). Mammals with restricted ranges include some species of shrews and lemmings, such as the Pribilof Island shrew *Sorex pribilofensis* and the Wrangel Island brown lemming *Lemmus portenkoi*, which inhabit islands that were once part of a broader land mass but became isolated by rising sea levels after the last ice age.

Therophytes (annual plant species) are rare in the Arctic because of short growing seasons, marked interannual variability and nutrient-poor soils. Conversely, polyploidy[2] is common across the Arctic vascular plant flora, in particular in the northern and longer-glaciated North Atlantic areas of the Arctic (e.g. Brochmann *et al.* 2004, Solstadt 2009). The evolutionary success of polyploids in the Arctic may be based on their fixed heterozygous genomes, which may buffer against interbreeding and genetic drift through periods of dramatic climate change. Moreover the ecological amplitude of polypoids is broad and thus they have a greater ability to cope with a changing climate and adapt to more diverse ecological niches than a dipoloid could (Brochmann *et al.* 2004, Daniëls *et al.*, Chapter 9). Among birds, plumage polymorphism is widespread (e.g. skuas/jaegers *Stercorariidae*, northern fulmar *Fulmar glacialis*, snow geese *Chen* spp., Iceland gull *Larus glaucoides*, nestling murres *Uria* spp.), perhaps as a result of population differentiation and introgression during the Pleistocene glacial and interglacial periods (see also Box 17.10 in Cook, Chapter 17).

In response to extreme seasonality, many Arctic species are migratory. This involves a high proportion of bird species and several marine mammals that migrate out of the Arctic entirely, whereas others such as reindeer/caribou migrate long distances within the Arctic or to adjacent sub-Arctic areas. Migratory birds, in particular, visit the Arctic to breed or feed intensively during the summer burst of productivity, both on land and in the sea. Many of them spend more than half the year outside the Arctic, where they may be found in practically every other part of the world, except inland Antarctica (Ganter & Gaston, Chapter 4).

A special kind of migration is shown by diadromous[3] fish, which either spend each summer in the sea to fatten up, or live there for most of their lives before going up rivers to reproduce in fresh water (Christiansen & Reist, Chapter 6).

Arctic ecosystems have generally been considered to possess shorter food chains with fewer trophic levels than other biomes (Callaghan 2005). However, this concept is increasingly challenged (see e.g. Hodkinson, Chapter 7 and Michel, Chapter 14), and Arctic marine ecosystems are found to be as diverse as more southern marine ecosystems (Smetacek & Nicol 2005, Josefson & Mokievsky, Chapter 8). However, the numerical dominance of relatively few key species in Arctic food webs, together with highly variable climatic conditions, makes them prone to strong food web interactions (for instance leading to community-wide cycles) and environmentally driven fluctuations with cascading effects through entire ecosystems (Post *et al.* 2009, Gilg *et al.* 2012, Hansen *et al.* 2013). Consequently, Arctic ecosystems are unstable in terms of species composition and abundance, but nevertheless have shown substantial resilience to natural variability in the Holocene, largely because of the wide distributions and mobility of their constituent organisms. This mobility, which enables much of the fauna and flora to move and seek new habitat elsewhere in response to unfavorable circumstances, is often an essential part of their adaptation to locally and regionally variable conditions. Mobility can be active, in which animals seek out new habitat, or passive, involving non-directed dispersal of animals, fungi and plants by wind, surface melt-water and streams, and local ocean currents or by phoretic dispersal on the bodies of vertebrates or larger flying insects. When planning for Arctic conservation, it is essential to consider the vast spatial scales over which many organisms operate as well as the existing barriers to mobility that influence the current distribution of some species (e.g. marine barriers to movements of some terrestrial mammals such as the Arctic ground squirrel *Spermophilus parryii*).

## 1.3. HUMAN USE OF WILDLIFE THROUGH TIME

> » *This is what I want to pass on to my descendants: good food from the land, caribou and fish. The land makes you live well and be healthy.*
>
> (Rosie Paulla, in Brody 1976).

> » *The reason I exist today as an Inuk is because of my ancestors that really tried and survived on wildlife and whales… When I go whale hunting … there are a lot of things that go through my mind, not about the world today, but about the world where we were before, where my ancestors were coming from. Yeah, you can almost hear echoes from the past when you are whaling.*
>
> (Johnny Mike, Pangnirtung, March 1995).

From the first arrival of humans in the Arctic to the modern day, the use of wildlife has been an essential contributor to individual and community well-being. Patterns and purposes of use have varied by time and place, with differing implications for biodiversity. The harvest of wildlife remains both a vital connection between humans and biodiversity and a source of impacts to at least some wildlife populations, whereas today other stressors pose a greater threat to Arctic biodiversity. This section provides a brief outline of such uses and impacts, from prehistory until today, by indigenous peoples and more recent arrivals.

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[2] More than two sets of chromosomes occurring in an organism.

[3] Fish migrating between fresh and marine waters.

People in the Arctic have harvested wild species for millennia with wild mammals, birds, fish and plants providing nutritional as well as cultural sustenance (Huntington *et al.*, Chapter 18). Arctic cultures have been more dependent on hunting than people in almost any other part of the world because of the limited availability of edible wild plants to complement hunted species. Some species, such as bears and whales, have great symbolic importance in Arctic cultures, and harvest of wildlife is deeply rooted in the self-perception of Arctic peoples (see pp. 18-19 for Arctic indigenous views on biodiversity). Although traditional foods typically account for a smaller portion of indigenous diets today (Hansen *et al.* 2008, Vaktskjold *et al.* 2009, Wheeler *et al.* 2010; see also Huet *et al.* 2012), biodiversity and the natural environment remain integral to well-being of Arctic peoples, providing not only food but the everyday context and basis for social identity, cultural survival and spiritual life (Huntington *et al.*, Chapter 18).

Indigenous cultures and technologies allowed people to thrive in the Arctic and to cope with a high degree of natural environmental variability. However, the Arctic has fewer resources and fewer alternatives in times of scarcity than the sub-Arctic and boreal zones, creating a higher degree of risk from changes in weather patterns or wildlife populations. The archeological record indicates, as one result, the repeated disappearance of whole cultures such as in Greenland and the Canadian Arctic since the Arctic was first inhabited (Born & Böcher 2001). Scarcity and even famine remained a part of life in much of the Arctic even into the modern era.

Climate change and human hunting probably worked together to force major changes in Arctic biodiversity in the late Quaternary (Lorenzen *et al.* 2011). Still, for several millennia human population density was so low in most parts of the Arctic[4], and the means of transport and hunting so limited in range, that significant human impacts on animal populations were probably limited to a number of long-lived and slow-reproducing species together with easily accessible colonies of breeding seabirds and marine mammals (see e.g. Krupnik 1993 and Freese 2000). It is also likely that hunting had marked impacts on the behavior of several species, which became wary of human presence, while most remained relatively little affected.

Arctic cultures often view human-environment interactions in terms of the relationship between individual humans and animals. For example, hunters may be admonished to treat harvested animals well, by using them fully, storing them properly and respecting their spirit. While such practices no doubt contribute to the well-being of Arctic societies and may have helped sustain animal populations, they should not be interpreted solely in light of modern conservation principles based on scientific understanding of population dynamics, reproduction rates and habitat needs (see e.g. Berkes 1999). Instead, such practices must be understood as part of the cultures and knowledge systems in which they were practiced, and can be incorporated into today's conservation efforts.

The perception of pre-modern sustainability of Arctic peoples' harvest of mammals, birds and fish varies considerably. Scholarly reviews are given, for example, by Berkes (1999) and Krupnik (1993) representing slightly differing 'anthropological' and 'natural science' views, respectively. There are well documented examples of measures such as rotational harvest to avoid overexploitation in the North, but most of these are from the sub-Arctic and boreal regions (Berkes 1999, Mustonen & Mustonen 2011, Christiansen & Reist, Chapter 6), where more alternative resources were available. As expressed by Krupnik (1993) "In contrast [to the Arctic], an overkill hunting strategy appears to have no parallel among the hunters and fishers of the northern forests or the temperate coastal zone, because the resources of the river valleys and maritime ecosystems are far less marked by instability and unpredictability." Similarly, people in the sub-Arctic Faroe Islands and Iceland practiced strong regulation of the take of birds and eggs in seabird colonies to avoid depletion of this very important resource (see e.g. Nørrevang 1986 and Olsen & Nørrevang 2005).

Indeed, people living in the Arctic often harvested more than they consumed, and for good reasons (Krupnik 1993). The living conditions in the Arctic – i.e. among people without access to alternative boreal resources – have always been unpredictable enough that it was a necessary strategy to use any opportunity to secure as much food and other materials as possible, as a reserve against future scarcity (see also Meltofte 2001). Animals were harvested in accordance with need, considering both immediate use as well as longer-term insurance against scarcity. In addition, if important local resources were depleted, there was room in most parts of the Arctic to move elsewhere.[5]

The migration of people from the south, particularly from the 17th century onwards, increased the pressure on several wildlife populations considerably. Several populations of marine mammals suffered sharp population declines due to commercial whaling and other new forms of exploitation. During the whaling era, two whale populations – the Atlantic gray whale *Eschrichtius robustus* and the Northeast Atlantic right whale *Eubalaena glacialis* – were driven to extinction (Krupnik 1993,

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[4] With the possible exception of reindeer herding areas in northern Eurasia, which to a large extent relied on boreal resources, the most densely populated Arctic areas were probably the highly productive coasts around the Bering and Davis Straits (SW Greenland) populated by Inuit and Yup'ik (see AMSA 2009).

[5] Famine is not considered here, since it most often was the result of unfavorable sea ice or other climatic conditions in certain years or periods reducing the availability of game (see e.g. Vibe 1967, Krupnik 1993).

Nowak 1999, Reid *et al.*, Chapter 3). A few species that were already reduced in population or distribution by local hunting were driven extinct by newcomers. The Steller's sea cow *Hydrodamalis gigas* was driven extinct within a decade of the arrival of southern expeditions and whalers (Doming 1978, Turvey & Risley 2006). The great auk *Pinguinus impennis* in the North Atlantic met a similar fate during the 19th century (Nettleship & Evans 1985, Meldgaard 1988). Later, commercially exploited fish stocks came under pressure until recently when more effective management measures were put in place in most places, although by-catch and the allocation of harvest remain problematic for some stocks, especially for some indigenous fishers (FAO 2005, Christiansen & Reist, Chapter 6, Michel, Chapter 14, Huntington, Chapter 18; also see Section 1.5.1.2 for a summary of impacts and trends of harvest on biodiversity.)

For the many Arctic species such as birds and whales that migrate to southern wintering areas, hunting and habitat degradation outside the Arctic have added to the pressure, which in some cases is more severe than in the Arctic. Dire examples of this are the likely extermination of the New World Eskimo curlew *Numenius borealis* by hunting and habitat change primarily in the late 19th and early 20th century (Ganter & Gaston, Chapter 4) and the highly endangered spoon-billed sandpiper *Eurynorhynchus pygmeus* of easternmost Siberia that appears to be at the brink of extinction due to habitat loss and harvest on its wintering grounds in Southeast Asia (Zöckler *et al.* 2010).

While Arctic biodiversity for thousands of years has formed the basis for human cultures in almost all parts of the Arctic, today the harvest of Arctic living resources cannot provide sufficient incomes to support a modern lifestyle across entire communities or regions. Thus, access to additional income from mineral resource exploitation or subsidies from southern societies (transfer payments) are necessary to maintain living standards considered basic in the 21st century (Duhaime 2004), though these economic changes have repercussions for biodiversity and human use thereof. Accordingly, in large parts of the Arctic the importance of Arctic biodiversity to human societies will increasingly emphasize cultural and ethical values including activities such as increasing tourism (see e.g. Hvid 2007 and Huntington, Chapter 18). Yet, harvest of wildlife has importance in securing people against the fluctuation and instability of the monetary economy, such as happened after the end of the Soviet Union (Duhaime 2004).

Marine fisheries form an important exception to this trend, in that some of the richest fisheries on Earth are found in the North, particularly along the sub-Arctic fringes. These commercial fisheries harvest millions of tonnes annually, including more than 10% of global marine fish catches by weight and 5.3% of crustacean catches, for an economic value in billions of US dollars (Christiansen & Reist, Chapter 6, Michel, Chapter 14, Huntington, Chapter 18). By contrast, harvest of Arctic species other than fishes and shellfish – even though an important part of the seasonal activities and nutrition of many humans in the Arctic – is an important source of income for a dwindling number of people (Huntington *et al.*, Chapter 18).

The rapid growth of human population in most other parts of the world was primarily due to the development of agriculture, followed more recently by the industrial revolution and modern health practices. Thanks to these innovations, southern societies have increased population densities by several orders of magnitude and at the same time – in most parts of the world – raised living standards to hitherto unknown levels. This was not possible in the Arctic as the 'carrying capacity' of Arctic biodiversity could not support dense human populations. Instead, recent Arctic population growth has resulted from increasing integration with southern economies and societies including the introduction of modern medicine and technology (such as rifles) together with the prevention of widespread starvation and death in periods of poor hunting. For example, the population of Greenland has grown by a factor of 10 since contact with Europe was established almost 300 years ago (Born & Böcher 2001, Danmarkshistorien.dk 2012). Within this general trend, there have been local and regional population decreases and other impacts resulting from impacts of commercial exploitation, environmental variability and economic downturns. However, the separation of human population levels from local carrying capacity and the advent of commercial hunting practices that reward higher harvests led to severe overexploitation of several animal populations such as walrus and a number of seabird species in W Greenland (Merkel 2004a, Witting & Born 2005, Reid *et al.* Chapter 3, Ganter & Gaston Chapter 4).

Human interactions with animals are not limited to hunting and fishing. In some cases, humans are the prey species, as is the case with biting flies and especially mosquitoes. Arctic ecosystems provide ideal aquatic breeding habitats for these insects. While the diversity of mosquito species is generally low, individual species often attain such high summer densities as to make life intolerable for humans and many other vertebrate species. The depredations of mosquitoes alter patterns of behavior in both humans and other vertebrates, including caribou/reindeer. A consequence of increasing abundance of mosquitoes is seen in the explosive emergence of infections of filarioid nematodes that over the past decade have driven mass mortality among reindeer in sub-Arctic Finland and represent direct threats to food security (Hoberg & Kutz, Chapter 15). It is predicted that such ephemeral events linked to patterns of high temperature and humidity may become increasingly common, due to accelerated warming at high latitudes. Currently, no major pathogens are transmitted by Arctic mosquitoes, but as climate warms there is potential for the spread of several insect-borne diseases of humans and other vertebrates into the Arctic. The effects of future warming on biting insects are highly uncertain, however, as they depend on interactions between insect life cycles and temperature, precipitation patterns and tundra hydrology.

Reindeer herding in Eurasia is one of the most extensive forms of human interactions with tundra ecosystems. Both herding practice (range use and migration pattern) and deer abundance (herd size) matter in terms of grazing impacts. Substantial increases of herd sizes both in northern Fennoscandia and on the Yamal Peninsula are associated with large impacts on vegetation, even to the extent that semi-domestic reindeer may counteract the processes of climate-induced encroachment of tall shrubs in tundra (Ims & Ehrich, Chapter 12).

Human-wildlife interactions also include activities such as birdwatching and tourism. These are increasing in the Arctic, especially through more voyages by cruise ships (AMSA 2009). Tourism can increase awareness of Arctic biodiversity and support for its conservation, but if not carefully managed can also lead to disturbance of animals, especially at areas of high aggregations such as bird colonies or marine mammal haul outs, which offer excellent wildlife viewing opportunities and thus attract visitors. The presence of tourists may also interfere with traditional hunting, fishing and herding activities, since these activities to some extent compete for the same locations or resources.

## 1.4. STATUS AND TRENDS IN ARCTIC BIODIVERSITY

An accurate accounting of the status and trends of the species of Arctic flora and fauna is impossible except for relatively few well-known vertebrates (see Box 1.4 on the Arctic Species Trend Index). For many species or species groups, we have data on distribution and sometimes also density, but lack the record through time to assess trends. In addition, many short-term trends reflect cyclical patterns rather than long-term increases or declines. Among the best known of these cyclical patterns are those of Arctic lemmings and lemming-dependent predators with their characteristic 3-5 year cycles (Reid *et al.*, Chapter 3, Ims & Ehrich, Chapter 12). Caribou populations may also fluctuate over the course of decades, making it difficult to distinguish natural variability from new impacts such as industrialization or climate change. For some species, monitoring is facilitated by formation of temporary aggregations associated with seasonal habitat preferences or predator-avoidance behaviors. Examples include caribou and beluga calving grounds, seal pupping areas, and goose and seabird colonies. In addition, migratory birds that breed in a dispersed fashion may aggregate on migration or during winter at southern staging and wintering areas, enabling satisfactory monitoring outside the Arctic (e.g. shorebirds and some raptors). Consequently, some of the species for which trends are best known are highly migratory and highly social, at least during some part of the year. Solitary or highly dispersed species are much harder to monitor and feature disproportionately among species for which information is lacking. This section presents a summary of current understanding by taxonomic[6], ecosystem and functional group in accordance with the chapters in the assessment.

Approximately 67 terrestrial and 35 marine **mammal species** are found in the Arctic, of which 19 terrestrial and 11 marine species are more or less confined to this biome (Reid *et al.*, Chapter 3). This represents about 2% of the world's estimated number of mammal species. Arctic mammals are unevenly distributed, with more species and generally higher abundances in the low Arctic than in nearby high Arctic areas. Regions that remained largely unglaciated (e.g. Beringia) during the last ice age now have the greatest diversity of terrestrial species. Among marine mammals, species richness is highest in the Pacific and Atlantic sectors of the low Arctic in the vicinity of the Arctic gateways, which provide corridors for seasonal migrations from temperate seas. There are several examples of population and range changes in Arctic mammals during historical times, in which direct actions by humans have had large effects on a number of species. Overharvest has caused extinction of one species, Steller's sea cow, as well as regional extirpations of carnivores such as the gray wolf *Canis lupus*. Excessive commercial harvest extirpated the Atlantic gray whale and NE Atlantic northern right whale. In some areas, subsistence overharvest reduced populations of walrus and beluga *Delphinapterus leucas* to low levels, but the introduction of quotas has allowed recovery in some populations. Humans have moved muskoxen around the Arctic, reestablishing historically extirpated populations such as those in Arctic Alaska and NE Siberia. The decreasing extent and duration of sea-ice cover due to climate change has resulted in decreased survival and body condition in some polar bear populations. Heavy and more frequent icing events following freezing rain and winter thaws have driven declines in some populations of muskoxen and caribou. Proliferation of shrubs in the low Arctic is allowing Eurasian elk *Alces alces*, moose *Alces americanus* and snowshoe hares *Lepus americanus* to spread further into the low Arctic. The amplitude and frequency of lemming cycles have changed in some Arctic regions, likely due to changes in timing and quality of snow accumulation in a warmer climate. The northwards expansion of the red fox *Vulpes vulpes* at the expense of the Arctic fox has been attributed to a warming climate, but recent evidence suggests that food supplementation by humans is an additional causal factor. Recently, several wild reindeer/caribou populations have shown pronounced population decreases, probably related to natural fluctuations, climate-induced crashes and overharvest, while other populations are increasing. Among terrestrial mammals only the Pribilof Island shrew *Sorex pribilofensis* is considered endangered according to IUCN criteria.

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[6] Taxonomy is the science of identifying and naming species and other systematic groups of organisms, and arranging them into a classification system.

## Box 1.4. The Arctic Species Trend Index

*Mike Gill, Circumpolar Biodiversity Monitoring Program, Environment Canada*

Evaluating trends in species abundance reveals much about broad-scale patterns of biodiversity change. The Arctic Species Trend Index (ASTI), developed for this purpose, uses population trend data from 890 populations of 323 vertebrate species (37% of known Arctic vertebrate species) using 1970 as the baseline year. It is the Arctic component of a global index of vertebrate species trends, the Living Planet Index (LPI). The ASTI data set can be used to dig deeper and look at patterns in species trends as well as to look at how these trends are related to other changes in Arctic ecosystems (e.g. pelagic fish and the Arctic Oscillation (see below)).

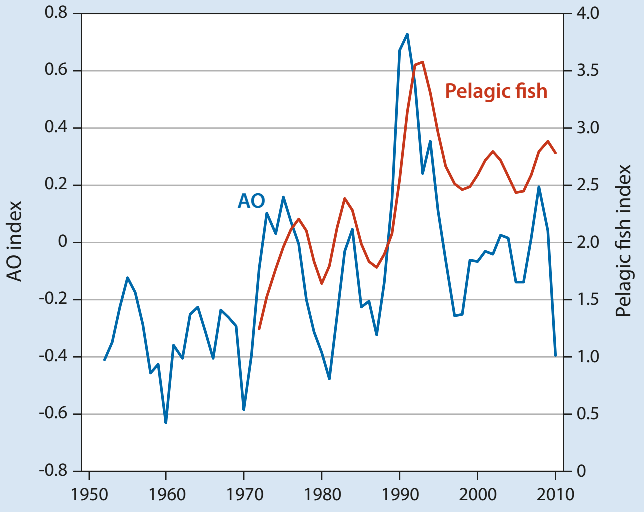
Recent analysis has yielded the following Key Findings:

### 1. The Arctic Species Trend Index: 2011 update

1.1. Average abundance of Arctic vertebrates increased from 1970 until 1990 then remained fairly stable through 2007, as measured by the ASTI 2011.

1.2. When species abundance is grouped by broad ecozones, a different picture emerges, with the abundance of low Arctic species increasing in the first two decades much more than high Arctic and sub-Arctic species. The low Arctic index has stabilized since the mid-1990s whilst the high Arctic index appears to be recovering in recent years and the sub-Arctic index has been declining since a peak in the mid-1980s.

1.3. The trend for Arctic marine species is similar to that of the overall ASTI, while the trend for terrestrial species shows a quite different pattern: a steady decline after the early 1990s to a level below the 1970 baseline by 2005.



### 2. Tracking trends in Arctic marine vertebrates

2.1. The trend for marine fish is very similar to the trend for all marine species, increasing from 1970 to about 1990 and then levelling off. This indicates that the ASTI is strongly influenced by fish trends. Overall, marine mammals also increased, while marine birds showed less change.

2.2. The three ocean regions, Pacific, Atlantic and Arctic, differed significantly in average population trends with an overall decline in abundance in the Atlantic, a small average increase in the Arctic and a dramatic increase in the Pacific. These differences seem to be largely driven by variation in fish population abundance – there were no significant regional differences for birds or mammals.

2.3. Pelagic fish abundance appears to cycle on a time frame of about 10 years. These cycles showed a strong association with a large-scale climate oscillation. See Box 1.4 Fig. 1.

2.4. The ASTI data set contains population trends for nine sea-ice-associated species. There were mixed trends among the 36 populations with just over half showing an overall decline.

2.5. The Bering Sea and Aleutian Island (BSAI) region of the Pacific Ocean is well studied, providing an opportunity to examine trends in more detail. Since 1970, BSAI marine fish and mammals showed overall increases, while marine birds declined. However, since the late 1980s, marine mammal abundance has declined while marine fish abundance has largely stabilized.

### 3. Tracking trends through space and time

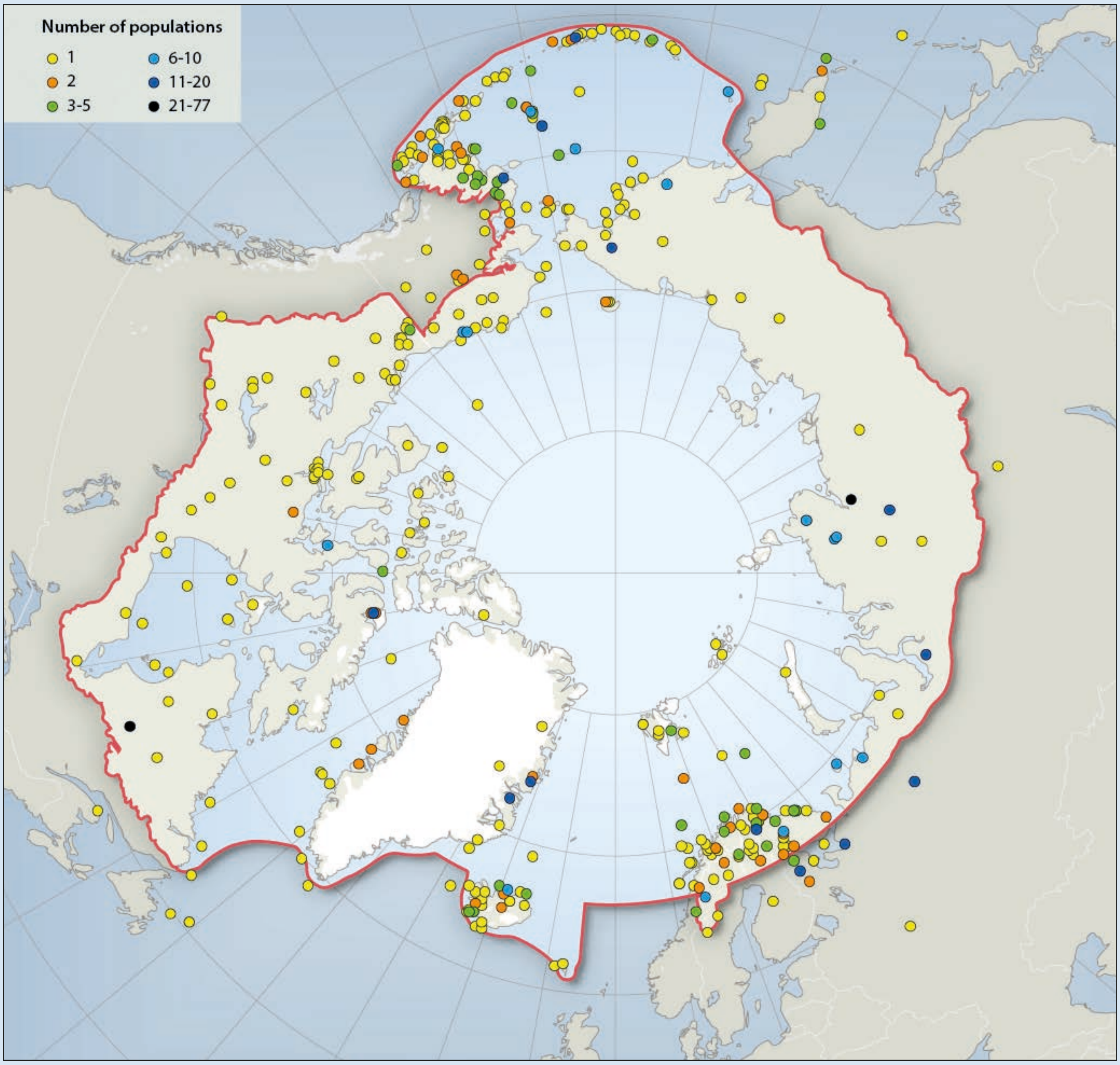
3.1. Spatial analysis of the full ASTI data set (1951 to 2010) started with an evaluation of vertebrate population trend data from around the Arctic. The maps produced from this analysis provide information useful for identifying gaps and setting priorities for biodiversity monitoring programs.

3.2. Mapping trends in vertebrate populations provides information on patterns of biodiversity change over space and time, especially when examined at regional scales.

3.3. Understanding of the causes of Arctic vertebrate population change can be improved by expanding the spatial analysis of ASTI data to include spatial data on variables that represent drivers of biodiversity change.

**Box 1.4 Figure 1.** Comparison of the three year running average for the CBMP pelagic Arctic fish index and the Arctic Oscillation (AO). Oscillation data from: esri.noaa.gov/psd/data/correlation/ao.data

**Box 1.4 Figure 2.** Distribution of population time series data across the political cooperation area of CAFF (red line).



Looking at spatial patterns in Arctic biodiversity trends, the ASTI can be used to assess not only areas of potential conservation concern around the Arctic but also to assess our current and historical monitoring coverage. With over 366 sites with trend information in the ASTI, the locations of these sites was not evenly spread across the Arctic region with concentrations of monitoring efforts found in the Bering Sea, northern Scandinavia and Iceland with more sparse monitoring efforts in northern Canada, northern Russia and northern Greenland. This pattern largely reflects the reality of remote areas and limited human populations associated with areas of limited monitoring coverage. When investigating areas showing concentrated declines, the Labrador Sea, Queen Elizabeth Islands and NE Siberia were three areas where broad scale declines have been occurring. And finally, when investigating the percent of the 366 locations with increasing or stable populations by decade, we see a continual decline in the percentage of stable or increasing populations from the 1950s to the 2000s. Analyzing the main purpose of the monitoring programs that provided this data, it appears that a bias towards increasingly monitoring species of conservation concern (e.g. declining species) cannot explain this trend.

Two hundred **bird species,** about 2% of the global total, occur regularly in the Arctic (Ganter & Gaston, Chapter 4). The majority of these are waterfowl, shorebirds and seabirds, with relatively few songbird species. The Bering Strait region is the richest in species, and for several shorebird species it also supports the highest population densities. Most species spend only a few summer months in the Arctic while dispersing to virtually all parts of the globe during the northern winter. Population trends among Arctic birds are best known for geese and seabirds. Most Arctic-breeding goose populations have increased markedly in the last 30-50 years, many of them recovering from low populations in the mid-20th century. Goose populations breeding in the eastern Russian Arctic and wintering in East Asia (mainly China) are an exception; they have undergone steep declines in the late 20th century. Similarly, eight Arctic-breeding shorebird species migrating through East Asia to winter in Australia have suffered severe declines over the last 25 years or so. However, nearly all shorebird populations in the West Palearctic appear to be stable or increasing, while about a third of the Nearctic-breeding shorebird populations may be decreasing. Several Arctic seabirds appear to have declined in recent decades (e.g. thick-billed murre *Uria lomvia* and the ivory gull), as have several populations of sea ducks. Population sizes and trends of many migratory Arctic birds are influenced by overharvest, disturbance and habitat loss outside the Arctic, with the probable extinction of the Eskimo curlew, mainly due to hunting on its migration areas, as a grave example. Likewise, there is evidence that the critically endangered spoon-billed sandpiper faces extinction due to habitat loss and harvest on its wintering areas in Southeast Asia, while disturbance and mortality on migration and wintering areas probably contribute to the threatened status of the lesser white-fronted goose *Anser erythropus*, red-breasted goose *Branta ruficollis*, bristle-thighed curlew *Numenius tahitiensis* and Siberian crane *Leucogeranus leucogeranus*.

Due to physiological constraints in these cold-blooded animals, **amphibians** and **reptiles** are few in the Arctic and only found along the southern periphery (Kuzmin & Tessler, Chapter 5). Only five primarily boreal and temperate amphibians – four in the Palearctic and one in the Nearctic – together with a single Palearctic lizard range into the low Arctic with all of them considered stable. However, population and distribution data are lacking from most of their Arctic ranges.

Approximately 250 marine and 127 diadromous and freshwater **fish species** inhabit Arctic seas and freshwaters (Christiansen & Reist, Chapter 6). Altogether, the c. 378 fish species within the Arctic correspond to 1.3% of the global total. If the adjacent sub-Arctic seas are included, i.e. the Norwegian, Barents and Bering Seas, the number of marine fish species rises to nearly 640. By far the highest marine diversity is found in the 'Arctic gateways' i.e. the sub-Arctic seas connecting the Arctic Ocean with the Atlantic and the Pacific Oceans. Only 63 marine fish species are considered genuinely Arctic specialists, and none is regarded as endangered. However, due to lack of data, 95% of the Arctic marine fish species have not been evaluated for threat status according to IUCN criteria. High local diversities of fishes also occur in the mouths of the large Arctic rivers where freshwater forms intermingle with diadromous forms and nearshore marine species. Local fisheries of mostly freshwater and anadromous[7] fishes along the Arctic coasts and during autumn migrations upstream into rivers have been ongoing for centuries. Local harvests are often quite high with fish primarily used as food for people and dogs; limited commercial fisheries exist in some areas, although landings are small in comparison to marine fisheries. Several freshwater and diadromous species are listed as 'at some form of risk' according to national conservation definitions which parallel IUCN criteria; in most cases these are taxa with limited distributions in sensitive habitats subject to anthropogenic stressors. There are no clear cases of extinction of freshwater or diadromous fish species, although local populations have been extirpated in some areas. Such populations are often unique forms, but are not described as separate species. For marine fishes, landings from commercial fisheries can be high, amounting for example to an excess of two million tonnes from a single stock of Atlantic herring *Clupea harengus* in the NE Atlantic. Whereas herring and other pelagic fish stocks show negative or highly variable trends, the overall trend for marine groundfishes, and codfishes in particular, appears strong and positive. In 2012, the total allowable catch (TAC) for Alaska pollock *Gadus chalcogrammus* in the Bering Sea was about 1.2 million tonnes, whereas the 2013-TAC for Atlantic cod *Gadus morhua* in the Barents Sea makes history with one million tonnes – the latter quota being shared between Norway and Russia.

There are upwards of 4,750 species of **terrestrial and freshwater invertebrates** living in the Arctic representing 27 classes of animals spread across at least 16 phyla (Hodkinson, Chapter 7). One class, the Micrognathozoa is known only from Greenland and the sub-Antarctic Crozet Island. The most speciose groups are testate amoebae, rotifers, water bears, water fleas and copepods, ostracods, enchytraeid worms, eelworms, spiders, springtails, mites and insects. Among insects, the true flies (Diptera) are the dominant group. In several groups, many species remain to be described. Representation of the known world fauna in the Arctic differs greatly among groups. Soil-dwelling, soil-surface-living or aquatic taxa such as testate amoebae and springtails often represent significant proportions of the described world species (7-18%). By contrast, the taxon with a high proportion of free flying and plant-feeding species, the insects, is far less strongly represented (0.3%). Arctic endemism is similarly highly variable across taxa. It is high in enchytraeid worms (19%), mesostigmatid mites (31%) and calanoid copepods (28%), but low

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[7] Anadromy is a particular form of diadromy in which summer sea-feeding species return to fresh water to reproduce and/or overwinter.

in stoneflies (0%), cyclopoid copepods (0%), testate amoebae (3%) and Collembola (3%). Some globally rare Arctic endemic species, such as the Svalbard aphids *Sitobion calvulus* and *Acyrthosiphon svalbardicum* and several elements of the Beringian beetle fauna, have highly restricted distributions and appear particularly susceptible to disturbance and climate change. Population densities of some individual invertebrate species such as nematode worms, springtails and mites can reach tens of thousands to millions per square meter. Life cycles are highly variable within and among groups. Some aphids produce 2-3 generations per year; other species, such as some springtails, mites, craneflies and moths, have free-running life cycles lasting from three to eight years. The precise life-history and general biology of most Arctic invertebrate species is unknown. Herbivorous species are relatively few, but invertebrates play essential roles in several ecosystem processes, especially organic matter decomposition and nutrient recycling. They are crucial for the pollination of many Arctic plants and serve as the major food resource for many breeding birds and freshwater fish species, such as Arctic char *Salvelinus alpinus*. There is a lack of good quantitative data sets that demonstrate long-term trends in Arctic invertebrate populations and community composition. Nevertheless, a growing body of casual observational evidence among indigenous peoples and scientists suggests that invertebrate communities are changing. Some larger species, notably beetle, are now being observed at sites where they were previously unknown, and in some places the seasonal patterns of occurrence and abundance of biting flies is changing.

Excluding microbes, about 5,000 species of **marine invertebrates** in 17 phyla are found in the Arctic (Josefson & Mokievsky, Chapter 8). These organisms are associated with sea-ice, pelagic or benthic realms, with the benthic realm being clearly dominant (about 90% of described species found there). However, since several areas, in particular the East Siberian Sea, the Canadian Arctic and deep sea areas of the Central Arctic Basin and at the Arctic-Atlantic frontier, are under-sampled, this figure is likely to increase substantially as more studies are made. In contrast to the terrestrial biomes, the marine invertebrate fauna is not impoverished compared with more southern biomes, but is intermediate in species richness. Marine arthropods, by far the most species-rich group in the marine Arctic and accounting for 37% of all marine invertebrate species in the Arctic Ocean, show high species richness in the Arctic compared with some adjacent non-Arctic areas. However, our current knowledge indicates that the Arctic Ocean is largely a sea with species originating from outside the Arctic, and there are few endemic Arctic species. One reason for this may be the low degree of isolation of the Arctic Ocean from adjacent oceans since the Pliocene. Although data are limited, a few studies suggest that boreal species are increasing in Arctic waters – including some invasive alien species such as red king crab *Paralithodes camtschaticus* in the Barents Sea – with negative effects on native species.

Among **plants** (Daniëls *et al.*, Chapter 9), about 2,220 vascular species (including subspecies, apomictic aggregates[8] and collective species) are found in the Arctic, less than 1% of the world total. No fewer than 106 species (about 5% of the Arctic vascular plant flora) are endemic to the Arctic. Almost all are forbs and grasses with high ploidy[9] levels. Distribution patterns and ecological features of the native Arctic vascular plants are considered still intact, and no native species are known to have gone extinct due to human activities. No such information is available for bryophytes (mosses and liverworts) and algae. An estimated 900 species of bryophytes have been recorded in the Arctic, which is about 6% of the world's total. They occur in almost all vegetation types and locally dominate mires, fens and snow beds. Together with lichens, they contribute strongly to the high species diversity of high Arctic ecosystems in particular. Endemism is not well developed among bryophytes. A conservative estimate of 4,000 algae species are found in circumpolar regions, including both freshwater and marine algae (micro- and macroalgae such as kelp), which represents about 10% of world's recognized species. However, only about 10% of the estimated global total of algae has been described.

**Fungi**, including both 'true' fungi (i.e. non-lichenized fungi, here called fungi) and lichenized fungi (lichens), are one of the most species rich groups of organisms in the Arctic (Dahlberg & Bültmann, Chapter 10). The known number of fungal species in the Arctic is about 4,300, of which 2,030 are macrofungi with apparent sporocarps and 1,750 are lichens. This corresponds to about 4% of the presently known number of fungi species in the world, but 10% of the global total for the lichens alone. However, due to their largely cryptic nature, fungi – especially microfungi – have been insufficiently studied, and the total fungal-species richness in the Arctic may exceed 13,000. Fungi are pivotal in Arctic terrestrial food-webs, since vascular plants largely rely on mycorrhizal[10] and decomposing fungi to drive nutrient and energy cycling, and lichens such as reindeer lichens, i.e. *Cladonia* (subg. *Cladina*) and *Stereocaulon* spp., are important primary producers. Different fungal species contributes differently to these processes. The ongoing greening of the Arctic driven by climate change will alter fungal diversity and fungal ecosystem services such as plant's uptake of nutrients, decomposition and long-term carbon sequestration in soil. Most species appear to be present throughout the Arctic and also occur in alpine habitats outside the Arctic. Few fungi are endemic to the Arctic. Of lichens, 143 species have been found only

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[8] Group of genetically closely related microspecies originating by asexual reproduction through seeds.

[9] Variations in chromosome number involving more than the diploid number of complete chromosome sets.

[10] Mycorrhiza is a widespread symbiotic relationship between fungi and roots of most Arctic plants in which the fungus obtains its sugars from the plant, while the plant benefits from the efficient uptake of mineral nutrients and water by the fungal hyphae.

in the Arctic, but it is likely that the majority will prove to be synonyms of other species or be found outside the Arctic. Arctic fungi have not been evaluated for threat status, but no species are considered endangered. In contrast, up to 296 lichens are possibly endangered, i.e. very rare in the Arctic and either endemic (126 species) or also rare outside the Arctic (170 species). However all rare taxa require an evaluation of their taxonomic status. No data on trends exist.

**Microbes**, defined here as bacteria, archaea and single celled eukarya (protists), are ubiquitous and diverse members of all biological communities with c. one million cells per milliliter of seawater and most freshwaters and contributing to the complexity of microbial food webs with a multitude of trophic interactions (Lovejoy, Chapter 11). The historic dichotomy of autotrophic 'algae' and heterotrophic 'protozoa' is not borne out in modern classification systems, and many photosynthetic microalgae (Daniels *et al.*, Chapter 9) are also heterotrophic. This mixotrophic life style is particularly common in Arctic marine and freshwaters enabling photosynthetic organisms to maintain active populations over the winter and under ice when sunlight is limited. Indeed, microbial community interactions and dominant species largely determine the efficacy of the biological carbon pump, where carbon dioxide is drawn down from the atmosphere and sequestered in the deep ocean. However, there is a lack of long-term comprehensive baseline data on microbial biodiversity in terrestrial, freshwater and marine systems, which largely impedes understanding ecosystem structure and resilience[11] over both local and regional scales. Because of their small size and often large populations, microbes in principle may have global distributions as they are transported by moving masses of air and water. Since for the most part they cannot be identified morphologically, sound historical records are lacking, and new tools are being used to taxonomically identify these small species from DNA and RNA collected from the environment. In the Arctic, where terrestrial, freshwater and marine heterotrophs[12] and microalgae are particularly poorly known, this approach has been used to identify likely Arctic endemics among mixotrophic microalgae and heterotrophic single-celled grazers.

For **terrestrial ecosystems** the expected effects of global warming are increasingly being seen in empirical observations (Ims & Ehrich, Chapter 12). June snow cover has decreased by 17.8% per decade since satellite records began in 1979, i.e. more than the concomitant reduction in Arctic summer sea ice. Vegetation seasonality in the Arctic region has had a 7° latitudinal shift equator ward during the last 30 years, and plant flowering has advanced up to 20 days during one decade in some areas. As a result, primary productivity and vascular plant biomass ('greening of the tundra') have increased rapidly – in particular in terms of increased growth and expansion of tall shrubs. Other plants belonging to the lowest vegetation stratum, i.e. cryptogams such as mosses and lichens, have been found to be declining in abundance. Altogether, these structural changes alter the function of the ecosystem in terms of reduced albedo, increased soil temperature, higher ecosystem respiration and increased release of trace gases. The extent of greening (both earlier onset in the season and increased plant biomass) as assessed by remote sensing is, however, regionally highly heterogeneous, which to some extent can be due to spatial variation in the rate of climate change, but also a host of other factors including anthropogenic stressors. Changing abundances of keystone herbivores, such as lemmings, reindeer/caribou, geese and insects, sometimes accentuate the greening of the tundra, and sometimes counteract it. Consequences of regional collapse of lemming cycles, human-induced overabundance of ungulates and geese, and new phenology-driven trophic matches and mismatches are also beginning to be seen as cascading impacts in terrestrial food webs with negative consequences for endemic Arctic species and positive effects for expanding boreal species. Among such impacts are reproductive failures in caribou (phenological mismatch with food plants) and in lemming predators and their alternative prey (resulting from collapse of cycles), as well as the spread of new insect pest species and plant pathogens north to the forest-tundra transition zone.

Arctic **freshwater ecosystems** are important trans-ecosystem integrators (i.e. they link terrestrial, freshwater and oceanic environments) of multiple environmental and anthropogenic drivers and stressors (Wrona & Reist, Chapter 13). Hence, freshwater ecosystems and their related structural and functional biodiversity serve as important ecological transition zones within and between ecosystems since they concentrate key processes and drivers. Freshwater ecosystems are undergoing rapid environmental change in response to the influence of both environmental and anthropogenic drivers. Primary drivers affecting the distribution, abundance, quality and hence diversity of freshwater ecosystems and associated habitats include climate variability and change, landscape-level changes to cryospheric components (i.e. permafrost degradation, alterations in snow and ice regimes) and changes to ultraviolet (UV) radiation. Directly and indirectly, these drivers and interactions among them are being increasingly shown to affect the types, number and distribution of freshwater ecosystems in the Arctic region and, correspondingly, associated biological and functional diversity. Observed changes in freshwater geochemistry including enhanced nutrient additions (eutrophication) arising from the release of stored nutrients from thawing permafrost and deepening of the active layer, increases in the length of the open water season related to diminishing ice cover duration, warmer winter and spring water temperatures, and enhanced UV radiation regimes have been shown to affect the resource availability, productivity

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[11] Resilience is the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same structure, function and identity.

[12] A heterotroph is an organism that relies on other organisms for food.

and trophic interactions and dynamics of freshwater organisms. For example, changes in ice regimes, increased terrestrial productivity combined with permafrost degradation of tundra and associated slumping into water bodies (both of which are effects of climate change) may increase freshwater habitat suitability, food availability and use by migratory waterfowl and aquatic mammals, thereby increasing the 'natural eutrophication' of Arctic lake, pond and wetland ecosystems. Moreover, other secondary environmental and anthropogenic drivers that are gaining circumpolar importance in affecting Arctic freshwater ecosystem quantity and quality include increasing acidification and pollution from deposition of industrial and other human activities (wastewater, release of stored contaminants, long-range transport and biomagnification of pollutants), landscape disturbance from human development (dams, diversions, mining, oil and gas activities, together with development of linear corridors like roads, trails and cut lines, and population increase) and exploitation of freshwater systems (fisheries, water withdrawals).

The marine Arctic spans a wide range of environmental conditions including extremes in temperature, salinity, light conditions and the presence (or absence) of sea ice, leading to diverse Arctic **marine ecosystems** (Michel, Chapter 14). Approximately half of the Arctic Ocean area overlays shelf areas, i.e. areas with water depths < 200 m. Consequently, the Arctic Ocean has the most extensive shelf areas of the world oceans, accounting for nearly 30% of the global shelf area. The Arctic marine ecosystems are experiencing rapid changes in their chemical, physical and biological characteristics together with unprecedented socio-economic pressures. Changes in the distribution and abundance of key species and cascading effects on species interactions, structure and functionality of marine food webs are already being observed. Range extensions are taking place throughout the Arctic, with a northward expansion of sub-Arctic species and a narrowing of Arctic habitats. Range expansions associated with shifts in the distribution of Pacific and Atlantic water masses are already influencing the distributions of invertebrate and fish species and that of parasites, particularly among seabirds (Hoberg & Kutz, Chapter 15). Changes in water mass distribution also have downstream impacts on sub-Arctic marine systems through trans-Arctic transport of marine species (Michel, Chapter 14). The rapid decline in summer sea ice extent, with an overall average sea ice loss of 39% in September 2010-2012 compared with the 1979-2000 average and occurring faster than predicted by climate models, if maintained, is predicted to lead to a largely summer ice-free Arctic Ocean within the next 30-40 years. The impacts of the ongoing changes in sea ice are seen at all ecosystem levels, from the composition of protist communities to the distribution and abundance of top predators such as killer whales *Orcinus orca* and polar bears. Unique Arctic ecosystems, such as multi-year ice and millennia-old ice shelves are currently in rapid decline. Marine resource exploitation is also changing. In addition to a renewed interest in hydrocarbon exploitation, some fisheries have shifted. For example, landings in W Greenland have shifted, as in other areas of the North Atlantic, from a strong dominance of Atlantic cod to northern shrimp *Pandalus borealis* (see Fig. 6.15 in Christiansen & Reist, Chapter 6 and Michel, Chapter 14). Another example is the significant population changes in fish and seabirds that happened in the Barents Sea in the late 1980s (Fig. 1.3).

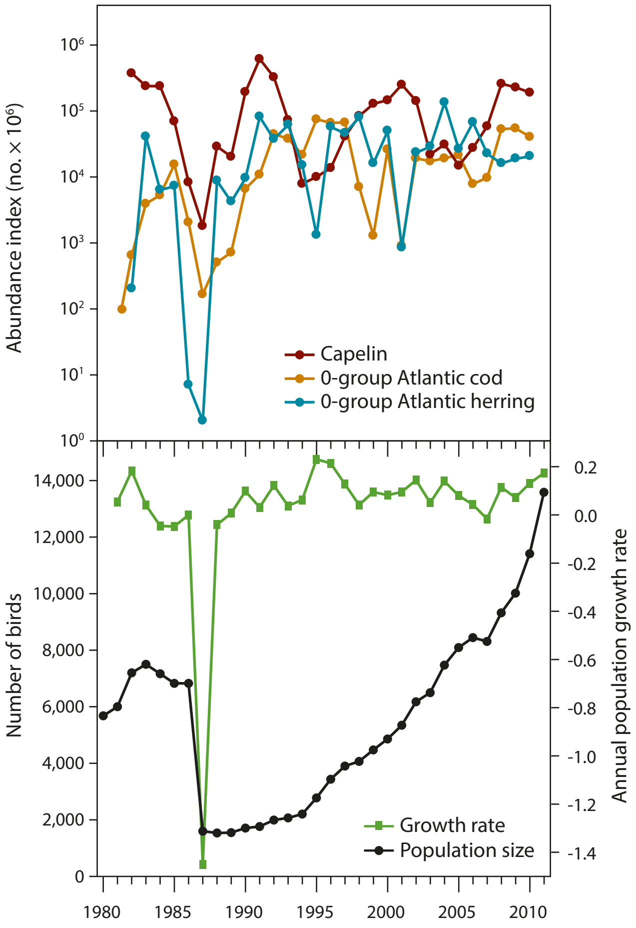

**Figure 1.3.** In 1987, the breeding population of common murre *Uria aalge* in the Barents Sea collapsed as a result of concomitantly low populations of their preferred prey, 0-group Atlantic cod *Gadus morhua*, capelin *Mallotus villosus* and 0-group Atlantic herring *Clupea harengus*. These low fish population levels were probably caused by a combination of climate variability, ocean current variability and overharvest with different weight of these causes between populations. Since such a situation of concomitantly low populations has not occurred since then (upper panel), the annual common murre population growth on Hornøya in NE Norway has remained high, and the murre population on this island is now higher than before the collapse (from Erikstad *et al.* 2013).

**Parasites** represent in excess of 40-50% of the organisms on Earth, are integral components of all ecosystems, and have considerable involvement in at least 75% of trophic links within food webs (Hoberg & Kutz, Chapter 15). Recognition of this complex web of interactions serves to establish the remarkable significance of parasites in ecological structure and biodiversity. Macroparasites (worms and arthropods) and microparasites (viruses, bacteria and protozoans) have at least one life stage that must live on or in another species, or host. Parasites are taxonomically complex and diverse, even in high latitude systems characterized by relatively simple assemblages, and are considerably more species rich than the vertebrate hosts in which they occur. Based on global estimates, there are between 75,000 and 300,000 species of helminths (worms) that infect terrestrial and aquatic vertebrates. In the Arctic, diversity for helminths in marine fishes (c. 3,780 species), freshwater fishes (720), birds (1,700) and mammals (900) is estimated near 7,100 species, but this value is conservative. As a generality, species richness for parasites declines on a gradient from south to north in terrestrial, freshwater and marine systems reflecting an interaction of historical processes and current ecological conditions. However, even for the best known host species, there is a general lack of long-term and comprehensive baselines for parasite biodiversity in the Arctic, and considerable cryptic diversity represented by currently undescribed species remains to be documented. Paradoxically, the presence of diverse assemblages of parasites is indicative of a healthy ecosystem because their presence denotes stability and the maintenance of connections among fishes, birds or mammals within and across complex food webs. Parasites are particularly sensitive to ecological conditions, environmental perturbation, migration pathways and habitat use because transmission is most often directly linked to food habits and foraging behavior for hosts.

Relatively few **invasive species**, i.e. human-introduced alien species that are likely to cause economic or environmental harm or harm to human health, are currently known in the Arctic (Lassuy & Lewis, Chapter 16). However, ecosystem altering invasive plants are known to have invaded the low Arctic in Alaska; over a dozen terrestrial invasive plant species are already known from the Canadian low and high Arctic, and 15% of the flora from the high Arctic archipelago of Svalbard was reported to be alien. Nootka lupin *Lupinus nootkatensis* has now invaded disturbed sites and sub-Arctic heathland vegetation in almost all of Iceland and even occurs in SW Greenland but without spreading into the tundra vegetation so far. The status of aquatic invasive species in the Arctic and sub-Arctic is less well known, but benthic communities in northern Norway and the Kola Peninsula are already likely facing significant disturbance from the introduced red king crab.

**Genetic** perspectives are keys to understanding population fluctuations, identifying and characterizing endemic species, tracking the invasion of species, recognizing emerging pathogens, revealing the status of threatened species, and demonstrating adaptations that allow species to thrive in the Arctic environment (Cook, Chapter 17). To mitigate the impact of climate-induced perturbations, an essential first step is to develop an understanding of how high latitude species and ecosystems were influenced by past episodes of dynamic environmental change. A history of ecological perturbation and faunal interchange in both terrestrial and aquatic environments driven by cyclical changes in climate is a general theme for high latitude biota. Reconstruction of past Arctic climates and biomes has been accomplished over different time scales using the fossil and sub-fossil remains of organisms such as diatoms, dinoflagellate cysts, beetles, chironomid midge larvae, ostracods and testate amoebae (Hodkinson, Chapter 7), in addition to the pollen record. Molecular genetics provides another powerful window into past change in Arctic populations. Integrated genetic studies have indicated the importance of mechanisms for episodes of geographic expansion (or retraction), genetic introgression, altered levels of sympatry and parasite host colonization in establishing broader patterns of biodiversity (Hoberg & Kutz, Chapter 15). Understanding that Arctic systems have evolved in this crucible of dynamic change provides an analog for identifying the possible outcomes of accelerated global warming and environmental change. DNA-based views, especially when integrated with ecological niche or other modeling approaches, provide a basis for exploring how biomes and individual species will respond in the future and thus are a key component of an advanced early-warning system for natural systems in the Arctic. Yet, because Arctic environments are remote and difficult to access and few specimens are available, there is limited information about geographic structure or the genetic basis for adaptation for most species. A number of Arctic species are now experiencing a reduction in their distributions, abundance and ability to exchange individuals among populations that will ultimately reduce population variability. These factors will hamper or dampen the capacity for adaptation under changing conditions and perhaps the potential to maintain resilience under exposure to novel pathogens and parasites.

When considering biodiversity, it is essential to recognize and understand **the functional significance** of the various species and species groups within Arctic ecosystems. By functional significance we mean the precise quantifiable role of each group of organisms in driving the essential ecosystem processes, such as primary production, decomposition and nutrient cycling that sustain life in the Arctic. This is particularly important for the less charismatic and often microscopic groups of organisms, including some plants, many invertebrates, many fungi, phytoplankton and bacteria, which are of overriding ecological significance in terms of energy flow through ecosystems yet frequently receive less attention and recognition than their ecological importance warrants. An example is the functionally highly important decomposer microorganisms that are responsible for the greater majority of soil respiration during the decomposition process (Heal *et al.* 1981). The chemical breakdown of cellulose and lignin, the major components of soil leaf litter, is almost exclusively the preserve of these micro-organisms, together with a strictly limited number of soil invertebrate species. Soil invertebrates, however, accelerate the decomposition process by reducing litter particle size and by feeding on and thus stripping out senescent microfloral colonies, thereby re-stimulating their activity. Microorganisms are the groups primarily responsible for the release of the major greenhouse gasses carbon dioxide and methane from tundra soils and are of paramount importance in contributing to change within the Arctic climate system. The actual composition of biodiversity in terms of its more cryptic components may determine whether the Arctic will become a source or a sink for greenhouse gases in a warming climate, and whether the Arctic amplification will become stronger or weaker.

**Provisioning and cultural services** are two of the ecosystem services provided by Arctic biodiversity, along with regulating and supporting services (which were not addressed in the ABA due to lack of information) (Huntington, Chapter 18). These services change over time for various reasons, but on the whole are relatively strong, with few signs of serious declines. There have been major changes in at least some aspects of reindeer herding, but these are predominantly the result of societal changes such as the break-up of the Soviet Union and its support system for remote herders. In some North American migratory caribou, rapid recent declines have forced heavy reductions in subsistence harvest. Commercial fisheries remain major economic activities in the Barents and Bering Seas and in Greenland and Icelandic waters, even if some areas have seen major shifts, such as the cod-to-shrimp transition in SW Greenland (see Fig. 6.15 in Christiansen & Reist, Chapter 6). Traditional hunting, fishing and gathering remain essential contributors to diet and to overall well-being in many Arctic communities, although such foods provide smaller proportions of daily energy intake than in the past. Sport fishing and hunting are increasing as the Arctic becomes a more popular destination for tourists, with the potential for additional stress on mammal, bird and fish populations. Perhaps as an indication of the increasing global scarcity of wild places and species, Arctic wildlife and wilderness are increasingly valued by people around the world simply for existing as they are (Huntington, Chapter 18). In other words, these services remain strong in the Arctic.

Trends in **disturbance, feedbacks and conservation** are not as positive in outlook (Huntington, Chapter 19). Increasing industrial activity is leading to disturbance in more and more areas, especially through construction of new roads. Modern construction, extraction and transportation techniques, however, offer the potential for developments to have less impact than they used to, but the overall trend is towards a greater human footprint in the Arctic. Feedbacks within the climate system tend to exacerbate greenhouse gas induced warming in the Arctic (see Section 1.5.2.1). Terrestrial protected areas are a major contributor to Arctic conservation, but marine protected areas are nearly nonexistent. Protective measures for species are increasing, which may indicate greater commitment to this conservation method, but could also indicate that more species are in need of protection. On a more positive note, the involvement of local communities in monitoring and conservation activities appears to be increasing.

The Convention on Biological Diversity (CBD) recognizes that **linguistic diversity** is a useful indicator of the retention and use of traditional knowledge, including knowledge of biodiversity. Twenty-one northern languages have become extinct since the 1800s, and 10 of these extinctions have taken place after 1990, indicating an increasing rate of language extinction (Barry *et al.*, Chapter 20). Thirty languages classified as critically endangered are in dire need of attention before they, too, are lost forever. Over 70% of the indigenous languages of the North are spoken only in single countries, and so are particularly exposed to the policies of a single government, which may also allow more responsive conservation of these languages as no cross border efforts are required. The remaining languages are spread across a number of jurisdictions and are therefore subject to differing approaches when it comes to addressing their revitalization. Language revitalization is possible, and there are multiple examples to illustrate it. However, the investment of time and resources needed to make revitalization a reality is a matter that needs to be addressed sooner rather than later. Many northern indigenous groups have already begun working on language revitalization, viewing it as an important component of their identity. In this context, the CBD provides an opportunity for indigenous peoples of the North to maintain their subsistence and traditional lifestyles. It expands the role and scope of conservation measures and allows a deeper understanding of relevance of indigenous cultures, practices and languages in the context of biodiversity conservation. Article 8j of the Convention has enabled local communities to become actors in biodiversity discussions in the North and helps to contribute to the preservation of 'knowledge and practices' of indigenous peoples, including their languages.

Considering all aspects of biodiversity, **the most prominent climate related changes in Arctic biodiversity** are northward (and upward on mountain slopes) range shifts observed by both scientists and Arctic residents in mammals, birds, amphibians, fish, terrestrial and marine invertebrates, parasites, plants and marine plankton (including new pest and invasive species) (Reid *et al.*, Chapter 3, Ganter & Gaston, Chapter 4, Kuzmin & Tessler, Chapter 5, Christiansen & Reist, Chapter 6, Hodkinson, Chapter 7, Josefson & Mokievsky, Chapter 8, Daniëls *et al.*, Chapter 9, Lovejoy, Chapter 11, Ims & Ehrich, Chapter 12, Wrona & Reist, Chapter 13, Michel, Chapter 14, Hoberg & Kutz, Chapter 15, Lassuy & Lewis, Chapter 16). Decreasing extent and duration of annual sea-ice cover are impacting marine species, including some polar bear and walrus populations, and heavy and more frequent icing events have caused declines in some populations of muskoxen and caribou (Reid *et al.*, Chapter 3). Lemming cycles have changed in some Arctic regions likely due to changes in timing and quality of snow accumulation, with consequent impacts to lemming predators and alternative prey (Reid *et al.*, Chapter 3, Ims & Ehrich, Chapter 12). Earlier snowmelt is stimulating advanced plant and arthropod phenology in some areas resulting in potential timing mismatch with caribou and bird migrations and reproductive cycles (Reid *et al.*, Chapter 3, Ganter & Gaston, Chapter 4, Hodkinson, Chapter 7). Rapidly increasing primary productivity, vascular plant biomass and shrub extension has resulted in 'greening of the tundra' and a transformation of some low Arctic to sub-Arctic conditions, while cryptogams have been found to be declining in abundance. These vegetation changes involve higher ecosystem respiration and increased release of trace gases (Ims & Ehrich, Chapter 12). Floristic changes have also been observed in moist to wet sites such as snow beds, mires, fens and shallow ponds, likely resulting from habitat warming and/or drying of the substrate associated with climatic warming and earlier snow melt (Daniëls *et al.*, Chapter 9). Climate-related shifts in range and seasonal movement patterns have altered predator-prey relationships, resulting e.g. in changes in diet of seabirds (Ganter & Gaston, Chapter 4). Similarly, distributions and rates of infection by such diverse pathogens as lungworm (in caribou/reindeer and muskoxen), helminths, protozoans (in salmon) and avian cholera have changed under a regime of contemporary warming and increasingly benign environments (Hoberg & Kutz, Chapter 15). Marine Arctic ecosystems are also experiencing dramatic climate-related changes that impact their chemical, physical and biological characteristics. Changes in the distribution and abundance of key species and cascading effects on the species interactions, structure and functionality of marine food webs are already being observed (Josefson & Mokievsky, Chapter 8, Michel, Chapter 14, Hoberg & Kutz, Chapter 15). The impacts of rapidly declining summer sea ice cover are seen at all ecosystem levels, from the composition of protist communities to the distribution and abundance of top predators. Unique Arctic ecosystems, such as multi-year ice and millennia-old ice shelves, are currently in rapid decline (Michel, Chapter 14). Further, apparent expansion of parasites in alcid seabirds from the Bering Sea through the Arctic Basin has coincided with the development of new oceanic current patterns linked to climate warming (Hoberg & Kutz, Chapter 15).

## 1.5. STRESSORS AND THEIR ALLEVIATION

As a contribution to halting the loss of biodiversity, the Arctic Council initiated the Arctic Biodiversity Assessment and asked for scientific advice on what could be done to alleviate stressors that put Arctic biodiversity under pressure. Detailed advice is given in the individual chapters, and in this section we the lead authors of the scientific chapters of the ABA present an overview of stressors on Arctic biodiversity together with possible actions to enhance biodiversity conservation. Our aim is to suggest appropriate, scientifically based actions, which should be seen as facilitative and not prescriptive. Arctic biodiversity is at risk from climate change and other human-caused stressors, and these pressures need to be addressed by prompt and concerted action at the local, national, circumpolar and global levels. Within the Arctic, stressors that directly affect habitats and populations include human infrastructure, unsustainable harvests, disturbance and pollution. Stressors coming from outside the Arctic include climate change, pollutants, invasive species, expansion of boreal species into the Arctic, and threats to migratory species in staging and wintering areas.

Arctic ecosystems are resilient to considerable climatic variability and change (Payer *et al.*, Chapter 2). However, continued warming is likely to be too rapid and intense for many species and processes to adapt or adjust *in situ*. Global warming is already causing local changes in Arctic climate regimes corresponding to biome shifts (see Section 1.4). Much depends on whether Arctic species and biological communities can shift distributions along with changing climate regimes, or persist in refugial regions where change is less rapid or extreme. Moreover, climate-related alterations to many cryospheric components (e.g. glaciers, ice sheets, permafrost and sea ice) are likely to produce new biophysical states that will not easily return to previous conditions within the timescale of centuries or even millennia (AMAP 2011a), creating repeatedly novel living conditions for most species and biological communities whose demographics and interactions operate in annual to decadal timescales. This not only involves temperature, wind and precipitation changes, but perhaps of equal importance the increasingly pronounced interannual variability and interactive feedbacks of climate change that are ongoing and expected. All of these will influence biodiversity across many interacting scales.

Many Arctic ecosystems bear signs of human activity from decades ago, indicating slow regeneration. This is because the growing season is very short, and the input of solar energy is low, meaning that Arctic habitats and many populations are particularly slow in regenerating from physical or other changes (Freese 2000). Since the true Arctic species are adapted to demanding Arctic conditions, but not to competition from 'southern' species, they could be more vulnerable to competition from southern intruders benefiting from climate change (Callaghan *et al.* 2004b). Arctic ecosystems also consist of relatively few species with even fewer keystone species in the food chains, which implies that population changes in just one keystone species may have strong cascading effects in the entire ecosystem (Gilg *et al.* 2012). Yet, the recovery of some bird, mammal and fish species from overharvest demonstrates the potential for effective conservation action.

Stressors affecting Arctic biodiversity originate from a multitude of sources, some of which are indigenous to the Arctic, while others originate fully or partially outside the Arctic. Section 1.5.1 discusses 'internal' stressors and related suggestions for actions, highlighting the stressors Arctic nations are responsible for. The second Section (1.5.2) deals with 'external' stressors, which require cooperation from countries where they originate. In this and the next section the focus is on anthropogenic stressors (i.e. factors created by or induced by humans), which human societies can do something about.[13]

## 1.5.1. Stressors originating from within the Arctic

In much of the world, nature conservation is now a question of protecting what little is left or of trying to restore what has been damaged. In this respect, the Arctic offers a rare opportunity to put sustainable development into practice and to apply solid conservation measures not as an afterthought, but as a priority (CAFF 2002).

### 1.5.1.1. Direct human impacts on habitats

Many Arctic regions have seen little or no locally-driven, human-induced habitat change compared with other parts of the world (MEA 2005). In particular, there is very little agriculture and animal husbandry – with the important exception of reindeer husbandry – and no forestry, factors that are the main drivers of wild species population decreases in many parts of the world (MEA 2005). Furthermore, in large parts of the Russian north, marked human population declines took place following the breakdown of the Soviet Union in 1991 (Bogoyavlenskiy & Siggner 2004), temporarily reducing the direct impact from human activities.

Many Arctic species have wide distributions with most habitats still intact, and relatively few have restricted ranges. This means that many species may be relatively resilient to some habitat loss from conversion, degradation and infrastructure. However, most Arctic species respond to habitat patchiness and seasonality with significant selection for certain localized habitats during certain times of the year or across years. Large bodied species may be most at risk because they tend to have smaller population sizes and larger ranges intersecting more potential human activities at the landscape scale.

Heavy grazing and trampling by domesticated reindeer may be the most widespread direct human-induced pressure on terrestrial Arctic habitats, especially in Eurasia, but its causes are often a combination of regulatory, economic and ecological factors (Ims & Ehrich, Chapter 12). Such human-induced impacts by one species may propagate to other species through food web interactions. Hence, overabundant semi-domestic reindeer in northernmost Fennoscandia (see Section 1.3) appear to have resulted in range expansions and increased abundance of boreal generalist predators and scavengers such as the red fox, with detrimental effects on the Arctic fox (Ims & Ehrich, Chapter 12).

Oil, gas and mineral extraction and transport are important stressors in parts of the Arctic and are expected to increase in the near future. However, on land this activity is largely limited to geographically small areas with oil and gas pipelines and access roads to mines and wells having the greatest geographical extent in most of the Arctic. Furthermore, onshore accidental oil releases will usually cover a much smaller geographical area than releases at sea and are therefore easier to address. In contrast, oil spills in the marine environment are not easily managed and pose a serious threat to marine ecosystems and particularly to seabirds and marine mammals (AMAP 2009b; see Section 1.5.1.4).

Dams, impoundments, diversions and water withdrawals produce physical and geochemical (e.g. enhanced mercury mobilization) impacts affecting freshwater systems and their surrounding and downstream environments including wetlands, deltas, estuaries and nearshore marine habitats. Ecological issues surrounding the development of hydroelectric facilities (in particular in the Canadian and Russian Arctic regions) and other reservoirs are projected to increase, resulting in implications for local and regional freshwater biodiversity (Prowse *et al.* 2011a, Wrona & Reist, Chapter 13). Similarly, from a terrestrial landscape perspective, crossings of linear corridors (roads, trails, cutlines, railways, pipelines) over rivers and creeks can have impacts on water quality. Equally important are seismic exploration lines in winter, which compress vegetation and may form drainage channels and alter landscapes. These can be many thousands of kilometers in length in a single year in some areas.

Off-road driving with tracked vehicles poses a problem in parts of the Arctic, and especially in Russia. Tracks form drainage channels that may erode into gullies draining wetlands and changing vegetation (see Kevan *et al.* 1995 and Forbes 1998). Under some conditions, severe impacts to tundra vegetation can persist for decades following disturbance by tracked vehicles (Jorgenson *et al.* 2010).

Although more common in the boreal forest, wildfires have scorched thousands of square kilometers of low and sub-Arctic tundra in particularly warm and dry summers (see e.g. Krupnik 1993, ACIA 2005). However, the extent to which such fires are natural phenomena or are ignited by humans is unknown. Fire has been largely absent from most of the tundra biome since the early Holocene epoch (Higuera *et al.* 2008), but its frequency and extent are increasing, probably in response to global warming (Hu *et al.* 2010) with a positive feedback effect (Mack *et al.* 2011).

In some areas, fishing practices such as bottom trawling may pose serious threats to benthic communities and remain an important stressor that needs to be studied and monitored (Christiansen & Reist, Chapter 6, Josefson & Mokievsky, Chapter 8, Michel, Chapter 14). Conventional bottom trawl fisheries for groundfishes are highly efficient, but can be damaging to the environment, as they can perturb and change the composition of benthic

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[13] In this report, we do not take a position with regard to efforts to establish an international treaty for the protection of the Arctic (see Nowlan 2001 and Ebinger & Zambetakis 2009).

communities (Tillin *et al.* 2006, Thurstan *et al.* 2010). Restrictive measures have been put in place in some areas to address this (Michel, Chapter 14).

Tourism concentrated on particular sites may have impacts on habitat through wear on sensitive vegetation or erosion of unconsolidated substrates. However, this pressure is still negligible in most places (e.g. Daniëls & de Molenaar 2011) and is relatively easy to regulate if unacceptable levels arise. Furthermore, tourists fascinated by the Arctic and its wildlife can be strong advocates of conservation needs for Arctic nature and environment and thereby enhance motivation for conservation (Prokosch 2003). (See also Sections 1.5.1.3 and 1.5.2.3.)

Managing and understanding the impact of human activities on biodiversity and ecosystems is increasingly important as direct impacts on Arctic habitats will increase significantly in the future (Nellemann *et al.* 2001). Future management will require modeled projection of possible impacts, empirical monitoring of potential trouble-spots and consultation with a wide-ranging team of knowledge holders from scientific disciplines as well as indigenous and local knowledge.

**Possible conservation actions**

- To succeed, biodiversity conservation needs to be a cornerstone of natural resource management and land and marine planning throughout the Arctic for the benefit of Arctic residents and biodiversity in general. To achieve this, a diversity of legal, regulatory and best management practice tools could be employed at diverse scales. Possible detrimental cascading effects on nearby endemic Arctic biodiversity and unique Arctic habitats are important considerations in land and marine planning and monitoring.
- Comprehensive national approaches to protected area planning and establishment are effective biodiversity conservation mechanisms. Eco-regional representation, connectivity, critical areas for various life stages, biodiversity hotspot analyses and maintenance of the most productive and/or resilient areas are important approaches to consider.[14] This work could build on work already done, such as AMSA IIC (AMSA 2009) and RACER (Christie & Sommerkorn 2011).
- Given the scale of changes forecast for the Arctic that will often result in substantial habitat displacements (c.f. Section 1.5.2.1), it is important that protected areas are: (1) large enough to safeguard critical habitat for target populations, (2) strategically selected (i.e. forming ecological networks of sites) and (3) actively managed in coordination with other approaches that support the overall resilience of regional ecosystems and species species (see also Section 19.4.1.3 in Huntington, Chapter 19).
- To secure species representation, protection of areas with many *unique* species should be given high priority, so that a total Arctic network is based on the 'complementary species richness' method and covers as much of the entire biodiversity as possible (Vane-Wright *et al.* 1991, Myers *et al.* 2000).
- Productive and varied areas deserve high priority in protected area planning and management. Especially in the high Arctic, such areas often constitute 'oases' that may function as source habitats for surrounding areas (Hodkinson, Chapter 7, Daniëls *et al.*, Chapter 9, Michel, Chapter 14). Such hotspot areas are found in terrestrial, marine and freshwater biomes, and include biologically important polynyas, persistent areas of perennial sea ice, large river deltas, unique lake systems, hot springs and cold seeps, and seasonally important areas for reproduction, molt and fattening of many birds, fishes and mammals (Reid *et al.*, Chapter 3, Ganter & Gaston, Chapter 4, Wrona & Reist, Chapter 13). The same priority applies to important areas for endangered species and particularly sensitive or vulnerable populations (see also Section 5.1.2).
- The design and implementation of mechanisms to ensure the maintenance of ecosystem structure, functions and processes and the representativeness of marine habitats and refugia with low human impact should be considered. A circumpolar Marine Protected Area (MPA) network could be an important part of such an effort. As many important areas cross jurisdictional boundaries, cooperation is essential. Such a network could include the establishment of an effective management system of deep-sea areas and large estuaries, which contain a relatively high proportion of endemic invertebrate species as well as several members of the species-rich fish families (Christiansen & Reist, Chapter 6, Josefson & Mokievsky, Chapter 8).
- Arctic fish species are largely bottom-living (Karamushko 2012), and since Arctic groundfish fisheries are expected to increase in the coming years, the development and deployment of fishing practices that minimize by-catch and seabed destruction are critical.
- Since protected areas are of little conservation value if their legal protections are moderated when economic or other conflicting interests appear (see section on protected area failure in Sutherland *et al.* 2011), the status of protected areas needs to be maintained and enforced.
- When unavoidable alteration of high priority areas takes place, these impacts could be mitigated by improved protection of other important habitat. However, true compensatory measures in the form of 're-wilding', which are used in other parts of the world, are of little relevance in the Arctic where there is almost no modified habitat to return to a

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[14] Targets for area coverage were agreed upon internationally at the 10th meeting of the CBD parties in Nagoya, Japan, in October 2010, i.e. the Aichi goals of protection of > 17% and > 10% for land and sea territory, respectively. In 2009, 11% of the Arctic as defined by CAFF (i.e. includes large tracts of sub-Arctic and boreal forest together with much of the Greenland ice shelf) had some form of protection. More than 40% of Arctic protected areas have a coastal component, but for the majority of these areas it is not possible at present to determine the extent to which they incorporate or extend into the adjacent marine environment (Barry & McLennan 2010).

more natural state. Areas already impacted by bottom trawling and heavy grazing and trampling by reindeer are exceptions to this, as there is room for recovery of affected areas by reducing the impacts and allowing for re-generation.

- Mitigation and restoration of disturbed or damaged habitat needs to be incorporated into development projects at the planning stage. This should include consideration of the full cost of restoration and remediation activities.

See further discussion in Sections 1.5.1.2, 1.5.1.3 and 1.5.2.1.

### 1.5.1.2. Harvest of mammals, birds and fish

According to Article 2 of The Convention on Biological Diversity *"Sustainable use" means the use of components of biological diversity in a way and at a rate that does not lead to the long-term decline of biological diversity, thereby maintaining its potential to meet the needs and aspirations of present and future generations.*

The harvest of mammals, birds and fish has formed the basis of Arctic societies since humans first arrived in the Arctic (see Section 1.3). Key species such as ringed seal *Pusa hispida* and fishes were able to sustain local human populations for millennia, although periods of famine and population declines show that the Arctic environment lay on the margins of human habitability. Today, harvest of living resources remains vital to the cultures of Arctic peoples, and contributes important protein and other nutrients for many Arctic residents (Huntington, Chapter 18).

During the last few hundred years, harvest of wildlife in the Arctic changed from a small-scale practice by scattered human populations to the use of modern hunting and catching technologies, more efficient means of transport such as snowmobiles, all-terrain vehicles, power boats and ocean going vessels, and increased accessibility through more extensive road systems. In combination with population growth and commercial markets in some regions for wildlife products, this increased the pressure on several wildlife populations (Huntington, Chapter 18).

Even though historically overharvest was one of the most common pressures on Arctic wildlife, it is also the most manageable (Klein 2005). In most areas, hunting and fishing are regulated, at least for species of conservation concern. Indeed, the pressure from overharvest has been largely removed as a major conservation concern for most species due to improved management and conservation actions. The switch from dog teams to snowmobiles has contributed to reducing harvests in many areas, and changing tastes and the increased availability of agricultural foods have also led in some places to lower harvests (Huntington, Chapter 18; see also Michel, Chapter 14).

In the Russian Arctic, where marked human population declines took place after the break down of the Soviet Union, a major shift has happened in the harvest of wildlife. The reduced population has lowered hunting pressure on wildlife in general, but has increased local dependence on harvest of local wildlife as a result of decreasing subsidies (Duhaime 2004, Wheeler *et al.* 2010). Since regulation and law enforcement decreased at the same time, the result has been that hunting, egg collection and fishing pressure on some populations have increased, while other populations have benefited from reduced harvest (K.B. Klokov & E.E. Syroechkovskiy in litt.).

In many regions of the Eurasian Arctic, the adoption of reindeer herding by indigenous hunting cultures led to the extirpation or marked reduction of wild reindeer and drastic reductions of wolves, lynx *Lynx lynx*, wolverines *Gulo gulo* and other potential predators of reindeer (Nuttall 2005).

> » *I could say for sure that there are much more bowhead whales now than there used to be when we were children. Where today you now could see a single whale, 2, 3 or 4 whales in one group. While in the olden days we used to only observe single bowhead whales and never more than one…*
>
> (Elijah Panipakoocho, in Hay *et al.* 2000).

Some populations (for example some whales, muskox and common eider *Somateria mollissima*; Fig. 1.4) have recovered or are recovering from overharvest following conservation and management measures that have been put in place over the past few decades (Reid *et al.*, Chapter 3, Ganter & Gaston, Chapter 4). Similarly, sound regulation of bowhead whale hunting in the Bering-Chukchi-Beaufort region has helped populations increase from previously depleted levels (see Box 14.6 in Michel, Chapter 14). Others are not recovering or are only slowly recovering (several sub- and low Arctic carnivore

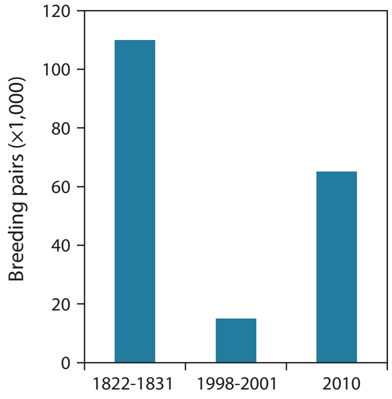

**Figure 1.4.** Common eider *Somateria mollissima* population depletion and recovery in W Greenland from the early 19th century to the present (estimates by F. Merkel in litt. based on data from Müller 1906 (down collection), Merkel 2002, 2004a, Christensen & Falk 2001 and annual growth rates from 2001 to 2007 in NW Greenland from Merkel 2010). The depletion was probably mainly caused by overharvest (hunting and egg collection), while the recovery was the result of tightened legislation and cooperation with local hunters since 2001 (Gilliland *et al.* 2009, Merkel 2010).

populations, some polar bear populations and some reindeer/caribou populations together with W Greenland walrus, harbor seal *Phoca vitulina* and thick-billed murre; the three latter being red-listed in Greenland; Boertmann 2007, Rosing-Asvid 2010, Reid *et al.*, Chapter 3, Ganter & Gaston, Chapter 4).

In addition, overharvest has not only caused depletion of some target populations, but in some cases it has had cascading ecosystem effects. For example, the elimination of large whales by commercial whaling may have been followed by increasing populations of smaller marine mammals together with some seabirds (Springer *et al.* 2003). Another example is the depletion of large populations of predatory fish (Smetacek & Nicol 2005) that may have resulted in reduced genetic variability (Cook, Chapter 17). Generally, however, the impact of historical harvest of marine mammals, fish and seabirds on current Arctic marine ecosystem structure is not well documented, but the removal of such a large biomass of targeted species would have affected the flow of energy and trophic interactions that shaped the Arctic marine food web that existed previously (Michel, Chapter 14).

> » *There has been improvement on the salmon stock. It was in the 1970s that the Norwegians prohibited this trawl-like sea fishing. Already in the next year we had small salmon swimming upstream. Nowadays the sea is being fished out of shrimp that is leaving the salmon with only little shrimp to feed on. This has caused the color of salmon to fade. It is not as red as Atlantic salmon from the Arctic Sea used to be. And the flesh or meat, that used to be much thicker in the past. Back then a salted salmon fillet was like a wood board. This is also due to overcatching shrimp.*
>
> (Late salmon fisherman Jouni Tapiola from Kaava, Finland; Helander *et al.* 2004).

In several species of seabirds and small cetaceans, by-catch in fishing nets and on hooks is related to overharvest in that it results in additional mortality on top of other harvests. However, by-catch in gill-nets in the Arctic seems to have diminished in recent decades, at least in the Atlantic sector, due to reduced use of gill nets in the high seas of Greenland and Norway (Bakken & Falk 1998). However, it still is of major concern in coastal fisheries, e.g. in W Greenland and the NW Pacific (Chardine *et al.* 2000, Merkel 2004b, 2011).

Fisheries conservation and management measures put in place over the last few decades have resulted in large Arctic commercial fisheries which from a global perspective are relatively well managed, although there have been management failures, and high harvest pressure continues on some fish stocks (Christiansen & Reist, Chapter 6, Huntington, Chapter 18). Arctic countries are at the forefront of development of sustainable fisheries. Examples of improvements include national and subnational regulations, restrictions and large-scale management planning processes and international cooperation (Huntington, Chapter 18, see especially Box 18.3). The need for using a precautionary approach for fisheries and resources management is reinforced by the paucity of baseline data and long-term monitoring in the Arctic compared with other marine ecosystems, combined with rapid climate-associated changes (Michel, Chapter 14). In US waters of the Arctic, for example, commercial fishing has recently been prohibited as per the Arctic Fisheries Management Plan until more information is available to support sustainable management of potentially harvestable species (NPFMC 2009).

Accurate statistics on by-catch are crucial in upcoming Arctic fisheries and call for adaptable management policies to meet conservation aims. No single harvesting practice is foolproof (Pitcher & Lam 2010). Catch Quota Management (CQM; Danish Ministry of Food, Agriculture and Fisheries 2012), a new policy that is currently being tested in North Sea fisheries, may provide urgently needed by-catch data, which is a first step to better controlling the impacts of by-catch.

While harvest can be a major force influencing ecosystem structure and function by altering community composition and species interactions, it also interacts with other stressors and influences as well. For example, while trends in some areas may imply 'fishing down' of the ecosystem, the shift in community structure and landing composition also coincides with a rapid change in climatic and oceanographic conditions, and other stressors. Nevertheless, the contribution of climate change and direct human intervention will have profound impact on marine ecosystems (Christiansen & Reist, Chapter 6, Michel, Chapter 14).

Harvest of animals inside the Arctic is not the only source of harvest stress, as migratory species are also harvested outside the Arctic (see Section 1.5.2.4).

#### Possible conservation actions

- To maximize the adaptive capacity of harvested populations of mammals and birds, with respect to harvest, climate change and genetic viability, populations should be allowed to achieve and maintain healthy population levels that meet sustainable harvest management goals. This step includes allowing depleted populations to recover (see text above for examples). Maintaining viable populations can be achieved by, for example, regulation of the take itself, harvest methods and the establishment of protected zones e.g. for reproduction, molting and feeding.
- The principles of ecosystem-based management (EBM) distribute risk such that ecosystem sustainability is enhanced and ecosystems do not disproportionately suffer the impacts of tradeoffs resulting from management decisions concerning utilization of Arctic resources. This approach would help support the resilience and sustainability of ecosystems in the face of harvests and the many other uses of and impacts to Arctic resources and areas.
- Ongoing improvements in data gathering and analytical techniques for estimating sustained yield are needed. Ideally, such information would include an ability to differentiate populations and stocks, re-

peated estimations of stock or population abundance, and accurate and complete harvest or catch data including individuals not retrieved. The same applies to by-catch of mammals and birds – and non-targeted fish species – in fishing gear.
- Continued and increased international cooperation on the gathering and assessment of data on population structure, harvest monitoring and harvest methods and regulations is needed, so as to improve the planning and management of harvests. Existing examples include the International Agreement on the Conservation of Polar Bears and cooperation through the North Atlantic Marine Mammal Commission. Many other species and inter-jurisdictional issues require such attention (see also Section 1.5.2.4).
- Improved means of accessing and exchanging information between hunters, fishermen, scientists and management authorities is of paramount importance. This can involve implementing community monitoring programs, public education, information campaigns on sustainability, involvement in public debates, and more.[15]

### 1.5.1.3. Displacement of animals from important habitats

The effects of disturbance on displacing mammals and birds from important habitats are closely related to shyness of the individual species (Madsen & Fox 1995, Laursen *et al.* 2005). This shyness has both an inherited (genetically fixed) and an acquired element. Both are related to the level of population pressure created by such disturbance through death and injury over the course of generations. Usually, the more a population of mammals or birds has been subject to hunting, the shyer it is, and potentially the more effect further disturbance (e.g. in the form of human presence) can have on the population. The exceptions to this are species that rely on cryptic behavior, such as ptarmigan.

Most mammal and bird species in the Antarctic are indifferent towards humans when on land, where there are no mammalian predators (see Box 1.3). Similarly, in the Arctic much wildlife is relatively indifferent to human presence, so that they can be approached by humans to within 10-20 m – similar to the escape distance from foxes and other mammalian predators. This is not the case for hunted populations, which often have flight distances of several hundred meters, at least during the time of the year when they are hunted. Conversely, birds and mammals can sometimes reduce their flight distances surprisingly quickly when protected from hunting (e.g. mallards *Anas platyrhynchos* and other waterfowl in 'city parks' such as in larger cities in Greenland – a situation that was unthinkable until few decades ago; H. Meltofte, pers. obs.).

Few studies have documented the effects of disturbance at the population level (see Madsen & Fox 1995), probably because they are hard to disentangle from other effects of human presence such as direct mortality or habitat disturbance. Large aggregations of breeding, molting and wintering waterbirds, marine mammals at haul outs and calving caribou may be most sensitive to disturbance, with heavy and continued disturbance having an effect similar to habitat loss, since the birds or mammals are prevented from utilizing important habitat. Such behavioral changes may lead to reduced foraging time, increased energy expenditure and poorer physiological condition leading to reduced fecundity and increased mortality. Disturbance may also have indirect effects such as increased predation, when birds leave their nests due to human disturbance and predators can move in easily to take eggs or chicks. This effect is especially severe in dense bird colonies. In some cases it may be hard to separate the effect of disturbance from the direct effect of the take of individuals from the population. For example, when walruses no longer haul out on land in W Greenland (Born *et al.* 1994), it is hard to know whether this is an effect of continued shooting at haul out sites or the extermination of the local animals, but most likely it is a combination of these pressures.

The potential disturbance due to human presence is closely related to the level of hunting that the populations in question are subject to. For instance, tourists may approach incubating black-legged kittiwakes *Rissa tridactyla* and thick-billed murres to within a few meters in Svalbard, while these and other harvested species may flush at distances of several hundred meters in areas where they are hunted such as in Greenland (Merkel *et al.* 2009, pers. com., Egevang 2011, H. Meltofte, pers. obs.). The balance between hunting-induced shyness and the interests of non-hunters, including tourists, in being able to enjoy wildlife will ultimately depend on the priorities of the individual jurisdictions responsible for hunting and recreational activities.

Other potentially harmful disturbances are ship traffic, seismic operations and aircraft, which may have the same effect as direct human disturbance. Low-flying aircraft – especially helicopters – may displace birds and mammals from key habitats and can even cause destruction of eggs and young on bird cliffs (Mosbech & Glahder 1991, Chardine & Mendenhall 1998, Overrein 2002, Moore *et al.* 2012). The properties of sound in water are of particular concern, since increasing ship traffic may hamper the ability of whales to communicate over large distances (Southhall *et al.* 2007). Underwater noise from seismic operations and icebreakers is particularly difficult to mitigate, because the attenuation is slow and it spreads widely.

Indeed, disturbance will inevitably increase in the future, and it remains a challenge to avoid harmful disturbance to sensitive species such as whales and other marine mammals or particularly sensitive areas such as molting areas for waterfowl and breeding areas for seabirds.

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[15] The appropriateness of co-management systems is outside the scope of this report to make recommendations on. However, much experience exists in Arctic countries on how to handle this, if such methods are desired (see Huntington, Chapter 19).

The rapidly diminishing Arctic sea ice cover including the decline in multi-year ice will open up large sea territories for economic development such as exploitation of natural resources that were previously physically or economically unfeasible. This also involves new shipping routes and increased tourism (AMSA 2009).

**Possible conservation actions**

- The effects of human disturbance on population size and fecundity is largely unknown. As human activities increase, the impact of this as a stressor needs to be better understood and monitored.
- Human disturbances should to be kept at a level that does not significantly alter animals' patterns of utilizing existing food resources, natural behaviors and ability to breed, molt and rest. One of the tools for achieving this is the establishment of reserves and other low-disturbance areas as refugia especially for hunted populations (see e.g. Madsen & Fox 1995). Other tools include seasonal restrictions, speed limits, reducing or minimizing travel in key areas during sensitive periods[16], height restrictions for aircraft and minimizing noise in marine ecosystems including stand-off distances and a ramp-up period at the start of seismic activities.
- For species coming under severe pressure from climate change, alternative habitat should be or safeguarded such as safe coastal haul out sites for walrus, in areas where ice haul out sites are no longer suitable due to loss of ice or distance from feeding areas.

### 1.5.1.4. Pollutants originating in the Arctic

People living in the Arctic probably consume, individually, as many goods and as much energy as people from the industrialized world (e.g. Grønlands Statistik 2011), thus likely contributing as much to global pollution on a per capita basis as humans elsewhere. However, there is relatively little industrial production in the Arctic, and human density is very low. Total emissions of toxic contaminants are thus minimal in the Arctic when compared with more southern latitudes. Pollution within the Arctic is both direct via local releases (e.g. carbon dioxide and black carbon from energy production and combustion of waste often on open dumps, ozone depleting substances from refrigerators etc.) and indirect via the consumption of imported goods whose manufacture and transport contribute to global pollution – which then may disperse to the Arctic. Reducing local pollution will benefit biodiversity around Arctic communities and will contribute to global pollution-reduction efforts. In addition, larger sources such as mining, oil and gas activities, and legacy sites such as military bases are substantial sources of pollution within the Arctic (e.g. AMAP 1998, 2004, 2009b).

Oil, gas and other mineral extraction and use is probably the single most important human-induced contributor to pollution, both locally in the form of release of toxic compounds and accidents (AMAP 2009b) and globally in the form of greenhouse gases, black carbon and mercury emitted when fossil fuels are combusted. This is particularly relevant for the Arctic, since the region potentially holds one fifth of the world's yet undiscovered resources (USGS 2011, Michel, Chapter 14). Oil spilled both on land and at sea decomposes more slowly in the cold Arctic environment than at warmer latitudes, and hence remains bio-active for a longer time (AMAP 2007). Furthermore, response capabilities in the Arctic are typically far below what they are in other oil-producing regions (AMAP 2007). A risk assessment by two major insurance and risk analyses companies, Lloyd's and Chatham House (2012) concluded that "while particular risk events – such as an oil spill – are not necessarily more likely in the Arctic than in other extreme environments, the potential environmental consequences, difficulty and cost of clean-up may be significantly greater, with implications for governments, businesses and the insurance industry."

Accidental release of oil into the Arctic marine environment threatens all trophic levels (see Michel, Chapter 14). Most obvious to the public are effects on birds and mammals, especially compromising their feathers and fur, resulting in hypothermia and potential mortality. In addition, metabolic effects are documented for invertebrates, birds and mammals. Furthermore, Arctic seabirds and marine mammals are particularly susceptible to oil spills should one occur where and when they congregate in large numbers to nest, rear young and molt each year (Reid *et al.*, Chapter 3, Ganter & Gaston, Chapter 4).

According to the Arctic Oil and Gas 2007 overview report from Arctic Council (AMAP 2007) "There are no effective means of containing and cleaning up oil spills in broken sea ice." The same conclusion was reached by the US National Research Council (2003): "No current cleanup methods remove more than a small fraction of oil spilled in marine waters, especially in the presence of broken ice." However, recent experiments under optimal conditions have been able to achieve 'in situ burning' of significant shares of oil in waters covered with 70% drift ice (Sørstrøm *et al.* 2010).

Oil spill accidents of cargo, military and cruise vessels pose a serious local threat particularly in areas with seabird colonies and similar concentrations outside the breeding season (staging, molting and wintering congregations in particularly important areas; AMSA 2009). Yet, the magnitude of spills from ships – even with oil tankers – is significantly smaller than the potential magnitude of a spill from an oil blowout from an under-sea well. The Deepwater Horizon accident in the Gulf of Mexico released on the order of twenty times as much oil as at the Exxon Valdez spill in Prince William Sound, Alaska (c. 790,000 m$^3$ vs. c. 37,000 m$^3$; AMAP 2009b,

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[16] Of particular concern is some parts of the tundra during sensitive time periods, including spring calving (caribou and muskoxen), den selection (foxes), nest initiation (e.g. geese, owls and raptors) and molting (geese and other waterfowl).

Graham *et al.* 2011). Although spills on land are generally more readily contained, they are still a serious threat to tundra, lake and river systems.

Legacy contaminants (e.g. PCBs in Svalbard) and radioactivity from legacy military activity can potentially have an impact on biodiversity (e.g. AMAP 1998, Bustnes *et al.* 2010). Open rubbish dumps may have a negative impact on wildlife population dynamics through an increase in predators and parasites and the spread of contaminants (e.g. from industrial wastes) and pathogens (see e.g. Pamperin *et al.* 2006, Weiser & Powell 2011, Stirling & Derocher 2012).

**Possible conservation actions**

- A major oil spill in ice filled Arctic waters would be detrimental to biodiversity and very difficult to clean up, particularly under problematic weather, light and ice conditions. However, if oil development is undertaken, a precautionary approach adhering to regulations and guidelines specific to the Arctic and based on the best available science would reduce risks, including that development activities in the most sensitive areas are avoided.[17]
- Research efforts into understanding the consequences of oil spills in sea-ice environments remain essential to ensure advances in knowledge and development of improved technologies specific to oil and gas development in the Arctic.[18]
- Some tools that may help to reduce other pollution originating from within the Arctic are: (1) for ship operations in the Arctic, a mandatory polar code encompassing vessel construction, maintenance and operations (e.g. routes, speeds) would help minimize the risks, (2) best management practices for local waste management are desirable throughout the Arctic, (3) minimizing black carbon emissions would reduce the impact of this important driver of climate change, and (4) ongoing clean-up of legacy contaminated sites from military activity and historic mining and oil and gas exploration will continue to reduce contaminant inputs to the environment.

See further discussion in Sections 1.5.2.1 and 1.5.2.2.

## 1.5.2. Stressors originating from outside the Arctic

### 1.5.2.1. Climate change

Since 1980, the rate of increase of atmospheric temperatures in the Arctic has been twice that of the rest of the planet (McBean 2005, IPCC 2007a, AMAP 2009a, AMAP 2011a), and projections show that the Arctic will experience the largest future temperature changes on the planet (Overland *et al.* 2011). This is the result of 'polar amplification' caused by a combination of feedback mechanisms such as snow and ice melt leading to lowered albedo (which leads to further snow and ice melt and so on) and increased heat transport from lower latitudes (Graversen *et al.* 2008, Screen & Simmonds 2010, AMAP 2011a).

In addition to the well-known effect of greenhouse gases on global warming (IPCC 2007a), incomplete combustion of fossil fuels and biomass by human action or in forest fires releases black carbon which, when deposited on ice and snow, increases melt by reducing albedo. Hence, black carbon adds to the positive feedback of snow and ice melt (AMAP 2011c, UNEP *et al.* 2011; see also Section 1.5.1.4) and may – together with a decline in reflective sulphate aerosols – have played a significant role in the warming of the Arctic in recent decades (Lenton 2012).

Full implementation of the measures recommended by UNEP *et al.* (2011) for reducing warming globally is estimated to be able to reduce warming in the Arctic in the next 30 years by about two-thirds compared with projections.

Increased vegetation growth following global warming is another potential feedback mechanism operating through a reduction of the albedo and hence, leading to further warming (McBean 2005, Ims & Ehrich, Chapter 12). Finally, massive amounts of peat-based carbon and gas hydrate deposits, bound in permafrost both on land and in marine shelf areas, may be released at accelerated rates. This process will release both carbon dioxide and the much more potent greenhouse gas, methane (Zimov *et al.* 2006, Shakhova & Semiletov 2007, AMAP 2009a, Lenton 2012; see also Huntington, Chapter 19). However, the extent to which this will be counterbalanced by enhanced carbon uptake by increased vegetation growth on the tundra is uncertain (Callaghan 2005, AMAP 2009a, 2011a). Contributing to this uncertainty is the possibility that increased plant growth and compositional shifts in vegetation communities induce net loss of carbon to the atmosphere via mycorrhiza activity that increases the rate of decomposition of soil organic matter.

The ten year period 2001-2010 had the highest global mean temperature recorded for a 10-year period since records began in 1850 (WMO 2012), and there are indications that summer temperatures in the Arctic during recent decades have been warmer than at any time in the

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[17] See AMAP 2007 for management recommendations.

[18] The work of EPPR significantly advanced this issue in its 2011 report *Behavior of oil and gas and other hazardous and noxious substances spilled in Arctic waters* and its other work on pollution prevention. Similar work by others continues to advance the science of oil and gas development in ice-filled waters, including a Norwegian project led by SINTEF (www.sintef.no/jip-oil-in-ice) and Canadian work done by Environmental Studies Research Fund (www.esrfunds.org/) and the Program on Energy Research and Development (www.nrcan.gc.ca/energy/science/programs-funding/1603). As well, new research is proceeding on the potential for microbes to degrade oil in ice-filled environments.

past 2000 years (Walsh *et al.* 2011). Within this century, temperatures in the Arctic are projected to continue to increase at a greater rate than the global average, with the most pronounced increase in autumn and winter and an annual increase of between 2.8 and 7.8 °C (Kattsov & Källén 2005, Dahl-Jensen *et al.* 2011, Overland *et al.* 2011). June snow cover in the northern hemisphere (almost entirely within the Arctic) has already decreased by more than 45% since records began in 1979 (Derksen & Brown 2012; see Fig. 12.14 in Ims & Ehrich, Chapter 12). Similarly, Arctic summer sea ice cover – and particularly the amount of multi-year ice. – is decreasing at an accelerating rate, so that total ice cover at the summer minimum reached an all time low in September 2012 with only half the extend as compared with the 1979-2000 average (Fig. 1.5). Current projections suggest that the Arctic Ocean will become largely ice-free in summer within the next 30-40 years (Meier *et al.* 2011). Similarly, negative mass balance of Arctic ice caps and glaciers are projected to contribute to an expected global sea level rise of 0.7-1.6 m at the end of the 21st century (Grinsted *et al.* 2010, Dahl-Jensen *et al.* 2011).

> *Long ago [it] used to be [a] long spring. Used to stay out there [at his hunting camp] for months. In the springtime (...) we do fishing first. After that, hunt geese; then go fishing again after that. Now we don't even go fishing after goose hunting because it melts too fast.*
>
> (Geddes Wolki in Nichols *et al.* 2004).

The impacts of climate change include a long list of changes in the physical environment, which will have profound effects on Arctic biodiversity. The conditions will vary spatially, but aside from temperature increases, the most pronounced changes are likely to include (cf. Callaghan 2005, Kattsov & Källén 2005, AMAP 2011a):

- increased precipitation with more winter snow
- increased frequency of winter thaw-freeze events including rain-on-snow resulting in ice crust formation
- earlier and more variable snow melt
- earlier drying of ponds
- disappearance of perennial snow beds
- increased periods of summer drought but with more severe rains
- thawing permafrost and thermokarst development with drainage of peatlands and ponds or establishment of new ponds
- increased freshwater discharge into the Arctic Ocean
- disappearance of coastal ice shelves
- flooding of low coasts
- coastal erosion
- later onset of autumn snow
- more frequent and severe extreme events (icing, erosion, storms, flooding, fire)
- accelerating loss of sea ice cover, especially multi-year ice, and
- ocean acidification.

The extent to which these effects are expected to develop varies between projections, but the overall direction is clear, and several of them are already evident now (AMAP 2011a).

In addition to linear changes comes the risk of reaching tipping points, where a system (geophysical or ecosystem) moves from one state to another from which it is hard to change back across a certain threshold (ARCUS 2009, Rockström *et al.* 2009, Barnosky *et al.* 2012). Here, "we may already be at (or very close to) a tipping point for some large-scale systems in the Arctic" such as the Greenland Ice Sheet (Richardson *et al.* 2011, Lenton 2012). That the risk of reaching such tipping points is higher than was anticipated earlier is due to the fact that recent trends in a number of climate related elements have been more pronounced than the IPCC projections (e.g. AMAP 2011a); i.e. the 'Earth System' may be more sensitive to carbon dioxide forcing than previously thought (Fig. 1.6; Lunt *et al.* 2010, Richardson *et al.* 2011).

The most profound effect will be the loss of ice on land (permafrost), in freshwater and in the ocean (AMAP 2011a, Prowse *et al.* 2011b). This is expected to have major and often non-linear effects on Arctic biodiversity

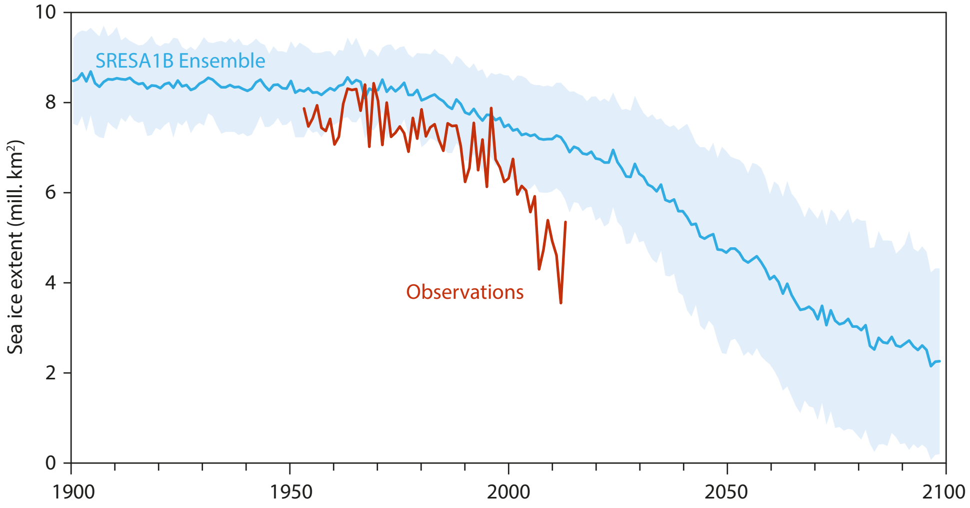

**Figure 1.5.** The loss in summer extent of Arctic Ocean sea ice has occurred much faster than the initial projections had anticipated, so that the total ice cover at the summer minimum reached an all time low in September 2012 with only half the extend as compared with the 1979-2000 average (modified from Stroeve *et al.* 2007; see also photo on page iv). Similarly, the loss in monthly averaged Arctic Ocean ice volume for August 2013 was 76% lower than the maximum in 1979 (Polar Science Center 2013).

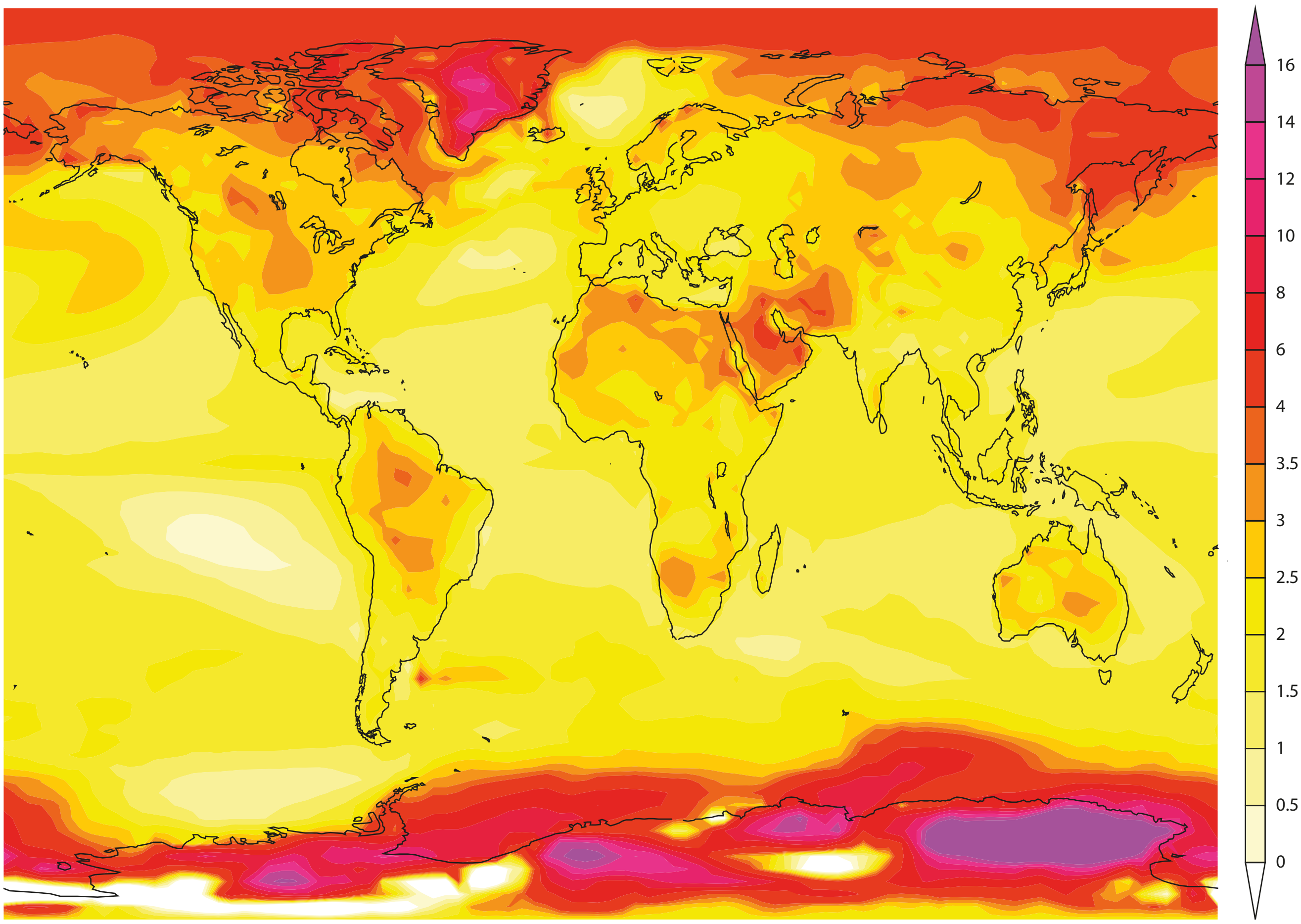

**Figure 1.6.** Temperature response (°C) to an increase of $CO_2$ from 280 to 400 p.p.m. calculated as 'Earth System Sensitivity' resulting in significantly larger sensitivity than in 'traditional' models. From Lunt *et al.* (2010) and Richardson *et al.* (2011). Reprinted with permission from Nature Publishing Group.

because of complex feedbacks and interactions between freeze-up and melt cycles and species assemblages (Callaghan 2005; see also Walther 2010). These feedbacks are anticipated to accelerate changes in the physical environment and in biodiversity (AMAP 2011a). The direct effects of higher temperatures, and in some cases higher precipitation, may at first involve increased plant growth and abundance and possibly increasing populations of some animals, but in the longer term the effects are likely to include the disappearance of large tracts of what we recognize today as Arctic ecosystems and populations and hence surpass the effects of all other stressors taken together (Callaghan 2005, Meltofte *et al.* 2007).

> » *We never saw them before. This is what we have observed. New plants have arrived here and on tundra. Rivers and lakes are filled with small-flowered a kind of duckweed* **[Lemnaceae]**, *and the lake started to bloom. Life of the fish is more difficult and likewise peoples fishing opportunities as lakes grow closed up with the new plants…*
>
> (Larisa Avyedeva, Saami, from Luujavre, Russia, on new species of plants which have arrived to the territories of the Kola Saami 2001-2004; Cherenkov *et al.* 2004).

A meta-analysis of data from the last 40 years has shown that a wide range of species' distributions has moved away from the Equator by a median speed of 16.9 km per decade and uphill by a median speed of 11.0 m per decade, and that these range changes tracked temperature trends (Chen *et al.* 2011). Similar northward range extensions have been recorded in sub-Arctic and Arctic species, where also a marked 'greening' has taken place in large regions since relevant satellite pictures became available in 1982 (Jia *et al.* 2007; see Section 1.4 for a range of observed climate-related changes together with references to relevant chapters). It is possible that about half the present tundra may be replaced by the end of the 21st century by shrubs and trees from the south (Callaghan 2005, Kaplan 2005, SNAP 2012, Pearson *et al.* 2013) – provided that the spread of woody vegetation is not counterbalanced by drought (Callaghan *et al.* 2011a), outbreaks of insect pests or intense herbivory (Ims & Ehrich, Chapter 12). Similar changes are taking place in the marine environment including changes in the timing and duration of land fast ice and a reduction of little-studied biota associated with coastal ice shelves, which imply the loss of a globally unique ecosystem (Michel, Chapter 14). Furthermore, the retreat of summer sea ice from continental shelf seas altogether means the loss of an entire type of marine polar ecosystem at a global scale. With these impacts occurring already, the reduction of human-induced climate change is the most urgent action in securing Arctic biodiversity for the future or, as concluded by AMAP (2011a; summary report): "Combating human-induced climate change is an urgent common challenge for the international community, requiring immediate global action and international commitment."

> » *You got an example of that [ice crust] now with the caribou coming around here, a lot of people wondering why they didn't stay around right. They want them to stay around and they're in the woods. Why are they down there? Because the hills are all iced up. They're pure ice in places and they can't get their food so, they're not going to stick around where they can't dig now. They know more than we do. And they know what's coming, they can, I don't know how they know, but they know that it's going to be icy, they move on.*
>
> (Ron Webb in Davies 2007).

Because of the rapidity of change, the dominant response of many Arctic species to climate change is more likely to be by phenotypic[19] adaptation rather than genotypic[20] adaptation (Callaghan 2005, Gilg *et al.* 2012). This may involve northward displacement of whole habitats resulting in a reduction in the area occupied by Arctic ecosystems – particularly those characteristic of the high Arctic – because of the reduction in the available surface area when moving north towards the pole. In terrestrial species and ecosystems this loss of surface area ultimately stops at the northern shores of continents and islands, so that sub-Arctic and boreal species expanding from the south squeeze Arctic habitats – and particularly high Arctic habitats – up against the Arctic Ocean (Callaghan 2005, Kaplan 2005, Meltofte *et al.* 2007, Hof *et al.* 2012, Hope *et al.* 2013). Considering the fact that during the last 0.8-1.0 million years, glacial stages sensu lato accounted for > 85% of the time with much more extensive steppe-tundra habitats than in interglacial periods like the present, the whole Arctic biome can already now be considered to be a refugium for Arctic biodiversity (Ims & Ehrich, Chapter 12).

Unlike many lower latitudes, where dispersal and colonization can, in theory at least, result in a rearrangement of ecosystems without necessarily involving species loss, global warming at high latitudes if allowed to proceed unchecked is certain in the long run to cause the extinction of many specialized high Arctic organisms together with small island endemics (Cook, Chapter 17). However, in absolute numbers, relatively few Arctic species may be subject to extinction in the 21st century. A number of true Arctic vertebrates and sea-ice-associated biota are likely to be most at risk (Callaghan 2005, Smetacek & Nicol 2005, Michel, Chapter 14; yet, see Section 1.5.2.2 for the potential effects of ocean acidification). Moreover, a substantial proportion of land area currently classified as high Arctic consists of islands well isolated from continental land masses (e.g. Svalbard, Franz Josef Land, the Canadian Arctic Archipelago). Future changes in these island ecosystems will be strongly affected by their isolation. Simple expansion of existing low Arctic ecosystems will be inhibited by water/ice barriers, and become increasingly so as the open-water season lengthens. Highly mobile species such as birds and some insects may expand their ranges to these islands as the climate moderates, while terrestrial mammals, non-flying invertebrates and plants with animal-dispersed seeds may take much longer to reach them. The protection of high Arctic biota, especially animals such as lemmings, Arctic hare *Lepus arcticus* and muskoxen, is likely to be easier in such refugia, the more so because their maritime climates are likely to remain cooler than those of continental regions (Gaston *et al.* 2012).

Nevertheless, predictions of such changes are fraught with large uncertainties. Current ecological projection models are often mechanistically naïve in the sense that differential dispersal capacities and interspecific interactions are not taken into account (cf. Guisan & Thullier 2005, van der Putten *et al.* 2010). Thus, novel types of habitats and ecosystems may emerge under rapid climate change. Moreover, within the range of projections from Global Circulation Models there are outcomes that represent 'novel climates' with no analogues (Williams *et al.* 2007), which naturally limit inferences about how biota are likely to respond.

In the marine environment, the northward expansion of sub-Arctic species takes place via dispersion and transport of planktonic larvae or adult animals. In addition, increasing temperatures and the opening of migration corridors as the ice retreats favor range extension of marine species such as the killer whale, with expected impacts on marine food webs (Michel, Chapter 14). In addition, global warming will increase the potential for exchange of species and populations between the Pacific and the Atlantic sectors (Cook, Chapter 17). The same applies to alien invasive species (Lassuy & Lewis, Chapter 16).

The strong selection pressures inherent in the harsh and highly fluctuating Arctic environment, applied to organisms over periods of up to two million years, should ensure that those that persist display high fitness and resilience to climatic variability and change (see Beaumont *et al.* 2011 and Walsh *et al.* 2011). This does not mean, however, that climate variability and shifts will have little effect. A few degrees increase in mean winter temperature will result in more frequent and much more pronounced freeze-thaw events including winter rains resulting in ice crust formation (Rennert *et al.* 2009), which may pose severe problems or even extinction of several species and corresponding change in ecosystem structure. Similarly, a few degrees of temperature increase will result in extensive sea ice reductions, particularly of multi-year ice, as is already taking place (Smetacek & Nicol 2005). As a result, the global polar bear population has been predicted to decrease by about 30% during the next 45 years (Amstrup *et al.* 2008, Stirling & Derocher 2012), and the range of polar bears is forecast to contract significantly, particularly in the southern parts of their distribution (Durner *et al.* 2009).

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[19] The composite of an organism's observable characteristics or traits such as morphology, development, biochemical or physiological properties, phenology and behavior.

[20] The genetic makeup of a cell, an organism or an individual.

Furthermore, Arctic communities are not entirely composed of common and widespread species. Some invertebrate and lichen species, for example, are either widespread but uncommon elements of a particular community type or have a highly restricted distribution. We do not yet fully understand the ecology of rarity, the functional importance of these rarer species in ecosystem processes or their role in community resilience. The capacity for rapid adaptation by organisms to a changing Arctic environment will differ markedly between groups. For example, bacteria, microalgae and some smaller invertebrates are likely to adapt more rapidly *in situ* to change than birds or mammals, which are more likely to have to move to new areas in search of favorable conditions.

In ungulates, increasing temperature has already been shown to strongly influence development rates, population amplification, distributions and emergence of disease attributable to some helminth parasites. Temperature changes can facilitate expansion of parasite and host assemblages from the south, leading to a range of interactions with northern endemic faunas, including changing patterns of exposure for zoonotic parasites transmitted from animals to people (Hoberg & Kutz, Chapter 15).

To human societies in the Arctic, climate change and its impacts on biodiversity are now and will increasingly be a challenge (Hovelsrud *et al.* 2011). Some may see the multitude of changes as beneficial, such as less inclement winters, longer summers, easier boat traffic (including marine hunting and fishing, where this primarily takes place from boats; e.g. Hvid 2007 and Michel, Chapter 14), better possibilities for agriculture and aquaculture, together with improved access to mineral resources. Also, increased marine productivity and new fish and other wildlife species may become available for harvest and improve economic opportunities (MacNeil *et al.* 2010). However, to what extent these advantages will be outweighed by the negative impacts such as decreasing biological resources currently harvested, is uncertain and furthermore much dependent on individual situations and preferences including the sense of 'Arctic identity'. Successful adaptation will demand considerable adjustment to new pressures as well as the ability to make use of new opportunities (see e.g. Nuttall 2005). The conservation interest lies in keeping the change from all stressors as much as possible within the scope of adaptation and adjustment (i.e. resilience) for all socio-ecosystem components, including humans, so that massive disruption of ecosystems does not result.

When considering impacts of climate change on Arctic ecosystems, interactions between climate change and other stressors must be taken into consideration. Offshore oil and gas exploration, increasing terrestrial and marine traffic, fishing activity, and heavy metal and organic contaminants are all stressors that may be exacerbated by ongoing climate change (Callaghan 2005, Callaghan *et al.* 2011b, Wrona & Reist, Chapter 13, Michel, Chapter 14). Furthermore, warmer climates may enable – in addition to 'naturally expanding' boreal species – the expansion of a number of invasive species into the present Arctic (Lassuy & Lewis, Chapter 16; see also Section 1.5.2.3).

Climate change will also alter productivities of Arctic aquatic ecosystems (Wrona & Reist, Chapter 13, Michel, Chapter 14). Most Arctic salmonids (e.g. chars, whitefishes), important mainstays of coastal and subsistence fisheries, are represented by polymorphic forms and also exhibit variable life histories (Christiansen & Reist, Chapter 6). Stressors (e.g. climate change, river damming) will result in changes in the relative proportions of these variant forms with possible negative consequences for fisheries. An example is the present dominance of anadromy in the mid-latitudes of the range of Arctic char (i.e. 50-70 °N in North America), relative to non-migratory counterparts present in the same lakes, where sea-run fish are preferred in fisheries due to greater size/weight, larger abundances and lower parasite loads. Anadromy in fishes is believed to result from greater productivity in the sea relative to freshwater systems (Gross 1987); this is especially relevant in the Arctic where the differential is substantial. Climate-change driven increases in productivity from present levels are likely to be higher in fresh waters than in the adjacent marine waters. Accordingly, benefits from migrating to the sea (e.g. enhanced growth) will be lower relative to costs (e.g. migration, predation), thus, decreased anadromy may ensue with follow-on consequences to fish quality and quantity (Reist *et al.* 2006). Limited evidence accrued to date suggests that some char populations are already exhibiting a lower proportion of anadromy (Finstad & Hein 2012).

The huge variation between the effects that climate change has on different species and even on the same species in different parts of the Arctic may cause significant shifts in 'match' to occur between species assemblages and food webs such as simultaneity in plant flowering and emergence of insect pollinators (Gilg *et al.* 2012). This may result in improved 'matches' in some inter-species relations (Vatka 2011, Ims & Ehrich, Chapter 12), but it is more likely that such changes will result in trophic mismatches, leading to reduced reproductive success in many Arctic species (Ganter & Gaston, Chapter 4, Michel, Chapter 14; see also Miller-Rushing *et al.* 2010 for discussion) as hypothesized for Greenland caribou (Post *et al.* 2009).

Climate change is also predicted to have a significant impact on levels of contaminants and their effects on wildlife. Contaminants may become more mobile in the Arctic environment with climate change. For example, mercury is expected to increase in the Mackenzie River with increased discharge rates (Leitch *et al.* 2007) and with increases in primary productivity associated with warmer temperatures and less ice cover (Carrie *et al.* 2010). Similarly, climate change is expected to release contaminants accumulated in ice sheets, glaciers and permafrost that are now melting and thawing (Callaghan *et al.* 2011b, Kallenborn *et al.* 2011, UNEP/AMAP 2011).

**Possible conservation actions**

- Sufficient efforts to reduce global greenhouse gas emissions, and thereby human-induced climate change, are needed if the threat of climate change is to be addressed. Continued warming is overwhelmingly the most serious predicted threat to Arctic biodiversity, as it will fundamentally alter Arctic biodiversity at the habitat, species and ecosystem level. In fact, the global goal that world leaders have set for climate change mitigation, i.e. 2 °C (UNFCCC 2010), may not be adequate to protect Arctic biodiversity since the Arctic is warming twice as fast as the global average. Mechanisms to address climate change are presented by IPCC (2007b), UNEP *et al.* (2011) and elsewhere, recognizing that urgent and far-reaching global actions are required to address this problem that has worldwide causes and worldwide impacts.[21] This assessment provides additional evidence pointing to the urgency of addressing this issue.
- The reduction of black carbon emissions is a high priority, since a reduction in the emissions of black carbon (and tropospheric ozone) is the fastest way to reduce the 'polar amplification' of global warming in the Arctic (Lenton 2012).
- High priority for conservation planning should be given to the protection of networks of large, representative tracts of habitat. This should include northern 'refugia' areas to support and maintain the resilience of Arctic ecosystems, such as Arctic islands and mountainous areas together with the remaining multi-year sea ice areas, where unique Arctic biodiversity has the best chance of surviving climate change.
- Furthermore, the reduction or minimization of all other stressors to biodiversity will help mitigate the effects of climate change (IPCC 2007c).

### 1.5.2.2. Pollutants originating outside the Arctic

Aside from the climate drivers dealt with in Section 1.5.2.1., the most important pollutants reaching the Arctic from southern countries are

- environmental contaminants which are persistent, bio-accumulative and subject to atmospheric or oceanic long-range transport,
- aerosols causing ozone depletion and thereby increased UV radiation potentially harming living organisms.

In addition, atmospheric deposition of nitrate (a plant nutrient) brought to the Arctic from southern sources, which currently is at relatively low levels in the Arctic, can be expected to increase in the future (Callaghan 2005).

Most bio-accumulating contaminants found in the Arctic originate from industrialized areas in Eurasia and North America and are brought into the Arctic by atmospheric and ocean currents (AMAP 2010, 2011b). Bio-magnification takes place through food webs, resulting in the highest concentrations found in apex predators (and scavengers) including humans (Reid *et al.*, Chapter 3).

Significant levels of contaminants (heavy metals, organochlorines, brominated flame retardants, etc.) have been documented in several Arctic animals, but so far, there is little scientific evidence that contaminants have reached such levels that they have resulted in reduced populations. Exceptions to this may be glaucous gulls *Larus hyperboreus* on Bjørnoya, Svalbard (Verreault *et al.* 2010) and ivory gulls in Canada (Ganter & Gaston, Chapter 4; see also Miljeteig *et al.* 2012) together with marine benthic invertebrate species in areas with mine tailings (Josefson & Mokievsky, Chapter 8). In a number of other species the levels are high enough that detrimental effects to individuals may occur (Letcher *et al.* 2010, Dietz *et al.* 2013). However, some toxic contaminants such as the legacy POPs are declining across much of the Arctic (AMAP 2009c, Rigét *et al.* 2010, 2013), most likely as a result of international regulation of emissions, such as the Stockholm Convention on POPs, which was influenced by Arctic Council assessments under AMAP (e.g. Downie & Fenge 2003).

In contrast, the Arctic is a major sink for tropospheric mercury derived largely from industrial sources (e.g. coal combustion) (Ariya *et al.* 2004) and freshwater run-off, and mercury concentrations in marine animals are stable or increasing in the Canadian Arctic and W Greenland (Braune *et al.* 2005, Niemi *et al.* 2010, AMAP 2011b). A variety of recently emerging, but poorly studied, contaminants, such as polybrominated diphenyl ethers (PBDEs), are also increasing (Braune *et al.* 2005). See further in Section 1.5.1.4.

Carbon dioxide also has serious effects on the acidity of the oceans and thereby living conditions for calcareous organisms and maybe even fish (AMAP 2013, Christiansen & Reist, Chapter 6, Josefson & Mokievsky, Chapter 8, Lovejoy, Chapter 11, Michel, Chapter 14). These organisms (mollusks, echinoderms, etc.) are likely already under stress due to low temperatures because the cost of calcification varies inversely with temperature (Clarke 1992). Increasing temperature and acidification could mean that one stress factor is substituted by another, but whether or not they will balance is difficult to say. Furthermore, the solubility of gases, including $CO_2$, is higher in colder waters than warm waters, so that the Arctic Ocean is especially prone to harmful effects of acidification (Bates & Mathis 2009, Carmack & McLaughlin 2011, Lovejoy, Chapter 11). Global ocean acidification is now occurring at a pace likely unsurpassed over the past 55 million years, and regions of the Arctic Ocean are already showing the effects of acidification (AMAP 2013). The pteropods such as *Limacina helicina*, an important plankton species found in the top

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[21] Unless carbon capture and storage (CCS) becomes economically realistic, these actions include that $CO_2$ from "less than half the proven economically recoverable oil, gas and coal reserves can (…) be emitted up to 2050", if the maximum increase of 2 °C is to be achieved (Meinshausen *et al.* 2009).

layers of the Arctic Ocean, appear to be particularly at risk (Comeau *et al.* 2011, Michel, Chapter 14). This may have serious negative effects including cascading effects on commercially harvested fish populations in some of the richest fishing regions on Earth.

Increased UV radiation due to ozone-depleting substances emitted to the atmosphere has negative consequences for plants (Newsham & Robinson 2009) and potentially to other living organisms in the Arctic as well (Wrona & Reist, Chapter 13).

**Possible conservation actions**

- Efforts to identify and assess emerging contaminants that may pose a threat to Arctic biodiversity should continue, combined with implementation of appropriate control mechanisms to limit their input into the Arctic.
- The successful international efforts already made to ban the most problematic substances should continue, and could be expanded to limit the discharge of the rest.
- Enhanced integrated, multi-disciplinary research and monitoring could be established to improve our understanding of the fate, distribution and effects of contaminants on biota and on ecosystem structure and function, including achieving an improved mechanistic understanding of interactions with other relevant environmental stressors (e.g. climate variability/change) and cumulative effects.

### 1.5.2.3. Invasive species

In this assessment, invasive species are defined as alien species intentionally or unintentionally introduced by humans that are likely to cause environmental or economic harm or harm to human health. This includes invasive species that have expanded north after being originally introduced by humans to sub-Arctic ecosystems. The range expansions of species native to the sub-Arctic are not considered ‘invasive’ in the strict sense used here, although many may cause the same negative impacts.

Next to habitat loss and modification, invasive species are globally considered the most significant threat to biodiversity (Vitousek *et al.* 1997, Clavero & Garcia-Berthou 2005, IUCN 2012), but to date this problem is less acute in the Arctic than elsewhere. However, some well-known examples of alien invasive species with serious effects in near-Arctic areas are American mink *Mustela vison* introduced for the fur trade into some areas in northern Europe and now found over Iceland, Finland and Norway, together with Nootka lupin in Iceland and Pacific red king crab in the Barents Sea (Lassuy & Lewis, Chapter 16).

Many terrestrial alien species already invasive in sub-Arctic ecosystems may move northward facilitated by climate change, human settlement and industrial activity. Some of these are likely to be ‘human commensals’ benefiting from increased human waste in the Arctic and function as new predators possibly impacting Arctic wildlife (Ims & Ehrich, Chapter 12). A warming Arctic has already facilitated a sharp increase in shipping and energy exploration activity, which directly increases the risk of biological invasions from species borne through pathways and vectors such as ballast water, hull or rig fouling, and associated shore-based developments such as ports, roads and pipelines (Lassuy & Lewis, Chapter 16). Furthermore, it is anticipated that northward expansion and range shifts for complex assemblages of parasites among terrestrial, freshwater and marine vertebrates will result in new faunal associations, a changing spectrum of hosts and varying impacts at landscape to regional scales (Hoberg & Kutz, Chapter 15). Pathogens and disease vectors, too, may invade or arrive with invasive alien species.

Examples of such invasive species in the sub-Arctic include several introductions (i.e. intentional translocations) of freshwater and diadromous fishes in Norway and the White Sea in Russia that may be relevant to the Arctic in the future (Christiansen & Reist, Chapter 6 and references therein). These include both introductions of alien species (e.g. pink salmon *Oncorhynchus gorbuscha*) to areas well outside their geographic range and also to relocation of species (e.g. European whitefish *Coregonus lavaretus*, vendace *Coregonus albula*) to new drainages adjacent to their native ranges. Initial intentions of such translocations are typically to increase local fishery or aquaculture opportunities. However, the effects are usually detrimental in that increased competition or predation occurs on native fish species often resulting in displacement or extirpation from the area.

**Possible conservation actions**

- Cost-effective early detection monitoring networks for invasive alien species linked to a common repository would facilitate immediate and thereby effective response.
- Preventative approaches that block pathways of invasive species introduction are important to implement at both the national and international levels.[22]
- Expanded inventory efforts at points of entry into the Arctic (e.g. roads, airports and harbors) are needed to enhance rapid response capabilities to eradicate introductions such as rats on seabird islands early in the invasion process.
- For marine species, support for ongoing international efforts to reduce the risk of introducing alien species such as ballast water treatment and the effective cleaning and treatment of ship hulls and drilling rigs brought in from other marine ecosystems is important.

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[22] This could include more consistent use of basic prevention tools such as Hazard Analysis and Critical Control Points (HACCP) planning (ASTM 2009), which has been used effectively in animal and plant farming operations and is applicable to a wide range of operations.

### 1.5.2.4. Stressors on migratory species

The Arctic holds a high proportion of migratory species, and many of them spend more than half the year outside the Arctic. The most serious threats to Arctic migratory species when outside the Arctic are habitat loss and degradation (Ganter & Gaston, Chapter 4). This is particularly evident for many waterfowl and shorebirds, for which losses of staging and wintering habitat (wetlands such as marshes and intertidal flats) are occurring at an alarming rate, especially in East Asia around the Yellow Sea (Syroechkovski 2006, Wetlands International 2012, MacKinnon *et al.* 2012), but also in other parts of the world. Furthermore, loss of coastal and intertidal habitat can be expected to increase considerably with climate-induced sea level rise, since man-made infrastructure such as seawalls precludes landwards displacement of these habitats. This effect will be compounded by increasing coastal development.

In addition, excessive harvest takes place in some places, particularly in East Asia. Conversely, regulation of hunting in the form of shortened shooting seasons, improved reserve networks and limitations to harvest technology (bans on netting and trapping, limits to weapon capacity etc.) have caused several waterfowl population in the western Palearctic and North America to increase during the last half century (Ely & Dzubin 1994, Madsen *et al.* 1999, Mowbray *et al.* 2002, Alisauskas *et al.* 2009, Meltofte & Clausen 2011, Wetlands International 2012).

As mentioned above, overharvest has even led to the probable extermination of the Eskimo curlew and near extinction of the spoon-billed sandpiper (Ganter & Gaston, Chapter 4). Similarly, overfishing of Atlantic horseshoe crabs *Limulus polyphemus* at the final migration stop-over site in Delaware Bay has reduced the availability of crab eggs as prey for spring staging red knots *Calidris canutus rufa* on the American East Coast, thereby caused heavy reductions in the population. The Siberian crane *Leucogeranus leucogeranus* is one of the East Asian species suffering heavy population decline as a result of habitat loss and overharvest in combination with displacement from many potential staging and wintering areas due to human disturbance including hunting. The East Asian great knot *Calidris tenuirostris* population is also suspected to have suffered from loss of staging areas around the Yellow Sea (Moores *et al.* 2008).

For seabirds, the threat from oil spills (see Section 1.5.1.4) is at least as big outside the Arctic as inside. Millions of Arctic seabirds including seaducks winter in waters that carry a heavy traffic of oil tankers and ships in general such as the Baltic Sea and the waters off Newfoundland, where accidental as well as (illegal) intentional discharge of oil are a major concern (Wiese & Robertson 2004, Skov *et al.* 2011).

Recent rapid population increases of a number of goose species in the Arctic and sub-Arctic, caused by better feeding conditions in temperate wintering areas and made possible by improved protection of the geese both on the breeding grounds and during staging and wintering, have created 'overabundance', which is affecting their Arctic habitats (see Ganter & Gaston, Chapter 4 and Ims & Ehrich, Chapter 12). Although relatively limited in geographical extent, this has resulted in the degradation of sensitive marshland vegetation in some Arctic regions (e.g. around southwestern Hudson and James Bays in Canada (Batt 1997). Attempts have been made to reduce the lesser snow goose *Chen caerulescens* population by increased hunting on the staging and wintering grounds, but with limited success (Alisauskas *et al.* 2011). Similarly, a management plan for preventing the Svalbard population of pink-footed geese *Anser brachyrhynchus* from further increase is under development among the range states (AEWA 2012).

Other stressors include contamination with organochlorine pesticides of apex predators such as peregrine falcon *Falco peregrinus* during wintering in temperate and tropical areas resulting in reduced breeding success, although this problem has receded for most populations (Ganter & Gaston, Chapter 4). Also, although lead poisoning of wildlife as a result of ingestion of lead shot appears to be in decline at least in northern Europe and North America following national bans on lead shot for waterfowl hunting, it is still in use for hunting of some other species in many countries (Anderson *et al.* 2000, UNEP/AEWA 2008).

Most caribou/reindeer herds around the Arctic undertake extensive seasonal migrations with winter ranges often quite disjunct from calving and summer ranges. Calving grounds, and often the travel routes, are well defined and can receive site-specific conservation attention. Seasonal ranges could, however, decline in carrying capacity when caribou experience disturbance, barriers to movement and habitat modifications, resulting in reductions in survival (through facilitated predation and hunting) and reductions in productivity (through habitat alienation, displacement and changes in energy budgets). Climate change is a threat to caribou migration where herds cross sea-ice bridges at times of increasing ice melt. These risks will be compounded by an increase in commercial shipping (Poole *et al.* 2010). Industrial developments and landscape alterations also have the potential to alter caribou migration corridors.

Similar problems may exist but be limited in scope for whale and fish stocks, except that the past overharvest of whales took place all over the area of occurrence of these species, and hydroelectric plants may hamper or even prevent migratory fish from moving up and down rivers. Overharvest of migratory populations of diadromous fishes may occur when both harvested while at sea (e.g. Pacific salmon species) and upon their return to fresh waters to overwinter and reproduce (e.g. chars, whitefishes, Atlantic salmon *Salmo salar*) thus leading to locally significant impacts (Christiansen & Reist, Chapter 6). Managing such cumulative impacts for species exhibiting limited marine migrations in Arctic waters (i.e. chars and whitefishes) is difficult but achievable through regional cooperation. Management of species (e.g. Pacific and Atlantic salmons) exhibiting wide-ranging marine migrations outside of Arctic waters requires more complex actions.

**Possible conservation actions**

- Cooperation with non-Arctic states is crucial to address threats on the staging and wintering grounds of migratory species. This includes international cooperation through multi-lateral and bi-lateral agreements. One example is the Convention on the Conservation of Migratory Species of Wild Animals together with its agreements and management plans (see Scott 1998).
- Habitat loss is the most serious stressor today for most migratory birds, and hence conservation action should include conservation of wetlands and other important habitats for staging and wintering Arctic birds.
- Overharvest and poisoning of birds by lead shot should be reduced where these are still a problem.
- To protect Arctic seabirds from oil spills on their staging and wintering grounds, it is important that Arctic nations continue efforts to reduce this risk.
- For endangered species, such as the spoon-billed sandpiper, international recovery programs need to be developed and implemented (see also Section 1.5.1.2).
- Caribou/reindeer migrations could be facilitated by protecting calving grounds and major travel routes (see Section 1.5.1.3).
- Regulation of the take of fish and whale stocks through existing international agreements should be supported, adhered to and further developed in accordance with the best scientific advice.
- The large goose numbers established during the last half century need to be carefully monitored. Where not already existing, management plans could be developed, implemented and followed up in cooperation between range states of the populations involved.

## 1.6. KNOWLEDGE GAPS

Basic knowledge on the vast majority of Arctic biodiversity is limited. Often, only the distribution of mammals, birds and vascular plants is sufficiently documented. Comprehensive data for abundance, population densities and trends are generally available only for vertebrates considered to be of direct significance to people, for example for commercial or other harvest, and for many taxa even the taxonomic status is incomplete. Thus, substantial gaps in biodiversity knowledge are apparent, and a more synoptic approach is necessary to:

- Address critical gaps contributing to a fundamental and functional understanding of diversity as a basis for recognizing and predicting the effects of accelerating change driven by climate and other disturbances.
- Improve understanding of diversity (from species to populations) and interactions of vertebrates, invertebrates and microorganisms that collectively form the web of relationships within northern marine, freshwater and terrestrial systems.
- Improve understanding of the functioning of Arctic ecosystems as to provide a scientifically sound basis for ecosystem-based management.
- Build requisite knowledge that supports ecosystem sustainability and paths for mitigation and adaptation within Arctic societies responding to rapid change and increasing threats to food security.

The causes of some data gaps are found worldwide, whereas others emerge from factors more special for the Arctic, such as remote and harsh environments, challenging logistics and the dearth of permanent infrastructure for science. Extreme and difficult conditions increasingly converge with the continuing global decline in scientists with appropriate expertise to provide authoritative identifications as a basis for biodiversity survey, inventory and monitoring activities.

Specimen archives, both spatially broad and temporally deep extending into the Quaternary, must be developed in conjunction with permanent museum repositories holding geo-referenced samples backed by web-available databases for large-scale informatics analyses across the Arctic (e.g. Christiansen & Reist, Chapter 6, Hodkinson, Chapter 7, Daniëls *et al.*, Chapter 9, Dahlberg & Bültmann, Chaper 10, Hoberg & Kutz, Chapter 15, Cook, Chapter 17). International cooperative agreements and participation by local communities are essential to efficiently build this high-latitude resource. In the absence of such resources as the functional basis for information systems, rapid and real-time progress in developing a broad view of Arctic biodiversity is not possible. Specimen archives assembled over years and decades constitute essential baselines for documenting and assessing the causes of spatial and temporal change in northern systems, and they provide pathways to employ new and expanding analytical approaches to assess diversity.

A profound challenge to our understanding of Arctic ecosystem functioning and our capacity to perform ecosystem-based management, is the very few dedicated programs and research stations that maintain fully integrated ecosystem-based approaches to research and monitoring in the Arctic. Regularly repeated measurements according to sampling design that both targets specific hypothesis and allows for detection of surprises (Lindenmayer *et al.* 2010) are essential to monitor changes in community composition and structure, diversity, productivity, phenology and other critical aspects of biodiversity and ecosystem integrity. Further, knowledge about the effects of the range of drivers and stressors on Arctic biodiversity is basic to its management. In support of biodiversity assessment on the ground, remote sensing from satellites and aircraft can provide temporally and spatially replicated data essential for monitoring, with remarkable speed and cost-effectiveness.

Integrated data resources for archives (collections of specimens, survey, inventory and monitoring) along with field observations and census across circumpolar regions must be developed and coordinated. A potential model is seen in the Circumpolar Biodiversity Monitoring Program (CBMP), although this and similar resources must be explicitly tied to specimens, hard data and authoritative identifications to document current and changing ecological conditions (see Box 1.4).

In synergy, these form the foundations for comprehensive ecosystem-based approaches to research and monitoring that can reveal how biodiversity may be affected by stressors and disturbances that cascade though food webs. However, this requires more emphasis than present on ecosystem level integration through all stages of science-based inferences from sampling, through data management, statistical modeling and interpretation of empirical results.

Similarly, the International Study of Arctic Change (ISAC) formed by the International Arctic Science Committee (IASC) and the Arctic Ocean Science Board (AOSB) recommends increased efforts to understand and model the physical and biological interactions governing Arctic ecosystems and their relation to Arctic peoples and the rest of the globe (Murray *et al.* 2010).

> » *… scientific work is basically simply an estimation, and I never totally believe scientists with their estimations… The scientists' estimations tend to contradict the knowledge of the Inuit – Inuit rely on wildlife for food and they deal with wildlife on a daily basis all year round – while on the other hand scientists come up here and do a 3- to 4-day study and then they do a report, and they try to convince everybody of their findings and because of that they always contradict with Inuit knowledge… But today Inuit are working together collecting these kinds of information for the future generations. If in fact we had documents to back us up, I am sure that scientists would have to believed what we were saying all along.*
>
> (Joannie Ikkidluak, in Hay *et al.* 2000).

The traditional knowledge of indigenous Arctic peoples contains a wealth of information on the uses of Arctic organisms including present and historic locations of fish spawning grounds, phenological events, etc., often indicated by place names. Several initiatives have been undertaken to better engage traditional knowledge and to reduce conflicts between local hunters and fishermen and government authorities devising regulations (Freese 2000, Klein 2005). One example is the co-management program *Opening Doors to Native Knowledge* in Greenland (Huntington *et al.*, Chapter 19). Improved knowledge of the conditions and actions that foster such collaboration and mutual understanding will help in the design and implementation of local conservation programs.

Commercial bioprospecting of organisms is already underway in Arctic ecosystems, particularly the marine environment, and coordinated careful consideration is needed to balance community and commercial interests (Leary 2008). The potential of the genetic resources present in the Arctic remains poorly understood, however, making it difficult to assess their value in this regard. From the perspective of scientists, lack of information for particular areas can hamper acquisition of open and unbiased analysis and make accurate conclusions and predictions very difficult. Therefore, possibilities for acquisition, cooperation and sharing of data from all parts of the Arctic are important for scientific analysis as well as for resource management.

### Possible actions

Detailed suggestions for filling specific knowledge gaps are provided in the various chapters of this assessment. Here, we describe why major categories of knowledge gaps must be filled, urgently and to the best of our collective ability. A great deal is known about Arctic biodiversity, as demonstrated by the depth and detail of the chapters of this assessment, and the need for vigorous and prompt conservation action is strongly supported by current knowledge. At the same time, much remains to be learned, which will help design and carry out more specific and effective conservation measures in the context of rapid change and increasing industrial development in the Arctic.

- The lack of basic knowledge about many aspects of Arctic biodiversity hampers our ability to evaluate the effectiveness of conservation actions. The threat of overharvest has been greatly reduced in the Arctic in part because sufficient knowledge exists to develop effective conservation measures and to build support for those actions. This success applies, however, only to a relatively few harvested species. Other conservation measures make up for a lack of specific knowledge with a broad approach, as is the case with protection of large areas of habitat. A comprehensive approach to gathering data about species and ecosystems is needed to better understand how environmental change and changes in human activity will affect Arctic biodiversity and the conservation thereof.
- The lack of monitoring and modeling capability for many aspects of Arctic biodiversity and their drivers of change makes it difficult to assess change, its cause and implications, and what could be rational conservation actions. Change cannot be measured without a baseline. For many species and ecosystem processes, that baseline of knowledge does not exist. Similarly, modeling efforts have focused on the physical environment and a few key species or ecosystem parameters. A coordinated ecosystem-level oriented monitoring and modeling effort is needed to support biodiversity conservation efforts in a time of rapid change.
- The lack of specimens and museum collections means that a firm foundation for assessing biodiversity and changes thereto is missing. A solid baseline requires hard data and definitive specimens. This area has received insufficient attention to date. A collaborative approach to collection and archiving of specimens could help ensure that further change can be assessed and quantified.
- A great deal of research has been done on various aspects of Arctic biodiversity, but overall databases and knowledge bases do not exist for most topics. The circumpolar study of Arctic biodiversity is further

hindered by barriers to the access of field sites. Broad support for open science, from field work to analysis to archives, would help address this issue and provide a means to pool collective knowledge and expertise.
- The shortage of trained professionals in appropriate fields related to biodiversity means that filling knowledge gaps will remain a challenge. Too few scientists are available to work on many aspects of biodiversity, from taxonomy and systematics to integrative problem solving at the ecosystem level. Greater efforts could be made to recruit and support specialists in these fields, so that needed knowledge can be generated in a timely fashion to support conservation of Arctic biodiversity.
- The lack of awareness of most aspects of Arctic biodiversity, combined with the limited degree to which Arctic residents are involved in biodiversity research and conservation, reduces public and political support for important conservation actions. Charismatic species get a great deal of attention, which can help support species-oriented conservation measures. A commitment to conserving overall biodiversity as a vital legacy for all of humankind, however, will require broader public understanding of what is at stake, and broader participation in generating information and solutions.

## 1.7. SUGGESTED CONSERVATION AND RESEARCH PRIORITIES

The erosion of global biodiversity is not the only global crisis of our time. It has been argued that changes in climate, biodiversity, infectious diseases, energy supplies, food, freshwater, human population and the global financial system are part of one contemporary global challenge, and that they need to be addressed as such (Steffen *et al.* 2011). If this is not done in an integrated and sustainable way, efforts to address one challenge may very well worsen one or more of the others considerably. Also, global markets seek the exploitation of Arctic resources, resulting in greater interconnections between the Arctic and the rest of the world.

To safeguard Arctic biodiversity and the services we receive from it, three spatial levels of stressors must be addressed: (1) global and circumpolar stressors like climate change and long-range transport of contaminants by air and sea water, (2) regional stressors like overexploitation, expanding boreal and invasive alien species, and (3) more ‘localized’ stressors like mineral extraction, oil development and ship accidents. Here we provide a set of suggested priorities for actions defined according to these three geographical scales. These priorities flow from the suggested actions in the technical chapters and this synthesis. They are intended to provide guidance to CAFF in development of recommendations from this report.

The alleviation of stressors with circumpolar effects on species and ecosystems generally requires international cooperation for effective management (Steffen *et al.* 2011).[23]

- Conserving the unique Arctic biome will require all possible efforts to curb human-induced global warming.
- Global and regional actions to reduce both legacy and new environmental contaminants entering Arctic ecosystems should continue and, where necessary, intensify under existing international conventions.
- Effective conservation of Arctic biodiversity needs to be global in scope and requires significant international cooperation to succeed. Any action to solve one global challenge should take others into account so that measures to solve one stressor do not worsen others.

Since many fish, birds and mammals move between different regional and national jurisdictions, management can benefit from regional cooperation.

- To maximize the resilience of Arctic ecosystems, effective protection of large representative tracts of habitat, including hotspots for unique Arctic biodiversity and northern ‘refugia’ areas, is of paramount importance. This includes Arctic islands together with mountainous areas and multi-year sea-ice refuges, where unique marine Arctic biodiversity has the best chance of surviving climate change.
- A major oil spill in ice filled Arctic waters would be detrimental to biodiversity and very difficult to clean up, particularly under problematic weather, light and ice conditions. However, if oil development is undertaken, a precautionary approach adhering to regulations and guidelines specific to the Arctic and based on the best available science would reduce risks, including that development activities in the most sensitive areas are avoided.
- Focused harvest management of fish, birds and mammals is needed on those species and populations that have experienced major declines for which harvest is one of the causal factors (see Section 1.5.1.2).
- To protect staging and wintering wetland areas for Arctic waterbird migrants from both habitat loss and overharvest, concerted international efforts should be conducted to conserve a network of key areas and address overharvest.
- To effectively protect Arctic native species and ecosystems from devastating effects of invasive alien species, appropriate efforts are needed to prevent their establishment in the Arctic. Early detection and preventative actions should focus on areas of human activity and disturbance.

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[23] See e.g. Johnsen *et al.* (2010) for overview and discussion of international agreements relevant to the Arctic, their coverage among Arctic states and their efficiency.

Although local stressors can entirely be managed by national or local authorities, bilateral or international cooperation on common standards can be beneficial.

- To protect Arctic biodiversity from severe impacts from local development and industrial activity, biodiversity conservation needs to be a cornerstone of natural resource management and land and marine planning.
- Improved monitoring and research is needed to survey, map, monitor and understand Arctic biodiversity including integrated, repeated data collection following recommended standardized protocols and priorities, and involving Arctic citizens in the survey and monitoring, if we are to move ahead with science-informed decisions in the Arctic. Support for national and international coordinated efforts such as the CBMP and the BAR Code of Life is important to fill critical data gaps on population abundances and trends for many Arctic terrestrial and marine species as well as on changes in the functioning and services of Arctic ecosystems.

In order to effectively respond to these suggested priorities, international cooperation and direct action at the national level are required. Many such efforts are already underway, and the Arctic countries possess strong legal frameworks that can form the basis for effective conservation of Arctic biodiversity. The Arctic Council has also established mechanisms for regional cooperation and scientific collaboration on research and monitoring e.g. the CBMP. Nevertheless, such agreements and initiatives are of little use if not backed up by secure long-term funding, enforcement and popular support.

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Arctic biodiversity has been exposed to strong selection pressures in the harsh and highly fluctuating Arctic environment over periods of up to three million years with repeated glaciations interrupted by relatively short interglacial periods. Photo: dalish/shutterstock.com

*Chapter 2*

# Species Diversity in the Arctic

**Authors**

David C. Payer, Alf B. Josefson and Jon Fjeldså

## Contents

> **When there is an earthquake, we say that the mammoth are running. We have even a word for this, holgot.**
>
> Vyacheslav Shadrin, Yukaghir Council of Elders, Kolyma River Basin, Russia; Mustonen 2009.

## SUMMARY

Species richness is generally lower in the Arctic than at lower latitudes, and richness also tends to decline from the low to high Arctic. However, patterns of species richness vary spatially and include significant patchiness. Further, there are differences among taxonomic groups, with certain groups being most diverse in the Arctic.

Many hypotheses have been advanced to explain the overall decline of biodiversity with increasing latitude, although there is still no consensus about a mechanistic explanation. Observed patterns are likely the result of complex interactions between various biotic and abiotic factors. Abiotic factors include lower available energy and area at high latitudes, and the relatively young age of Arctic ecosystems. Among biotic factors, latitudinal differences in rates of diversification have been suggested, but empirical evidence for this as a general principle is lacking. Recent evidence suggests that 'tropical niche conservatism' plays a role in structuring latitudinal diversity.

Physical characteristics of the Arctic important for structuring biodiversity include extreme seasonality, short growing seasons with low temperatures, presence of permafrost causing ponding of surface water, and annual to multi-annual sea-ice cover. The Arctic comprises heterogeneous habitats created by gradients of geomorphology, latitude, proximity to coasts and oceanic currents, among others. Superimposed on this is spatial variation in geological history, resulting in differences in elapsed time for speciation.

Over 21,000 species of animals, plants and fungi have been recorded in the Arctic. A large portion of these are endemic to the Arctic or shared with the boreal zone, but climate-driven range dynamics have left little room for lasting specialization to local conditions and speciation on local spatial scales. Consequently, there are few species with very small distributions. In terrestrial regions, high-latitude forests were replaced by tundra about 3 million years ago. Early Quaternary Arctic flora included species that evolved from forest vegetation plus those that immigrated from temperate alpine habitats, but the most intensive speciation took place *in situ* in the Beringian region, associated with alternating opportunities for dispersal (over the Bering land bridge, when sea levels were low) and isolation (during high sea levels). In the marine realm, the evolutionary origin of many species can be traced to the Pacific Ocean at the time of the opening of the Bering Strait, about 3.5 million years ago.

More than 20 cycles of Pleistocene glaciation forced species to migrate, adapt or go extinct. Many terrestrial species occupied southern refugia during glaciations and recolonized northern areas during interglacials. Ice-free refugia persisted within the Arctic proper; species occupying these refugia diverged in isolation, promoting Arctic diversification. The most significant Arctic refugium was Beringia and adjacent parts of Siberia. Pleistocene glaciations also resulted in a series of extinction and immigration events in the Arctic Ocean. During interglacials, marine species immigrated mainly though the Arctic gateways from the Pacific and Atlantic Oceans, a process that continues today.

Throughout the Pleistocene, Arctic species responded to climatic cycles by shifting their distributions, becoming extirpated or extinct, persisting in glacial refugia, and evolving *in situ*. Although the last 10,000 years have been characterized by climatic stability, the Earth has now entered a period of rapid anthropogenic climate change that is amplified in the Arctic. Generalism and high vagility typical of many Arctic species impart resilience in the face of climate change. However, additional anthropogenic stressors including human habitation, overharvest, industrial and agricultural activities, contaminants, altered food webs and the introduction of invasive species pose new challenges. The consequences of current warming for Arctic biodiversity are therefore not readily predicted from past periods of climate change.

## 2.1. Introduction

Arctic ecosystems are relatively young in a geological sense, having developed mainly in the last 3 million years (Murray 1995), although some Arctic species' lineages diverged and adapted to cold, polar conditions much earlier (see Section 2.3). In general, species richness is lower in the Arctic than in more southerly regions (Fig. 2.1). This is consistent with the general observation that biodiversity declines from the Equator to the poles (Rosenzweig 1995, Gaston & Blackburn 2000, Willig *et al.* 2003). The strength and slope of latitudinal biodiversity gradients differ between regions and are more pronounced in terrestrial and marine systems than in freshwater environments, and, in general, most pronounced in organisms with greater body mass and those occupying higher trophic levels (Hillebrand 2004). With the recent development of global distributional and phylogenetic datasets, however, it has become apparent that the pattern is much more complex than previously assumed (Jetz *et al.* 2012).

A number of hypotheses have been advanced to explain the latitudinal trend of biodiversity, although no consensus exists for a mechanistic explanation (Currie *et al.* 2004). Hypotheses may be grouped into those based on ecological mechanisms of species co-occurrence, evolutionary mechanisms governing rates of diversification, and earth history (Mittlebach *et al.* 2007). Until recently, ecological hypotheses have dominated the discussion, but with the development of large DNA-based phylogenies there is now more focus on understanding the underlying historical processes. The hypotheses proposed to date are not necessarily mutually exclusive, and observed patterns are likely the result of complex interactions between various biotic and abiotic factors.

The decline of available energy (Allen *et al.* 2002) and decreasing biome area (Rosenzweig 1995) with increas-

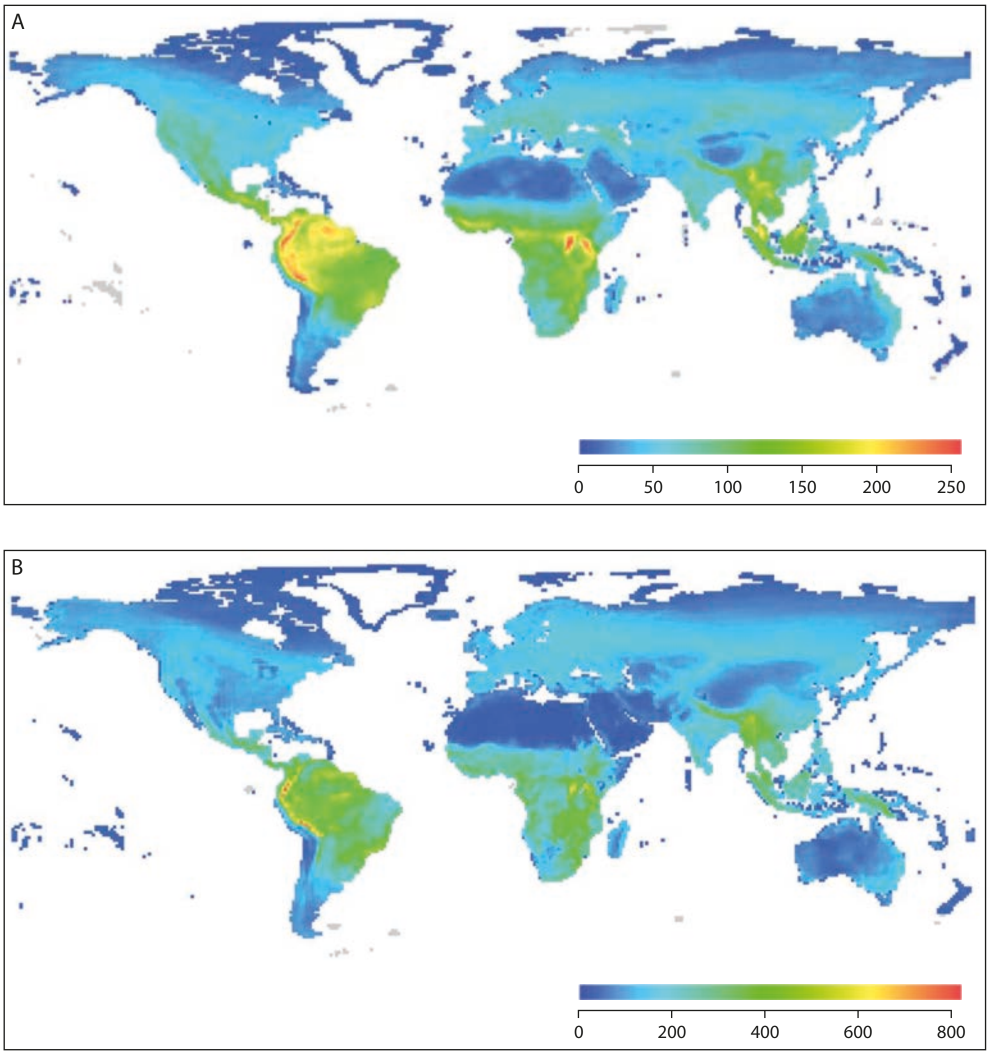

**Figure 2.1.** Global patterns of species richness for mammals (A) and birds (B). Maps produced by the Center for Macroecology, Evolution and Climate, University of Copenhagen. See also Fig. 1.1 in Meltofte *et al.*, Chapter 1.

ing latitude should both contribute to declining species richness in the North. Rohde (1992) posited that the ultimate cause could be a positive relationship between temperature and evolutionary speed. Relative to the tropics, the Arctic has limited insolation (lower solar energy input and thus colder temperatures) and a shorter elapsed time for diversification. In Rohde's (1992) view, all latitudes could support more species than currently exist, and, given adequate evolutionary time, the Arctic could support biodiversity rivaling that of lower latitudes. Because of great variation in speciation rates, however, the number of species in taxonomic groups is uncoupled from the age of groups (Rabosky *et al.* 2012). Further, several Arctic groups (notably waterfowl and gulls) underwent significant recent increases in speciation rates (Jetz *et al.* 2012). Thus, there is no general latitudinal change in speciation rates (as assumed, e.g. by Wiens *et al.* [2010]), and Jetz *et al.* (2012) instead point out hemispheric or even more local differences.

The recently proposed 'tropical niche conservatism' hypothesis may reconcile some of these diverging tendencies. This hypothesis assumes that most organismal groups originated during times when the global climate was warm (paratropical), and these groups tend to retain their adaptations to such conditions (Webb *et al.* 2002). Thus, as the global climate became cooler during the Oligocene, and again in the late Miocene, the ancient groups contracted their geographical distributions towards the Equator to maintain their original niches. The long time for speciation in tropical environments, compared with cold environments, would explain the large accumulation of species, and phylogenetically overdispersed communities, in the humid tropics (Wiens 2004). The most significant increases in speciation rates are associated with ecological shifts to new habitats that arose outside the humid tropics, notably in montane regions and archipelagos (Fjeldså *et al.* 2012, Jetz *et al.* 2012; see also Budd & Pandolfi 2010). However, only some groups have (yet) responded by adapting to these new environments, resulting in small and phylogenetically clustered communities in the Arctic.

The diversification process within the Arctic may have been strongly affected by the climatic shifts caused by variations in Earth's orbit known as Milankovitch oscillations. This includes a tilt in the Earth's axis that varies on a 41,000-year cycle (precession), an eccentricity in Earth's orbit that varies on a 100,000-year cycle, and 23,000 and 19,000-year cycles in the seasonal occurrence of the minimum Earth-Sun distance (perihelion; Berger 1988). Milankovitch oscillations cause variations in the amount of solar energy reaching Earth, and these variations interact with characteristics of the Earth's atmosphere such as greenhouse gas concentration and surface albedo, resulting in rapid, nonlinear climatic change (Imbrie *et al.* 1993). The present interglacial period, which has extended over the last 10,000 years, is a period of exceptional climatic stability; stable conditions have typically lasted only a few thousand years, and > 90% of the Quaternary Period (2.6 million years ago to present) has been characterized by more climatically dynamic glacial periods (Kukla 2000).

Webb & Bartlein (1992) noted that Milankovitch oscillations are associated with changes in size and location of species' geographical distributions. Dynesius & Jansson (2000) called these recurrent changes "orbitally forced species' range dynamics" (ORD), and noted that they constrain evolutionary processes acting on shorter time scales. The effects of Earth's precession and orbital eccentricity on surface temperatures are greatest at high latitudes (Wright *et al.* 1993), resulting in increasing ORD along the latitudinal gradient from tropics to poles. Predicted evolutionary consequences of enhanced ORD are apparent in general characteristics of Arctic biota, including enhanced vagility and larger species' geographic range sizes (Rapoport's rule), and therefore increased mixing of locally-adapted populations, increased proportion of polyploids within plant taxa, and reduced rates of speciation (Dynesius & Jansson 2000, Jansson & Dynesius 2002). There is spatial variation in these processes within latitude, however, which must be considered when evaluating current diversity patterns. For example, the Pleistocene temperature amplitude was lower in E Siberia and the Bering Strait region than in areas around the North Atlantic, leading to less glaciation (Allen *et al.* 2010) and enhanced opportunities for speciation in the Siberian-Beringian region (see below).

Although ORD increases risk of extinction associated with habitat change, this is mitigated by enhanced generalism, vagility and genetic mixing at high latitudes (Dynesius & Jansson 2000). This has important implications for risk of extinction associated with climate change and other stressors, as will be discussed in subsequent chapters of this Assessment.

## 2.2. Characteristics of Arctic biodiversity

### 2.2.1. Biotic and abiotic factors that structure diversity

Physical characteristics important for structuring Arctic biodiversity include extreme seasonality with dramatic intra-annual variation in insolation, generally cool summers, presence of permafrost resulting in unusual landforms, and annual to multi-year sea-ice cover. The resulting landscape is generally devoid of trees (a defining feature of the Arctic; see Section 2 in Meltofte *et al.*, Introduction) because tree growth, reproduction and survival are limited by short, cold growing seasons, lack of suitable substrates and nutrient deficiencies (Grace *et al.* 2002, Walker *et al.* 2012). Large areas of the Arctic's land surface are characterized by flat terrain underlain by permafrost, resulting in wetlands characterized by waterlogged soils and ponding of surface water (Gutowski *et al.* 2007). The Arctic Ocean has a deep central basin surrounded by the most extensive shelves of all the world's oceans, and is characterized by extensive (though declining) ice cover for much of the year (Michel, Chapter 14).

Species diversity is ultimately a product of both niche-based factors, e.g. adaptation to different environmental conditions, and dispersal-based factors, e.g. immigration from species pools. Of niche-based factors, adaptation to different environmental conditions or habitats is significant for generating diversity worldwide (Whittaker 1960). In general, complex, heterogeneous environments support higher diversity than homogeneous ones. Although the Arctic lacks the rich diversity provided by multistoried canopies in forested regions, it is far from homogeneous. The Arctic comprises vast numbers of different habitats created by gradients related to geomorphology (e.g. depth in the marine environment and elevation in the terrestrial realm), latitude, history of glaciation, proximity to coastlines, and oceanic currents, among other factors. In the marine environment, ice cover provides habitats unique to the Arctic with characteristic flora and fauna on both the bottom (secondary bottom habitats) and top (melt-water pools) of the ice surface. In the terrestrial Arctic, spatial heterogeneity in ice-associated processes such as freeze-thaw cycles and thermokarst create a dynamic mosaic of freshwater pools and shallow wetlands, which provide habitats for diverse taxa. This habitat heterogeneity is superimposed on spatial variation in geological history, resulting in differences in elapsed time for speciation.

In addition to these niche-based factors, barriers for dispersal affect status and trends in regional biodiversity, and, over the long term, opportunities for speciation. For example, terrestrial areas in the high Arctic comprise archipelagos separated from each other and from areas farther south by pack ice, which affects dispersal rates for several species (e.g. Daniëls *et al.*, Chapter 7). One well-known barrier in the marine environment is the huge ice plug occupying M'Clure Strait, Melville Sound and M'Clintock Channel in the Canadian High Arctic. This ice plug has persisted as a stable feature for > 1,000 years (although it is probably not stable on longer time scales), and effectively separates stocks of some marine mammals (Dyke *et al.* 1996). Polynyas (persistent open water areas within sea ice), which typically form in the shear zone between landfast and pack ice, provide important foraging areas during the breeding season and serve as winter refugia for a variety of seabirds and marine mammals (Stirling 1997), thereby contributing to Arctic biodiversity. Similarly, ice cover on land (glaciers and ice sheets) fragments terrestrial and freshwater habitats. Such fragmentation may enhance biodiversity (Fedorov *et al.* 2003), although the opposite effect of reduced range size leading to increased risk of extirpation or extinction must be considered (Rosenzweig 1995). This relationship is reversed for some ice-adapted Arctic species, with warming leading to habitat fragmentation, isolation and reduced ranges. Responses of Arctic biota to barriers related to climatic changes are therefore complex and not completely analogous to those of temperate taxa (Cook, Chapter 17).

Another feature of importance for Arctic biodiversity is regional heterogeneity in productivity. This is particularly true for the marine environment, where high productivity occurs in open waters close to the ice edge (Michel, Chapter 14). Diversity is often related to productivity in a unimodal (hump-shaped) fashion (Currie 1991, Currie *et al*. 2004), with diversity being highest in systems with mid-range productivity. However, this relationship is poorly documented in the Arctic, and may vary by taxonomic group or community type (Witman *et al.* 2008). Regardless of the exact relationship, differences in ice cover, mixing between warm- and cold-water currents, or currents with different nutrient content create a mosaic of oligotrophic and more enriched areas, which is reflected in differences in population density and species diversity. Good examples of enriched areas are the Bering and Barents Seas, which harbour species-rich invertebrate, fish and avian faunas (Ganter & Gaston, Chapter 4, Christiansen & Reist, Chapter 6, Josefson & Mokievsky, Chapter 8). In contrast, the deep seafloor of the central Arctic Ocean is oligotrophic and species poor.

In general, the terrestrial and marine Arctic are highly heterogeneous with many edge effects and potential dispersal barriers, creating the expectation of high species diversity associated with differential adaptation to distinct habitats. Despite this heterogeneity, however, the Arctic is less diverse than lower-latitude areas for several taxa, including mammals (Fig. 2.1a), most birds (Fig. 2.1b), plants (Fig. 1.1 in Meltofte *et al.*, Chapter 1) and especially herpetofauna (amphibians and reptiles), which are represented by just six species at the southern rim of the circumpolar Arctic (Kuzmin & Tessler, Chapter 5). As mentioned above, extreme seasonality, short growing seasons, overall harshness of climate, and widespread persistent or seasonal ice cover are all likely factors driving these relationships. Diversity in several other groups of organisms may equal or exceed that of corresponding groups at lower latitudes, however. Examples include marine benthic invertebrates (Renaud *et al*. 2009, Piepenburg *et al*. 2011), marine crustaceans and phytoplankton (Archambault *et al*. 2010), and *Calidris* sandpipers (Fig. 1.2 in Meltofte *et al.*, Chapter 1; Ganter & Gaston, Chapter 4). Very high species richness is also displayed in some terrestrial and freshwater invertebrate groups such as Collembola (springtails), which have the additional distinction of including many species that are endemic to the Arctic (Hodkinson, Chapter 7).

## 2.2.2. Spatial distribution of Arctic biodiversity

The Arctic supports > 21,000 species of mammals, birds, fish, invertebrates, plants and fungi, plus an estimated several thousand species of endoparasites and

**Table 2.1.** Selected characteristics of species occurring in the Arctic, by taxonomic group. In addition to those species listed, there are an estimated 7,100 described and as-yet undescribed species of endoparasites and several thousand groups of microorganisms.

| Group | Species occurring in the Arctic | Ratio of worldwide total | Mainly Arctic species | IUCN Endangered, Vulnerable, or Near Threatened | Extinct in modern times |
|---|---|---|---|---|---|
| Terrestrial mammals | 67 | 1% | 18 | 1 | 0 |
| Marine mammals | 35 | 27% | 11 | 13 | 1 |
| Terrestrial and freshwater birds | 154[a] | 2% | 81[a] | 17 | 0 |
| Marine birds | 45[a] | 15% | 24[a] | 3 | 0 |
| Amphibians/reptiles | 6 | < 1% | 0 | 0 | 0 |
| Freshwater and diadromous fishes | 127 | 1% | 18 | | |
| Marine fishes | c. 250[b] | 1% | 63 | 4[c] | |
| Terrestrial and freshwater invertebrates | > 4,750 | | | | |
| Marine invertebrates | c. 5,000 | | | | |
| Vascular plants | 2,218 | < 1% | 106[d] | 0 | 0 |
| Bryophytes | c. 900 | 6% | | | |
| Terrestrial and freshwater algae | > 1,700 | | | | |
| Marine algae | > 2,300 | | | | |
| Non-lichenized fungi | c. 2,030 | 4% | < 2% | | |
| Lichens | c. 1,750 | 10% | c. 350 | | |
| Lichenocolous fungi | 373 | > 20% | | | |

a) Includes only birds that breed in the Arctic. b) Excludes the sub-Arctic Bering, Barents and Norwegian Seas. c) Most marine fish species have not been assessed by IUCN. d) Includes Arctic endemics only.

microorganisms, many of which have yet to be described (Tab. 2.1). Species richness varies spatially and is not uniform across taxa. Consistent with the global latitudinal gradient in diversity described previously, species richness generally declines from the low to the high Arctic. There are also distinct regional hotspots of high biodiversity found throughout the Arctic, suggesting that despite general geographic trends, local factors are important contributors to regional diversity. For example, extraordinarily high species diversity occurs in microalgae of Hudson Bay (Archambault *et al.* 2010), and in terrestrial and freshwater invertebrates in the Disco Bay area of W Greenland (Hodkinson, Chapter 7). Beringia, which is defined as the area from the Lena River in northeastern Siberia to the Mackenzie River in northwestern Canada, and from the Arctic Ocean to southern Alaska and the middle Kurile Islands (Fig. 2.2), was first identified as a biodiversity hotspot for vascular plants by Hultén (1937). Subsequent work demonstrated its significance for diversity in other groups like birds and mammals. Henningsson & Alerstam (2005) suggested that the high diversity observed in shorebirds of Beringia results from geological history, high productivity and accessibility to multiple flyways. Similarly, species richness of mammals is greatest in Quaternary glacial refugia, particularly those such as Beringia that maintained connections to boreal regions (Reid *et al.*, Chapter 3). During and after the last glacial maximum (26,500-20,000 years ago), many herbivorous mammals persisted much longer in Beringia than western Eurasia, possibly because their favored forage (mesophilous herbs) persisted in this refugium (Allen *et al.* 2010). The role of Siberia and Beringia as the cradles of Arctic terrestrial biodiversity is reflected in a recent reassessment of the biogeographic regions of the World, based on linkages between distributions and phylogenetic relationships of > 20,000 terrestrial vertebrate species (Holt *et al.* 2013). This analysis identified a large Arctico-Siberian region, where the barren circumpolar Arctic environments associate with the wooded permafrost regions of Siberia.

In the marine realm, biodiversity tends to be high in the vicinity of the Arctic gateways from the North Atlantic and North Pacific Oceans (Christiansen & Reist, Chapter 6). This is true for such diverse taxa as mammals, fish and invertebrates. Diversity of marine fish (mainly teleosts and cartilaginous fishes) is particularly high in the Bering and White Seas (Christiansen & Reist, Chapter 6). Similarly, marine invertebrates have high species richness in Arctic areas close to the two gateways, with the highest diversity occurring in the Barents, Kara and White Seas (Josefson & Mokievsky, Chapter 8). For both fish and invertebrates, high diversity in the vicinity of the Arctic gateways is largely the result of mixing of sub-Arctic and Arctic fauna. Among marine mammals, the gateways provide corridors for seasonal migrations from temperate seas. The gateways are not true biodiversity hotspots, however, in that there are few endemic species present.

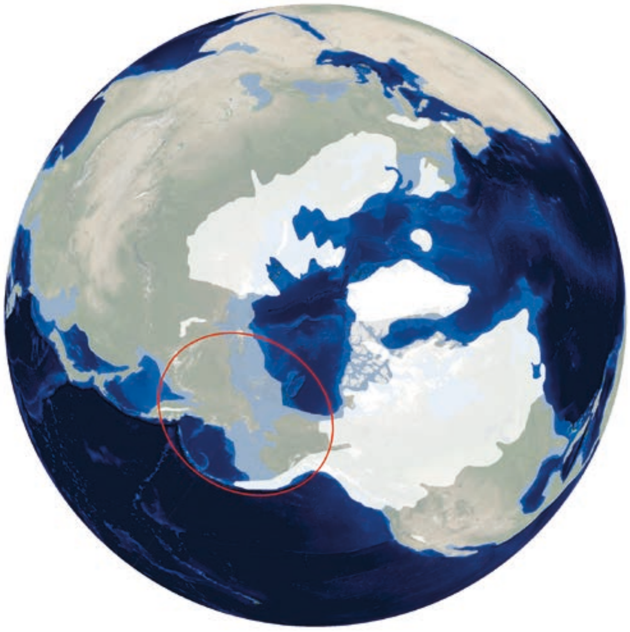

**Figure 2.2.** Beringia and other glacial refugia in the Arctic: distribution of ice cover (white shading) and ice-free areas in the Northern Hemisphere during the last glacial maximum, 18,000 years ago (after Ray & Adams 2001). Beringia is enclosed within the red oval.

## 2.3. Origins of Arctic biodiversity

It is evident that general conditions such as environmental harshness can only partially explain observed patterns of Arctic diversity. Although the proportion of Arctic biota comprising endemics is relatively low, there exist many examples of endemic species well adapted to harsh conditions. In the marine realm, for example, about 20% of mollusks and echinoderms are considered endemic (Briggs 2007). Endemic Arctic mammals include polar bear *Ursus maritimus* and two monotypic genera of whales belonging to the family Monodontidae, the beluga *Delphinapterus* and the narwhal *Monodon*. The degree of endemism at the level of both genera and species, however, is far lower than in the Antarctic, which has a similarly harsh environment. One likely explanation is the difference in geological age of the two systems. While Antarctic biota have evolved over about 25 million years with cold conditions persisting for the last 10-17 million years (Clarke & Johnston 1996, DeVries & Steffensen 2005, Patarnello *et al.* 2011; see also Box Box 1.3 in Meltofte *et al.*, Chapter 1), the corresponding elapsed time for Arctic biota is generally considered to be < 3.0 million years (Murray 1995, Briggs 2007). However, recent findings suggest that the modern circulation in the Arctic Ocean actually dates back 17 million years, with perennial sea ice cover formed about 13 million years ago (Krylov *et al.* 2008), so the difference may not be as great in the marine environment. The lower degree of endemism in the Arctic Ocean may also be a function of less isolation from adjacent oceans compared with the Antarctic seas, which are effectively isolated by the Antarctic Circumpolar Current (e.g. Hassold *et al.* 2009).

Within the Arctic, regional variation in rates of endemism appears to be related to elapsed time for speciation. For example, the opportunity for speciation has persisted longer in deep-sea areas than shelf and coastal marine areas, which have been free from bottom-covering glacial ice for a relatively short time (Weslawski *et al.* 2010). This is consistent with the observation that there are few endemic species in continental shelf and coastal areas (Dunton 1992, Adey *et al.* 2008).

Recent work in molecular phylogenetics suggests that some lineages of contemporary Arctic species adapted to cold, polar conditions as early as the Oligocene (34-23 million years ago), during the first Tertiary polar chill, although the precision of these estimates has been debated (Dornburg *et al.* 2012). For example, right whales (Balaenidae) may have originated as early as 27 million years ago (Sasaki *et al.* 2005). The *Pluvialis* sandpipers can be traced even further back, to 34 million years ago (Baker *et al.* 2007), and the divers *Gavia* represent a lineage that dates back > 65 million years to the late Cretaceous (Jetz *et al.* 2012), although it is not known when these birds adapted to Arctic conditions. See also Section 12.3.1 in Ims & Ehrich, Chapter 12.

### 2.3.1. Terrestrial and freshwater

Throughout most of the Tertiary Period (65-2.6 million years ago), high-latitude regions were forested (Murray 1995, McIver & Basinger 1999). Tundra first appeared during the late Pliocene in response to global cooling (Matthews & Ovenden 1990). Tundra communities were initially distributed discontinuously, then expanded to occupy a circumpolar belt by three million years ago (Matthews 1979). The early Quaternary flora of the Arctic included species that evolved from high-latitude forest vegetation of the late Tertiary by adapting to colder conditions, along with others that immigrated from alpine habitats in temperate regions of Asia and North America (Hultén 1937, Hedberg 1992, Murray 1995, Schönswetter *et al.* 2003, Ickert-Bond *et al.* 2009). Dramatic climatic shifts subsequently occurred throughout the Pleistocene, with more than 20 cycles of glaciation punctuated by warm interglacial periods.

The Pleistocene glaciations had a profound impact on Arctic biodiversity at all levels. Species had to migrate, adapt or go extinct. Many species occupied southern refugia during glacial maxima and recolonized northward following retreat of the ice sheets (Stewart *et al.* 2010). Ice-free refugia also persisted within the Arctic proper, including areas in eastern Europe, Siberia and North America. As mentioned above, the most significant Pleistocene refugium for Arctic and boreal biota was Beringia (Fig. 2.2; Hultén 1937).

Additional glacial refugia included exposed continental shelves and nunataks protruding above ice sheets in mountain ranges of the northern hemisphere (Abbott & Brochmann 2003). The existence of these refugia and their significance in structuring Arctic biodiversity has been supported by evidence from paleoecology, ecological niche modeling and molecular genetics (Cook, Chapter 17). Populations became fragmented and isolated in these ice-age refugia, which has likely promoted diversification in the Arctic (Fedorov *et al.* 2003).

An interesting example of the diversity-promoting effects of recurrent glaciations followed by interglacial periods is found in vascular plants of the Arctic. Arctic plants have a particularly high incidence of polyploidy, the presence of more than two sets of chromosomes. These polyploids have arisen through recurrent episodes of population fragmentation associated with glaciations followed by range expansions and hybridization during interglacials (Abbott & Brochmann 2003). New species resulting from this process (allopolyploids) are more successful than diploids in colonizing ice-free areas after deglaciation due to the buffering that their fixed-heterozygous genomes provide against inbreeding and genetic drift. Further, polyploids have broader ecological tolerances than diploids, and are thereby able to more readily adapt to diverse ecological niches and better cope with changing climate (Brochmann *et al.* 2004).

Beringia provided a land bridge between Eurasia and North America during most of the Tertiary, until it was severed by the Bering Strait at the shift between the Miocene and the Pliocene about 3.5 million years ago. The Bering Land Bridge repeatedly reformed throughout the Quaternary when sea levels fell during major glaciations (Hopkins 1973, Clark & Mix 2002), providing opportunities for biotic interchange between Eurasia and North America. This interchange included both terrestrial and freshwater species. An example of the latter is the Arctic grayling *Thymallus arcticus,* which apparently originated in eastern Siberia (Froufe *et al.* 2003, Weiss *et al.* 2006) and dispersed to Arctic North America via freshwaters of the Bering Land Bridge. The importance of this alternation between opportunities for dispersal and isolation is also well documented from fossil rodent faunas (Repenning 2001) and from phylogenies for other small mammals of the region (Hope *et al.* 2013).

### 2.3.2. Marine

Many marine mammals, invertebrates and algae of the Arctic Ocean appear to have an evolutionary origin in the Pacific at the time of the opening of the Bering Strait, about 3.5 million years ago (Adey *et al.* 2008). Throughout most of the Tertiary, the Arctic Ocean region supported a temperate biota, although intermittent polar sea ice formed as early as 47 million years ago and perennial sea ice was probably present by 13 million years ago (Krylov *et al.* 2008, Polyak *et al.* 2010). Harsh Arctic conditions developed only during the latter part of this period, however, beginning approximately three million years ago (Jansen *et al.* 2000).

Several endemic Arctic lineages started to develop during the glaciated periods of the Tertiary. For example, the bowhead whale diverged from the right whale 16 million years ago (Sasaki *et al.* 2005), several ice-associated seal species evolved 11 million years ago (Arnason *et al.* 2006), and the beluga and the narwhal evolved 10 million years ago (Xiong *et al.* 2009). Over the last 2.6 million years, recurrent glaciations punctuated with shorter periods of de-glaciation resulted in a series of extinction and immigration events, which are reflected in contemporary patterns of diversity. Further, historic events during the last 3.5 million years have driven re-distributions of species from the boreal regions of the northern hemisphere, and are likely still affecting Arctic diversity today. The most pervasive change occurred during the late ice-free Pliocene, after the opening of the Bering Strait, when extensive trans-Arctic movements of invertebrate species occurred (Vermeij 1989, 1991, Mironov & Dilman 2010). Known as 'The Great Trans-Arctic Biotic Interchange' (Briggs 1995), this movement was primarily from the species-rich Pacific center of diversity (Briggs 2003) to the North Atlantic, likely resulting in enrichment of the Arctic species pool. At least in the marine realm, there is little evidence for negative effects of these invasions on the native fauna (Briggs 2007).

Following this interchange, periodic glaciations eradicated faunas in the shallower areas of the Arctic Ocean. During inter-glacials, immigration of species from the Pacific and Atlantic boreal species pools was possible. This immigration occurred mainly through the two major gateways into the Arctic, the Bering Strait in the Pacific sector and the Fram Strait/Barents Sea area in the Atlantic sector. Water flux through the Atlantic gateway is currently up to 10 times that of the Pacific gateway, providing immigrating species much easier access through the former. Therefore, it's likely that the historic trans-Arctic enrichment of the Atlantic species pool contributes significantly to increased immigration through the Atlantic gateway to the Arctic Ocean today. This is consistent with contemporary observations in the White Sea/Barents Sea area, which has high species richness (Josefson & Mokievsky, Chapter 8). Further, Atlantic boreal species as well as species with Pacific origin that have invaded via the northern Atlantic co-occur here with true Arctic endemics (Mironov & Dilman 2010). Overall, species richness in the Arctic Ocean consists of a modest number of endemics together with species that immigrated from areas outside the Arctic in both historic and ecological time.

Effects of Pleistocene glaciation differed in shelf and deep-sea areas. While some shelf areas were severely affected by ice groundings, the bathyal (deep sea) parts of the Arctic Ocean were not. Further, bathyal areas were relatively more isolated from other oceans, in particular from the Pacific because of the shallowness of the Bering Strait. As a result, the bathyal zone contains a more endemic fauna with few Pacific elements compared with the shelves, as seen in the polychaetes (bristle worms) (Bilyard & Carey 1980) and several other groups (Vinogradova 1997). Differential effects of glaciation history are also seen in the bathymetric distributions of species. For example, the Pacific boreo-Arctic echinoderms have a limited bathymetric range in the Arctic (often < 100 m), while the Atlantic boreo-Arctic species are mostly eurybathic (capable of tolerating a wide range of ocean depths). This is believed to be the result of substantial shelf glaciation on the Atlantic side that caused primarily eurybathic species to escape to great depths for survival, and later re-invade the shelves when conditions changed (Nesis 1983).

## 2.4. Future prospects for Arctic biodiversity

Over the last 2.6 million years, throughout the cycles of Pleistocene glaciations, Arctic species have shifted their distributions, become extirpated or extinct, persisted in glacial refugia, undergone hybridization, and evolved *in situ*. Although the last 10,000 years have been characterized by a relatively high degree of climatic stability, the Earth has now entered a period of rapid anthropogenic climate change. Global temperatures have been warmer than today's for less than 5% of the last three million years (Webb & Bartlein 1992) and are within 1 °C of the maximum over the last one million years (Hansen *et al.* 2006). Further, the rate and magnitude of warming is amplified in the Arctic (McBean 2005, IPCC 2007, AMAP 2009, AMAP 2011). This trend of accelerating climate change and Arctic amplification is expected to continue (Overland *et al.* 2011). Global warming has caused species distributions to shift northward and to higher elevations for a wide range of taxa worldwide (Walther *et al.* 2002), including species occupying the Arctic (e.g. Sturm *et al.* 2001, Hinzman *et al.* 2005). The Arctic, being a region with high ORD and therefore populated by species that have experienced selection pressure for generalism and high vagility (Jansson & Dynesius 2002), should have inherent resilience in the face of climate change. Some extant Arctic species have survived population bottlenecks driven by climatic change, including cetaceans (e.g. narwhal [Laidre & Heide-Jørgenson 2005]) and waders (Kraaijeveld & Nieboer 2000), further suggesting some degree of climate-change resiliency. However, the rapid rate of change occurring now and the amplification of this change at high latitudes pose unique challenges for Arctic species. The Arctic has experienced less anthropogenic habitat change and fragmentation than lower latitudes, which favors the ability of species to track shifting habitats. However, because of the limited area available in the polar regions, terrestrial Arctic biota have limited ability to respond to warming by northward displacement (MacDonald 2010). Kaplan & New (2006) predicted that Arctic tundra will experience a 42% reduction in area if global mean temperature is stabilized at 2 °C above pre-industrial levels. Although the rate of change is debated (e.g. Hofgaard *et al.* 2012), there is general agreement that area of tundra will be significantly reduced in this century.

In addition to rapid and accelerating climate change, Arctic species are experiencing anthropogenic stressors that did not exist during past periods of warming, including human habitation, overharvest, industrial and agricultural activities, anthropogenic contaminants, altered food webs, and the introduction of invasive species (Meltofte *et al.*, Chapter 1). The many migratory species that occur only seasonally in the Arctic face additional and potentially cumulative anthropogenic stressors on migration routes and in overwintering areas that could further impact their ability to adapt. The suite of stressors experienced by Arctic species today is therefore novel, making past periods of climatic change an imperfect analogue for the challenges now facing Arctic biodiversity. Future efforts to preserve Arctic biodiversity must be similarly novel and broad-reaching.

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Polar bears are iconic species of the Arctic, representing the fascination for wildlife in the cold northern region shared by people living in the Arctic as well as beyond. Photo: Wild Arctic Pictures/shutterstock.com

*Chapter 3*

# Mammals

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## Contents

> **The bears are more hungry. There is a problem with the ice. The rough ice makes it hard for them to find seals, but there is the same number of seals. […] The only change I've noticed is when I was growing up the polar bears would scare easily and run away. Even when they were around shacks they didn't break windows or do damage but now they are not afraid. They used to avoid communities before and now they don't.**
>
> Dowsley 2007.

## SUMMARY

There have been substantial changes during the past 50 years in the distribution and abundance of numerous Arctic mammals. The intensity and scope of these changes have been more pronounced in marine than terrestrial mammals. However, the lack of quantitative information for many species means that our assessment is biased towards the larger, more conspicuous and more economically useful species.

One set of changes is driven by a warming climate. Reductions in the duration, extent and quality of sea ice are forcing ice-dependent mammals (notably polar bears *Ursus maritimus*, seals and walrus *Odobenus rosmarus*) to change feeding behavior and areas, change habitats for reproduction and resting, and often travel further, with consequent reductions in population productivity and size. Increased frequency of winter rain and melting temperatures create ice cover on the ground or in the snowpack, making it more difficult for caribou/reindeer *Rangifer tarandus* and muskoxen *Ovibos moschatus* to reach food, and sometimes causing die-offs. Warming temperatures are driving greater growth and spread of primarily shrubs, but also trees, transforming the low Arctic tundra to sub-Arctic conditions with resultant influx of species (notably moose *Alces americanus*, Eurasian elk *Alces alces*, American beaver *Castor canadensis* and snowshoe hare *Lepus americanus*) that can use this new habitat. Later onset of snow in autumn and earlier spring melt shorten the duration and quality of the snow cover that is essential for lemming winter reproduction, and are implicated in reduced amplitude and longer periods in lemming cycles, and therefore reduced availability of lemming prey for numerous predators.

In addition to these patterns, other processes related to a warming climate include: changes in the onset, duration and amount of plant growth, changing distributions of ice-associated marine productivity, increased frequency of boreal and tundra wild fires, changes in the relative abundance of particular plant groups in tundra habitats, changing insect distribution and abundance, changing distributions of parasites and pests, together with more extreme weather events and storms. These are likely to have direct or indirect effects on the distribution, carrying capacity, productivity and ultimately population size of various mammals (notably migratory tundra caribou and voles). However, at present we still lack sufficient information to draw strong inferences about causal mechanisms between these acknowledged climate patterns and mammal distributions and demography.

Ecological changes related to a warming climate are happening so fast and are so pervasive that stabilization and major reductions in emissions of greenhouse gases, at the global scale, are the highest priority conservation action for the Arctic.

A second set of changes is driven by human activities. Harvesting of Arctic mammals has a long history. Commercial interests have driven major declines in some populations of whales and reindeer, but intensive harvest management has demonstrated that many populations can recover, and that various species can sustain well-regulated harvests (e.g. whales, polar bears, seals, reindeer and caribou, Arctic fox *Vulpes lagopus*). Indigenous peoples have strong cultural and economic ties to the harvesting of mammals. These can be sustained with a combination of cultural tradition and better science-based monitoring of population sizes and harvest levels.

Humans have introduced or re-introduced populations of some species in the Arctic, considerably influencing their distributions and ecological roles. North American species such as muskrat *Ondatra zibethicus* and American mink *Neovison vison*, introduced to Eurasia, have spread into the low Arctic. Relocations of muskoxen have been successful in numerous circumpolar sites. We recommend against future introductions of mammals to previously unoccupied ranges, especially islands, because of uncertain and often disruptive ecological impacts.

The Arctic is experiencing more human activity and infrastructure developments at sea and on land in recent decades, as a result of hydrocarbon and mineral exploration and developments, new shipping routes, new roads and increased tourism. These bring risks of direct mortality (e.g. oiling from spills, ship collisions), of displacement from critical habitats (e.g. calving, pupping and feeding areas), of disturbance (e.g. aircraft, road or ship noise interfering with whale feeding or caribou suckling), and of increased human harvests.

The following are high priority actions to mitigate the risks of increasing human activities: (1) an expanded system of protected areas or more intensively managed zones, especially marine, with emphasis on coastlines, polynyas, deltas, the edge of the ice pack, and caribou calving grounds, (2) harmonized, cross-jurisdictional, regulatory and assessment regimes for ocean shipping, aircraft routing, seismic and drilling activities, hydrocarbon and mineral developments and tourism, and (3) a more complete mammal distribution and abundance monitoring program designed to test alternative hypotheses regarding mechanisms driving changes.

Arctic carnivorous mammals, especially marine, have increasing levels of contaminants, notably organochlorines and heavy metals, as a result of increased delivery of these substances to the Arctic food web as airborne pollutants or in runoff from freshwater Arctic drainages. There is little evidence of demographic consequences in wild mammals to date, but a growing need to better understand the origins of pollutants, with internationally coordinated efforts to reduce them at source.

The relative impact of current changes varies by species and biogeographic region. However, most changes have been, and will continue to be, in the low Arctic regions. This is where human activity is more intense, and where the most dramatic terrestrial and marine habitat changes

are taking place. Oceans pose an insurmountable barrier to any northward expansion of smaller-bodied terrestrial species currently confined to Arctic mainland, and these will experience the most significant range restrictions. Likewise many expanding boreal species within continental Eurasia and North America will be stopped by ocean barriers, and will be unable to reach the Arctic islands. This particular isolation of islands, such as the Canadian Arctic Archipelago, Novaya Zemlya and Severnaya Zemlya, to novel colonization by smaller mammals allows these islands to act as partial refuges for their existing mammal fauna in the face of climate-driven changes in distribution.

## 3.1. INTRODUCTION

Relatively few mammals occur in the Arctic. About 67 species of terrestrial mammals and 35 species of marine mammals occupy this biome, at least seasonally (Appendix 3.1), comprising about 2% of global mammalian diversity. This low percentage reflects the energetic constraints facing homeotherms in this environment, and the fact that large areas were covered in ice through various ice ages, and as recently as 7,000-14,000 years ago (Dyke 2004). As climates warmed in the late Pleistocene and the Holocene (i.e. the last c. 12,000 years), Arctic tundras changed in distribution and composition. Mammals redistributed themselves, evolved to the new conditions, or became extinct probably as a result of a complex combination of climate changes and hunting by humans (Lorenzen *et al.* 2011). The Arctic is now home to species belonging to the following mammalian orders: Rodentia (rodents), Lagomorpha (hares and pikas), Soricomorpha (shrews), Carnivora (dogs, bears, cats, weasels, walruses and seals), Artiodactyla (even-toed ungulates) and Cetacea (porpoises and whales). All of these are characteristic north temperate latitude groups, but representatives of two other such mammalian orders – Erinaceomorpha (hedgehogs) and Chiroptera (bats), both insectivorous – have not colonized Arctic latitudes in the Holocene.

The Arctic biome is generally defined in a terrestrial context, as tundra habitats where trees do not grow (see Section 2 in Meltofte *et al.*, Introduction for this Assessment's delineations of low and high Arctic). Such a tree-line is imprecise in definition, and the sub-Arctic includes extensive shrub tundra interspersed with trees (northern taiga forest). We include terrestrial species with predominantly boreal, including sub-Arctic, distributions whose habitat affinities and documented distributions include some of the low Arctic. For marine ecosystems there is nothing equivalent to the treeline to allow a convenient ecological definition of 'Arctic'. We discuss in detail those species with a well-documented and consistent occupation of marine areas encompassed by low and high Arctic. We do not discuss species using sub-Arctic marine waters. We also acknowledge the occasional occurrence of other species within low Arctic waters (Appendix 3.2).

The taxonomy of Arctic mammals is fairly well studied, partly because there are relatively few species. However, there are still some uncertainties, especially among the rodents, shrews and hares. Pleistocene isolation in different refugia, and Holocene isolation following sea level rise, may or may not have led to sufficient genetic differentiation to warrant species status (Jarrell & Fredga 1993, Edingsaas *et al.* 2004, Wilson & Reeder 2005, Hope *et al.* 2011). For this assessment we follow the nomenclature in Wilson & Reeder (2005).

The broad distributions of Arctic mammal species are fairly well known, especially for conspicuous and recognizable larger-bodied species, although the amount of fine-scale information on distribution varies by species. Our confidence in the broad distributions of small-bodied species (all terrestrial) is high. These patterns are largely extrapolated from locations of well-documented presence and absence, and consider likely barriers to dispersal (mainly stretches of ocean and major rivers). However, the detailed distributions of these small-bodied species remain poorly documented, because the animals are inconspicuous and have not been surveyed in a widespread and repeated fashion through this very extensive and relatively inaccessible biome. We rely on various standard sources for broad distribution patterns (Wilson & Reeder 2005, Andreev *et al.* 2006, MacDonald & Cook 2009, IUCN 2011), and also on detailed data from species experts.

We present the diversity of Arctic mammals as species richness within various geographic regions (Appendix 3.1). For terrestrial mammals, regional boundaries are primarily water bodies (oceans and large rivers) that coincide with the boundaries of distributions of a number of species, leading to a strong inference that the water bodies played a role in geographic isolation and, sometimes, speciation (e.g. Ehrich *et al.* 2000, Waltari *et al.* 2004). Occasionally, we also employ jurisdictional boundaries to define regions (e.g. Fennoscandia). For marine mammals, we present species richness within 12 marine regions defined generally by seas or archipelagos with some bathymetric or geographic separations (Appendix 3.2).

The quality of information on abundance varies a great deal among species and regions. Some mammals are central to the well-being of northern peoples as sources of spiritual meaning, food, income from hunting and trapping and as competitors. These relationships can be very old, and deeply embedded in northern cultures. Vyacheslav Shadrin, a Yughagir elder from Kolyma region of Siberia says: "…when there is an earthquake, we say that the mammoth are running. We even have a word for this, holgot" (Mustonen 2009). Some species attract scientific attention because they are key players in the food web or have particular conservation concerns. However, we have very little or no detailed information for numerous other terrestrial and marine species. In addition, there is a relative lack of accessible, published information for species occurring in Russia.

We present current knowledge on distributions, richness and abundance by species or population, depending on the detail available. We organize this information in four broad sections: (1) terrestrial herbivorous mammals, (2) terrestrial insectivorous mammals, (3) terrestrial carnivorous mammals, and (4) marine mammals.

## 3.2. BIOGEOGRAPHY

### 3.2.1. Terrestrial mammals

Much of the Arctic biome is relatively young in evolutionary and ecological time, having experienced numerous Pleistocene glaciations (ice ages), the most recent being the Last Glacial Maximum (LGM) or last ice age (Wisconsinan or Late Weichselian period), 12,000-18,000 years ago (Dyke 2004, Hjort *et al.* 2004). Various regions escaped glaciation as refugial tundra, including during the last ice age. Consequently, current patterns of terrestrial mammal distribution are prominently linked to these refugia during the LGM. In addition, these distributions reflect the patterns of colonization from refugia and from regions south of continental ice sheets into newly forming tundra habitats as the ice retreated in the Holocene (Macpherson 1965, Weider & Hobæk 2000, Waltari *et al.* 2004).

During the LGM, the great majority of N Asia and considerable parts of NW North America were ice free (Mangerud *et al.* 2002, Dyke 2004). A large ice sheet covered Fennoscandia, most of the Barents Sea including island complexes of Svalbard, Franz Josef Land and Novaya Zemlya, and portions of the Kara Sea from which it pushed onto land on the Taymyr Peninsula (Svendsen *et al.* 2004, Hjort *et al.* 2004, Mangerud 2004). There appears to have been a small refugium in the Andøya region of the present-day Lofoten Islands, Norway (Møller *et al.* 1992, Mangerud 2004, Parducci *et al.* 2012).

The eastern portion of the unglaciated region, including Asian Chukotka and much of Alaska and Yukon, was joined together as one land mass we now call Beringia. The west edge of Beringia may have been contiguous with the rest of unglaciated Asia and north Europe at the LGM, as far west as the Kanin Peninsula of Russia (Mangerud *et al.* 2002). Only small areas in the north Taymyr Peninsula and Putorana Plateau (east of Yenisey River) were covered in ice (Astakhov 2004, Hjort *et al.* 2004).

In the western hemisphere, there was another refugium, or a series of smaller refugia, along the northwest extremity of the present-day Canadian Arctic islands and continental shelf, comprising the Tuktoyaktuk Peninsula, most of Banks Island and parts of Prince Patrick, Eglinton and Melville Islands (Dyke 2004). In addition, tundra habitats existed south of the vast ice sheets to approximately 45° N (Dyke *et al.* 2002).

Of the 67 terrestrial species with distributions in Arctic regions, 49 (73%) are limited to the low Arctic, 15 (23%) occupy both low and high Arctic, and three (4%) are found only in the high Arctic (Appendix 3.1). These three, however, are somewhat anomalous. One (East European vole *Microtus levis*) was introduced (to Svalbard) from temperate regions. The other two (Wrangel Island collared lemming *Dicrostonyx vinogradovi* and Wrangel Island brown lemming *Lemmus portenkoi*) are restricted to Wrangel Island (Wilson & Reeder 2005), but their status as unique species remains unclear (see discussion in Section 3.3.1.1). Species richness falls dramatically from low to high Arctic, demonstrating that high Arctic regions are inhospitable and/or inaccessible for most mammals.

The distributions of most low Arctic species are predominantly outside the Arctic, in the boreal biome. These 'boreal' species can exist seasonally, or year-round, in Arctic regions, because their preferred habitats are grassland, sedge fen, shrub or alpine tundra habitats that spread quite seamlessly into low Arctic tundras.

The true Arctic terrestrial mammals are those whose distributions are almost entirely within the Arctic biome (18 species), and those with present-day, resident Arctic tundra populations that have paleo-historical links to a tundra refugium during the last ice age but also extensive boreal distributions (12 additional species) (Appendix 3.1). Species with distributions restricted almost entirely to the Arctic include the circumpolar Arctic fox *Vulpes lagopus* (found in all 20 possible zones), species that are less wide-ranging but still well dispersed (6-8 zones) such as Arctic hare *Lepus arcticus*, Nearctic collared lemming *Dicrostonyx groenlandicus*, Palearctic collared lemming *D. torquatus*, Siberian brown lemming *L. sibiricus* and muskox *Ovibos moschatus*, and also numerous species with very limited distributions (one or two zones) often on islands (four shrews *Sorex* spp., Alaska hare *Lepus othus*, Alaska marmot *Marmota broweri*, four collared lemmings *Dicrostonyx* spp., Wrangel Island brown lemming and insular vole *Microtus abbreviatus*). The 12 resident Arctic species with both refugial links and boreal affinities are: tundra shrew *Sorex tundrensis*, Arctic ground squirrel *Spermophilus parryii*, Norway lemming *Lemmus lemmus*, Nearctic brown lemming *Lemmus trimucronatus*, tundra vole *Microtus oeconomus*, singing vole *Microtus miurus*, caribou/reindeer *Rangifer tarandus*, gray wolf *Canis lupus*, brown bear *Ursus arctos*, weasel *Mustela nivalis*, stoat *M. erminea* and wolverine *Gulo gulo*. Most of these play prominent ecological roles in Arctic tundra ecosystems, and can be considered true Arctic species even though their distributions are not exclusively Arctic. One other species, the red fox *Vulpes vulpes*, appears to be a more recent Holocene colonizer of Arctic regions (Skrobov 1960, Macpherson 1964).

Arctic regions vary considerably in their composition of low and high Arctic species and in their species richness (Appendix 3.1, Fig. 3.1). Species richness is highest for regions that encompassed large refugia during the last ice age and also maintained land connections to boreal regions in the Holocene. These are Alaska/Yukon (37

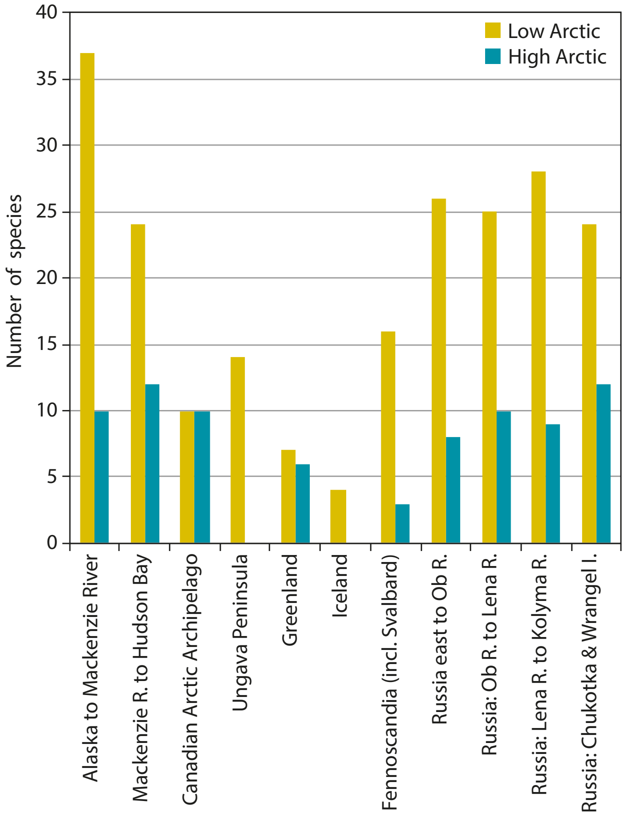


**Figure 3.1.** Number of terrestrial mammal species occupying low and high Arctic zones in each of the circumpolar Arctic regions. Data are summarized from Appendix 3.1.

species), Ob River to Lena River (26 species), Lena River to Kolyma River (28 species), and Kolyma River to Bering Strait (27 species). This richness is additionally enhanced in regions with extensive mountains (Alaska, Russia east of the Lena River) because of the additional habitat heterogeneity that diverse elevations provide.

Regions with smaller refugia in the last ice age (i.e. Fennoscandia and the Canadian Arctic Archipelago) have much lower species richness (Fig. 3.1; 17 and 10 species, respectively) probably because they sustained substantially fewer species through the last glacial advance. Their current diversity of low Arctic species strongly reflects their relative proximity to boreal habitats.

Regions completely covered in ice during the LGM, but well connected to refugia and to the boreal biome (i.e. Canadian mainland east of the Mackenzie, and western Russia), now have intermediate species richness (Fig. 3.1; 24 and 26 species respectively). This reflects colonization of newly formed habitats by tundra species from refugia and by boreal species from the south.

Greenland was likely completely covered by Pleistocene ice (Dyke 2004, Bennike *et al.* 2008) and remains largely covered to this day. Its sparse terrestrial mammal fauna (seven species) mostly originated from the refugium in the western Canadian Arctic Archipelago (Fedorov & Stenseth 2002, Waltari *et al.* 2004, Bennike *et al.* 2008). Ungava Peninsula in Canada and Iceland only have low Arctic habitats, but also low species richness (Fig. 3.1; 14 and four species, respectively) because they have been isolated from other tundra regions by large water bodies for most of the Holocene. Some Beringian tundra species, such as Arctic ground squirrel and muskox, have not been able to colonize Ungava without human assistance. The retreating Laurentide ice sheet over Hudson Bay, and massive pro-glacial lakes to its south, collectively formed an ice and water barrier, now largely Hudson Bay, that blocked colonization from the west (Dyke 2004, Occhietti *et al.* 2004). Some true Arctic species (Arctic hare and Arctic fox) apparently colonized from the Canadian Arctic Archipelago, and others arrived from the south (e.g. the Ungava collared lemming *Dicrostonyx hudsonius*) (Macpherson 1965, Dyke 2004). Iceland was likely completely glaciated in the last ice age and also isolated from other Arctic lands by the North Atlantic (Dyke 2004, Geirsdóttir 2004). Only the Arctic fox, the most itinerant of all Arctic species, has colonized Iceland in the Holocene, the other three species being introductions.

Terrestrial mammals that persisted in refugia, especially Beringia, through the LGM and into the Holocene represent a subset of a more diverse Pleistocene fauna, often characterized by species with large body size (such as mammoths *Mammuthus* spp.), 35 genera of which went extinct in the late Pleistocene (Webb & Barnosky 1989, Grayson & Meltzer 2002). A number of grazing herbivores went extinct at the Pleistocene-Holocene transition (13,000-11,000 years BP) at the end of the LGM, coincident with a warming climate as refugia began to expand in size (Guthrie 2001). The most coherent explanation for such a widespread set of extinctions of grazers, including mammoths, horses *Equus* spp. and Beringian bison *Bison* spp. (Shapiro *et al.* 2004, Guthrie 2006), was a major shift in climate patterns (notably cloud and precipitation) driving changes in vegetation from a steppe-like graminoid tundra to a wetter regime supporting woody shrubs and mosses where slower decomposition resulted in peatlands and shrub tundras (Guthrie 2001, 2006). Humans are unlikely to have been the primary cause of these extinctions (Grayson & Meltzer 2002). The dominant low Arctic herbivores we observe today are species that prosper on the dominant plants in relatively waterlogged and peaty habitats. The fates of extant herbivores in a changing climate will likely depend on the particular trajectories that vegetation composition and structure follow in response to regional shifts in temperature, precipitation and solar insolation.

### 3.2.2. Marine mammals

Arctic marine mammals have changed their distribution with climate variation over time (Vibe 1967, Harington 2008), and a common theme for marine mammals during the Pleistocene was northerly range shifts during warm phases and southerly shifts during cold phases (Harington 2008). For the cetaceans, Dyke *et al.* (1996) used radiocarbon ages of subfossils to demonstrate that distribution of bowhead whales *Balaena mysticetus* in the Canadian Arctic Archipelago expanded and contracted abruptly several times over the last 10,500 years. Those fluctuations allow for a reconstruction of the post-glacial sea ice history in the area, where bowheads were forced out of habitat due to year-round ice cover or allowed to expand their range into new habitat in the seasonal absence of ice cover. Evidence suggests Basque whalers harvested similar numbers of bowhead whales and right whales *Eubalaena glacialis* in the sixteenth century in the Strait of Belle Isle between Newfoundland and Labrador, a region far south of the present-day range of the bowhead whale, thus indicating a southward shift during the Little Ice Age (Cumbaa 1986, Rastogi *et al.* 2004, Weber *et al.* 2005). Furthermore, evidence that narwhals *Monodon monoceros* once occurred as far south as England during the Little Ice Age – observed in 1588 (Hay & Mansfield 1989) and post-Pliocene fossils in England and Germany (Owen 1846, Collings 1933) – indicate a substantial southerly shift of range with climate.

Polar bears *Ursus maritimus* evolved from brown bears but fossils are unfortunately rare (Harrington 2008). One of the oldest subfossils of a polar bear from the Palearctic is a left mandible found at Prins Karls Forland, Svalbard, and dated to Eemian-Early Weichselian (130,000-110,000 BP) (Ingólfsson & Wiig 2009). Based on a complete mitochondrial genome extracted from that bone, Lindqvist *et al.* (2010) suggested that polar bears evolved from brown bears about 150,000 BP. Analyses of mitochondrial DNA from another find dated to about 115,000 BP, from Kjøpsvik, Nordland, northern Norway revealed about the same age (160,000 BP) for the separation of polar bears from brown bears (Davison *et al.* 2011). A study using nuclear DNA indicated that polar bears evolved much earlier, in the mid-Pleistocene about 600,000 BP (Hailer *et al.* 2012). Edwards *et al.* (2011) suggest that there has been hybridization between polar bears and brown bears through time and that present day polar bears are closely related to earlier Irish brown bears. Miller *et al.* (2012) performed deep, high-throughput sequencing of the genomes of the polar bear mandible from Svalbard, two brown bears from the Alaskan archipelago, a non-archipelago brown bear, and an American black bear *Ursus americanus*. The comparative analyses demonstrated that these bear species evolved largely independently over a period of millions of years, which is in sharp contrast to the more recent estimates of polar bear origin mentioned above. Moreover, 5% to 10% of the nuclear genome of the archipelago brown bears was most closely related to polar bears, indicating ancient admixture between the species. Previously used gene-by-gene sequencing of single nuclear loci lacked sufficient power to detect such ancient admixture. These results are consistent with an ancient split between brown and polar bears approximately 4 to 5 million years BP, coinciding with the Miocene-Pliocene boundary, a period of environmental change that may have launched a radiation of bear species. This initial split was followed by occasional admixture until recently, leaving a clear polar-bear imprint on the nuclear genomes of archipelago brown bears. Genome-based analysis of historical fluctuations in effective population size (i.e. number of interbreeding bear individuals) strongly indicates that polar bear evolution has tracked key climatic events since the Middle Pleistocene. Ten finds of sub-fossil polar bears are known from southern Scandinavia, of which six have been dated to the period between 12,500 BP and 10,500 BP (Aaris-Sørensen & Petersen 1984, Blystad *et al.* 1984, Berglund *et al.* 1992), evidence that strongly suggests that the distribution of polar bears was influenced by climate variation during late Pleistocene and early Holocene and that they had a more southerly distribution than today.

The walrus *Odobenus rosmarus* was a part of the fauna in the North Sea during the late Pleistocene and early Holocene. In the late 1500s they lived (and reproduced) at the Orkney Islands in Scotland (59° N) (Ray 1960). On the Atlantic coast of North America many records of walruses are available from late glacial and post-glacial time periods making it possible to track the northward expansion of walruses as the sea ice retracted (Dyke *et al.* 1999). The northern limit for walruses at the LGM was in the vicinity of present-day Long Island, New York, after which it advanced to the Bay of Fundy by 12,700 BP, to southern Labrador by 11,000 BP, and to the central Canadian Arctic by 9,700 BP. The southern distribution limit also retracted and was in the Bay of Fundy by 7,000 BP. There are very few records of Pacific walrus *O. r. divergens* from late glacial and early post-glacial time. The oldest find, from Vancouver Island, is about 70,000 years old. Another was found in San Francisco harbor and dated to 27,200 BP (Dyke *et al.* 1999).

Similar to contemporary terrestrial mammals, contemporary marine mammals in Arctic regions include a substan-

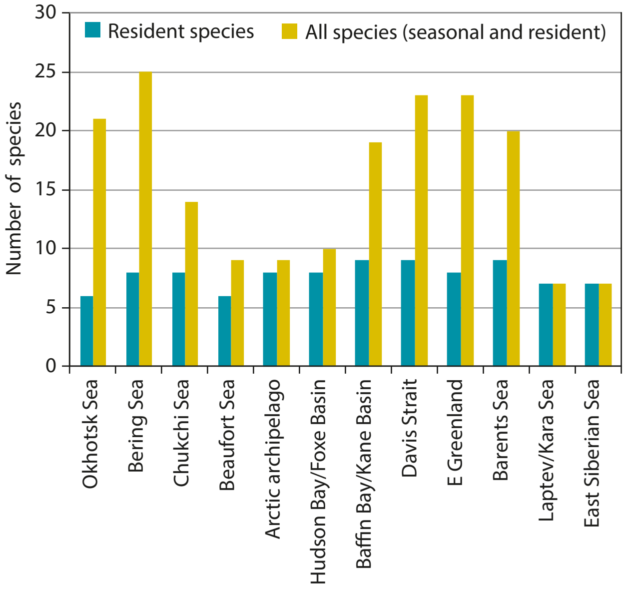


**Figure 3.2.** Number of marine mammal species in Arctic marine regions classified by resident species (n = 11 total) or all species (including seasonal visitors, n = 35 total).

tial number of low and high Arctic species. When all species of marine mammals that occur in low and high Arctic waters during some time of the year are considered (n = 35), species richness (total number of species) is highest in the Pacific low Arctic sectors (Sea of Okhotsk and Bering Sea, with 21 and 25 species, respectively) and in the Atlantic low Arctic (Davis Strait and E Greenland, each with 23 species) (Fig. 3.2). These areas are likely high in species richness because they are open to the large temperate ocean basins of the Pacific and Atlantic, from which many species seasonally migrate. When only resident Arctic marine mammals are considered (n = 11), species richness is lower and patterns are less variable. The highest species richness occurs in the Atlantic regions of Baffin Bay, Davis Strait and the Barents Sea (n = 9 species in each area). The lowest species richness occurs in the Sea of Okhotsk and the Beaufort Sea.

## 3.3. TERRESTRIAL HERBIVOROUS MAMMALS

Herbivores comprise the majority of Arctic terrestrial mammal species, and can be divided into three groups based on body size. The small-bodied voles, lemmings and pikas (24 species; 25-250 g) are relatively inconspicuous, but they are often the most numerous mammals in tundra ecosystems, providing food for most carnivores and playing a key role in energy flow through the ecosystem (Krebs *et al.* 2003, Legagneux *et al.* 2012).

Medium-bodied herbivores (nine species; 0.5-35 kg) include the hares and the larger rodents (ground squirrel, marmots, muskrat *Ondatra zibethicus* and American beaver *Castor canadensis*). These are generally found at lower densities than small mammals, but can be locally more abundant depending on habitat patchiness. By diversifying the food supply for carnivores, they can have a stabilizing role in tundra food webs (e.g. Reid *et al.* 1997).

Large-bodied herbivores (six species; 40-600 kg) include caribou/reindeer (one species with English names used interchangeably here), Eurasian elk *Alces alces*, moose *Alces americanus*, sheep *Ovis* spp. and muskox. Caribou and reindeer are essential food species for Arctic peoples (Hummel & Ray 2008), and, along with muskox, are widespread. Domesticated reindeer are mostly discussed by Huntington (Chapter 18).

### 3.3.1. Species richness and distribution

#### 3.3.1.1. Status

**Rodents**

Brown lemmings (*Lemmus* spp.) and collared lemmings (*Dicrostonyx* spp.) are the only small rodents with natural distributions in high Arctic regions. They are also found throughout the low Arctic, in conjunction with voles. In the Palearctic, there are four geographically separated species of brown lemmings: the Siberian brown lemming *L. sibiricus*, the Norway lemming *L. lemmus*, the Wrangel Island brown lemming, and also portions of the range of the Nearctic brown lemming *L. trimucronatus*. The Wrangel Island brown lemming is recognized by some as a unique species (Wilson & Reeder 2005) though others consider it a genetically distinct clade (Fedorov *et al.* 1999a, 2003). The Palearctic collared lemming is widespread. The Wrangel Island collared lemming *D. vinogradovii* is often considered a distinct species (Wilson & Reeder 2005), but genetic evidence indicates a close relationship with the Nearctic collared lemming (Fedorov & Goropashnaya 1999, Fedorov *et al.* 1999b).

The Nearctic brown lemming is the sole species of this genus in North America. However, the Nearctic is inhabited by four species of collared lemmings: the Nearctic collared lemming, Nelson's collared lemming *Dicrostonyx nelsoni*, Richardson's collared lemming *Dicrostonyx richardsoni* and the Ungava collared lemming.

Various boreal voles occupy portions of the low Arctic. In both old and new worlds we find the tundra vole *Microtus oeconomus* with robust tundra populations (Pitelka & Batzli 1993, Linzey *et al.* 2008), and the northern red-backed vole *Myodes rutilus*, just marginally into the tundra (Pitelka & Batzli 1993). Voles inhabiting only the Palearctic include Middendorff's vole *Microtus middendorffii* (Tsytsulina *et al.* 2008), the narrow-headed vole *M. gregalis* (Batsaikhan *et al.* 2008a) and the gray red-backed vole (grey-sided vole) *Myodes rufocanus* (Sheftel & Henttonen 2008). Some authors treat the North Siberian vole *Microtus hyperboreus* as a distinct species (Andreev *et al.* 2006), but Wilson & Reeder (2005) include it within *M. middendorffii*. In addition, the northern range extent of boreal birch mouse *Sicista betulina*, water vole *Arvicola amphibius* and mountain vole *Alticola lemminus* all slightly overlap southern Palearctic tundra (Andreev *et al.* 2006, Batsaikhan *et al.* 2008b, Meinig *et al.* 2008). There are fewer vole species limited to the Nearctic, and the two recognized species – singing vole and insular vole – may be one species (MacDonald & Cook 2009, Weksler *et al.* 2010). The long-tailed field mouse *Apodemus sylvaticus* was introduced to Iceland centuries ago and is now a habituated species even in the low Arctic (Schlitter *et al.* 2008).

The Arctic ground squirrel is the most widespread large rodent, found in both E Asia and North America (Linzey 2008). The Alaska marmot and the black-capped marmot *Marmota camtschatica* are found in specific mountain ranges (Brooks Range of Alaska, and Orulgan and Kolymskiy Ranges of Siberia, respectively), which are largely boreal but extend somewhat into the low Arctic (Tsytsulina 2008a, Gunderson *et al.* 2009).

The muskrat and American beaver are primarily boreal and native to North America, where their Arctic distributions are marginal and patchy and often associated with deltas of large rivers (e.g. Yukon and Mackenzie Rivers) (Baker & Hill 2003, Erb & Perry 2003). Muskrats have been introduced to various low Arctic regions of Eurasia (e.g. Yamalo-Nenetsky and Kolyma River) in the 20th century (Korytin *et al.* 1995, Andreev *et al.* 2006), and are now much more widespread (Lissovsky & Begletsov 2004).

### Pikas and hares

Three species of pikas have distributions extending into the low Arctic. Two are in Russia – the northern pika *Ochotona hyperborea* and the Turuchan pika *O. turuchanensis*. One is in North America – the collared pika *O. collaris* (Hoffmann & Smith 2005). The Turuchan pika has been considered a subspecies of northern pika (Smith *et al.* 1990, Sokolov *et al.* 1994). However, recent molecular analyses indicate the Turuchan pika is most closely related to the non-Arctic alpine pika *O. alpina*, with controversy remaining as to whether it merits full species status (Formozov *et al.* 2006, Lissovsky *et al.* 2007).

Four species of hare occur in the Arctic: snowshoe hare *Lepus americanus*, Arctic hare, Alaskan hare, and mountain hare *L. timidus*. The first three live in the Nearctic, whereas the mountain hare occurs across the Palearctic. The snowshoe hare is genetically distinct and primarily boreal. The Arctic, Alaskan and mountain hares are closely related; earlier treatments combined all three within one species, the mountain hare (Waltari *et al.* 2004, Hoffmann & Smith 2005, Waltari & Cook 2005). Genetic evidence suggests that the Alaskan and Arctic hares persisted separately in two North American refugia (Beringia and Canadian Arctic islands, respectively) during the last ice age, whereas current populations across the broad range of the mountain hare originated from multiple Eurasian refugia (Waltari & Cook 2005).

### Ungulates

Caribou or wild reindeer are classified by their behavior and ecology as ecotypes (Bergerud *et al.* 2008). In the Arctic we find two gregarious ecotypes: migratory tundra and Arctic island. Caribou and reindeer vary in the degree to which they are migratory and gregarious as their abundance changes. Gregarious behavior involves trade-offs between risks of predation and parasite infestation in relation to forage availability, which is the factor ultimately driving reproductive output (Bergerud *et al.* 2008, Hebblewhite & Merrill 2009, Gunn *et al.* 2011). The generally less gregarious populations of the Arctic island ecotype vary in their migratory behavior among years (Hansen *et al.* 2010), the causes of which are not fully understood.

Migratory tundra caribou and reindeer calve, summer and spend the fall on tundra ranges spread through the northern mainland of Eurasia and North America. Winter ranges for most herds extend into the sub-Arctic boreal forests (taiga), but some herds occasionally or usually winter on the tundra. The cows of any one herd migrate from their winter ranges to their calving grounds, which they tend to use repeatedly over many years.

In Russia, intensive reindeer husbandry, especially in western and far-eastern Siberia, has precluded wild reindeer from using the same ranges, and large wild reindeer populations are presently concentrated in central Siberia (Syroechkovskiy 2000, Klokov 2004). About 31 wild reindeer herds, of very variable population and range size, occupy Arctic tundra in Russia for at least part of the year, with the larger herds being Taymyr and Lena-Olenyok (Baskin & Miller 2007).

Semi-domesticated reindeer herds compete directly with wild reindeer for range. During the long history and wide geographic extent of semi-domesticated reindeer herding, during which semi-domesticated herds occupied ranges of wild herds, it is possible that some of the original wild herds have disappeared or inter-graded with semi-domesticated herds (Syroechkovskiy 2000, Baskin & Miller 2006).

In Alaska and Yukon, there are four wild caribou herds: Western Arctic, Teshekpuk, Central Arctic and Porcupine. East of the Mackenzie River, the Canadian mainland tundra is home to six large herds (Cape Bathurst, Bluenose West, Bluenose East, Bathurst, Beverly and Qamanirjuaq) that winter in the taiga forest. The Ahiak and Dolphin & Union herds, along with several smaller herds on the northeast mainland in Nunavut, spend all seasons on the tundra. The northern islands in Hudson Bay, and also Baffin Island, are occupied by migratory herds of tundra caribou. On one of these, Southampton Island, caribou were extirpated around 1953 and later re-introduced (Heard & Ouellet 1994). The Leaf River and George River herds occupy Ungava Peninsula.

In SW Greenland, the larger Akia-Maniitsoq and Kangerlussuaq-Sisimiut herds live year-round on tundra and undergo relatively short migrations. Five small populations also occur farther north on Greenland's west coast. A population in the Thule district of NW Greenland was apparently extirpated in the late 20th century, but the region has been recolonised by caribou from Ellesmere Island (Roby *et al.* 1984). Wild reindeer disappeared from E Greenland in the late 19th century (Vibe 1967) and have not recolonised the region. In Iceland, one of several introductions of reindeer from Norway in the 1700s has led to a robust wild population (Sigurdarson & Haugerud 2004).

Across the circumpolar high Arctic islands, caribou inhabit a more extreme environment than that faced by migratory tundra herds, and have adapted with proportionally shorter limbs, smaller bodies and paler pelage. Isolation on archipelagos has led to subspeciation, including the Novozemel'sk reindeer *R. t. pearsoni* on Novaya Zemlya archipelago, Svalbard's reindeer *R.t. platyrhynchus*, and Peary caribou *R.t. pearyi* on the Canadian Arctic islands. The crossing of sea ice between seasonal ranges is typical of Arctic island caribou (Miller 2003).

The muskox had a circumpolar distribution in the Pleistocene. Holocene climate changes, including warmer conditions than at present, along with heavy hunting may have contributed to its disappearance in the Palearctic and from Alaska and Yukon. The species currently occurs in most of the Canadian mainland tundra east of the Mackenzie River and west of Hudson Bay, and most of the well-vegetated tundra regions on the Canadian Arctic islands together with N and E Greenland (Gunn & Adamczewski 2003). In modern times, humans have reintroduced muskoxen to Alaska (Nunivak Island, Seward Peninsula, Cape Thompson, Nelson Island and the northeast). They were also successfully introduced to ranges unoccupied in the Holocene, in SW Greenland, Canada (Ungava Peninsula) and Norway, and to ranges in Russia (Taymyr Peninsula and Wrangel Island) that they may have occupied in the Holocene (Gunn & Adamczewski 2003).

The Eurasian elk is found in low Arctic wetlands and shrub-rich habitats from Norway through western Siberia (Henttonen *et al.* 2008). The moose occupies similar habitats in central and eastern Siberia and near the treeline of North America (Geist *et al.* 2008). Although considered here as two species (Wilson & Reeder 2005), differentiation at the species level may be tenuous (Hundertmark *et al.* 2002). Both have occurred in various low Arctic regions since the mid-20th century, using shrub tundra in summer and moving back to forest in winter (e.g. northern Norway (Fjellaksel 2010), Yamal (Korytin *et al.* 1995), eastern Siberia (Andreev *et al.* 2006) and N Yukon (Ruttan 1974)).

A subspecies of thinhorn sheep, Dall's sheep *Ovis dalli dalli*, and snow sheep *Ovis nivicola* are primarily found in northern boreal mountain ranges, but extend into the low Arctic in N Alaska and N Yukon, and in Chukotka and the Putorana Plateau of Siberia, respectively.

### 3.3.1.2. Trends

Arctic climates have changed sufficiently during the Holocene (last 10,000 years) that some landscapes which are currently tundra could have ranged from glacier to boreal forest cover, causing substantial shifts in species ranges. For example, low genetic diversity in most populations of Palearctic collared lemmings may be attributed to isolation of small populations on remnant tundra landscapes when the boreal forest expanded north during the warm period of the Holocene (Fedorov *et al.* 1999b). Palearctic brown lemming populations, by contrast, have generally high genetic diversity, indicating a relative lack of Holocene geographical separation, likely because their wet meadow habitats persisted through a warm period (Fedorov *et al.* 1999a, 2003, Ehrich & Stenseth 2001). On Franz Josef Land, a Russian archipelago, wild reindeer no longer occur, but radio-carbon dates from antlers indicate their presence when the climate was warmer (Forman *et al.* 2000).

We have few data regarding historical patterns or changes in mammal species distributions, because there have been few repeated inventories across this vast and relatively inaccessible region (Callaghan *et al.* 2005). For example, there is little information about distributions of pikas or hares. We know most about changes in species that are hunted or trapped, because these provide food and income and are the target of management actions.

Humans have driven the most dramatic recent changes in distributions by translocating species, sometimes to re-introduce them to previously occupied ranges and sometimes to introduce them in the hopes of economic returns. Muskoxen have spread out far from the numerous sites where they have been released, perhaps in search of new range as populations expanded (Reynolds 1998, Gunn & Adamczewski 2003). Reindeer on Svalbard have been released into areas where overharvest had occurred some 100 years previously (Hansen *et al.* 2010). Another example is the introduction of muskrats, formerly a Nearctic species, to numerous Palearctic locations (Erb & Perry 2003).

Various observers have witnessed changes in distribution, or inferred the changes through a series of observations. Yup'ik hunters and trappers report expansion of moose and American beaver distribution to the west in the shrub-rich habitats of the Yukon River delta in the past decade (Herman-Mercer *et al.* 2011). Eurasian elk and moose have expanded into new drainages and increased their use of upland tundra in various parts of Norway and Russia (Van Eerden 2000, Andreev *et al.* 2006, Lomanova 2007, Fjellaksel 2010). Similarly, there are more frequent sightings since the 1970s of moose in shrub-rich tundra regions north of treeline in the Northwest Territories and Nunavut (e.g. Thelon Game Sanctuary, Kazan River; NWT 2011). Russian researchers report that Siberian brown lemmings have almost disappeared over the past 20 years from the southern edge of their distribution on the southern Yamal Peninsula (Sokolov *et al.* in Reid *et al.* 2011a). Snowshoe hares have become well-established north of the Brooks Range in Alaska, occupying riparian shrub communities along several river drainages, and this expansion has coincided with a contraction of the range of Alaskan hares (D. Klein pers. com.). There may have been a general contraction of the southern boundary of the winter distribution for several caribou herds in the northern boreal forest since the 1800s and early 1900s, both in Canada and Russia (Banfield 1961, Syroechkovskiy 1995).

Animals do not occupy all parts of their general distribution every year. Some quite dramatic appearances and disappearances of species from fairly large Arctic landscapes do not represent a distribution change when viewed over a period of one or even many decades, because the animals often return to apparently abandoned ranges. Some species, such as the colonial Arctic ground squirrels, occupy sites intermittently in a meta-population process involving local extirpation and re-colonization. Caribou are particularly noted for shifting their seasonal ranges for periods of many years, with winter ranges shifting more frequently than calving and summer ranges (Syroechkovskiy 2000, Griffith *et al.* 2002, Schmelzer & Otto 2003, McNeill *et al.* 2005). When herds of migratory tundra caribou are at low abundance their large winter range tends to contract; as abundance increases, winter range expands (Bergerud *et al.* 2008). In the late 20th century some of the Porcupine caribou herd stayed on portions of the summer range in north Yukon through the subsequent winter (Kofinas *et al.* 2002). Inuit elders on southern Baffin Island report a process of winter range expansion, followed by range drift (expansion on one side and contraction on another), and ultimately a complete change in winter range to a new region, all coupled to long-term population increase in the caribou herd from the 1940s to 1980s, which they believe to be cyclic (Ferguson *et al.* 1998). Dolgan hunters of the Taymyr herd in Siberia report major shifts in the numbers of animals being accessible to hunt from the town of Dudinka (Sillanpää 2008). Such changes, often cyclic, span a period lasting about a human lifetime (Ferguson *et al.* 1998), making the interpretation of change in the relatively short-term context of recent memory and climate warming much more difficult.

Long term monitoring has revealed occasional changes in calving grounds. During 42 years of monitoring the Bathurst herd in Canada, the average annual overlap was 43%, forming two geographically consistent clusters (1966-1984 & 1996-2011) broken by a brief period at peak caribou densities, when the calving ground shifted (Gunn *et al.* 2012). The location of Alaskan calving grounds is relatively predictable although with variation in the degree of annual overlap (Kelleyhouse 2001, Griffith *et al.* 2002). In eastern Canada, the Leaf River calving ground has also shifted as herd abundance has changed (Taillon *et al.* 2012).

The seasonal and annual distributions of Arctic island ecotype caribou also change through time. The use by Peary caribou of some islands expands and contracts with abundance (Miller *et al.* 1977, Gunn & Dragon 2002). Some such changes are long-lived and appear permanent in recent memory, such as the near disappearance of Peary caribou from Prince of Wales and Somerset Islands between 1985 and 1990, even though about 6,000 migrated between the two islands in the 1970s and early 1980s (Gunn *et al.* 2006).

#### 3.3.1.3. Causes and prospects

Considering true Arctic herbivores, the lack of observed range expansion is probably best explained by the fact that these species already occupy most low and high Arctic regions, their expansion is blocked by insurmountable barriers, or their expansion may be limited by competition with closely related species. The Nearctic and Palearctic collared lemmings, Palearctic brown lemming and Arctic hare fit the first category. Oceanic, glacier and lowland habitats prevent the Arctic ground squirrel, the tundra vole, the Alaska marmot, and insular forms of lemmings and voles from any substantial expansion (Kerr & Packer 1998, Gilg *et al.* 2012). Richardson's and Nelson's collared lemmings would have to occupy habitats already occupied by Nearctic collared lemmings in any range expansion.

The remaining true Arctic herbivores could perhaps expand their distributions, and we mention these as hypotheses for future investigation. Alaskan hares could conceivably occupy the North Slope of Alaska and Yukon, a region they previously occupied (Klein 1995, MacDonald & Cook 2009). The Nearctic brown lemming might expand northwards across Lancaster Sound and Viscount Melville Channel to reach the northern Canadian Arctic Archipelago, though such a long distance ice crossing seems unlikely. By crossing substantial glaciers, caribou could recolonize E Greenland. Muskoxen could occupy substantial new ranges in Siberia and Alaska, mainly by expanding from regions of historical introduction. However, most true Arctic herbivores cannot readily expand their distributions, and we know of none that has done so in historical times without human assistance.

Low Arctic species with boreal affinities have greater opportunities for range expansion than the true Arctic herbivores, because low Arctic species are increasingly able to find suitable conditions for their survival as the southern tundra transforms to boreal shrubland and forest. In a time of changing climate and ecosystem conditions, factors that limit distributions are likely changing. Habitat changes are often the most noticeable. The most prominent of these are: an expansion of tree cover into the tundra (Hinzman *et al.* 2005), increases in primary production (Zhang *et al.* 2008), increases in cover of upright and prostrate woody shrubs (Tape *et al.* 2006, Forbes *et al.* 2009, Hudson & Henry 2009, Myers-Smith *et al.* 2011), increases in spatial extent of drier tundra plant communities (Hinzman *et al.* 2005), increases in cover of some graminoids and forbs (Kennedy *et al.* 2001, Walker *et al.* 2006) and decreases in moss and lichen cover (Cornelissen *et al.* 2001, Walker *et al.* 2006). However, these changes vary among sites, depending on local temperature and moisture regimes (Elmendorf *et al.* 2012). Herbivory, with associated nutrient additions, also alters the general patterns substantially (Gough *et al.* 2008, Post & Pedersen 2008, Ravolainen *et al.* 2011, Johnson *et al.* 2011) (see Ims & Ehrich, Chapter 12 for more detail).

> » *Willows, in Russian* ***talnik****, grow much faster now on the banks of Kolyma. As well in the summer pasture areas along the Arctic Ocean tundra willows are more plentiful and more now. On River Suharnaya the willow bushes are much bigger.*
>
> (Reindeer herders of the Chukchi community of Nutendli, reported in Mustonen 2009).

Most of the recorded changes in distribution have been in sub-Arctic species apparently responding to these habitat changes, especially the expansion and/or increased height of shrubs. More extensive and taller growth of willows *Salix* spp. increases the spatial extent and carrying capacity of habitats for species that feed heavily on these shrubs (e.g. moose, hares and beaver). By providing increased cover from predators, as a result of increased structure and increased trapping of snow, shrub expansion may also enhance habitat quality for some vole species. We may see new or continued expansions of the distributions of some boreal species such as the northern red-backed vole, snowshoe hare and perhaps American beaver into the expanding upright shrub communities, and the singing vole into the drying grass tundra. Much will depend on whether the resident Arctic species (such as brown lemmings and Arctic hares) are inferior competitors to the boreal species, and whether other limiting factors such as winter temperature regimes are also relaxed in a warming climate (e.g. the beaver, Jarema *et al.* 2009).

Most montane species such as Dall's sheep, snow sheep, black-capped marmot, Alaska marmot and northern pika currently range nearly to the northern limit of their mountainous habitats, so will not be able to expand appreciably. The collared pika may be an exception. Alpine tundra habitats exist in the Richardson and British Mountains well to the north of its present range limit, but we lack an understanding of what limits its northward colonization.

Distributions of many plants move slowly in response to warming, lagging behind the warmer conditions where they could potentially grow. Increased shrub growth alone will be insufficient to encourage substantive changes in animal distributions unless other necessary food and cover plants (e.g. berry-producing species, fungi, cone-bearing trees) are already present or have also expanded their distributions. For herbivores that depend specifically on certain slow-moving plants, distribution change may also have to lag behind. For example, moose and Eurasian elk mostly return to more sheltered forested valleys in the sub-Arctic for winter, and the extent of their summer movements onto tundra may become limited by the rate at which the treeline moves.

There are some herbivores, notably the graminoid-feeding voles, that inhabit both boreal and tundra biomes. Their distributions seem to be currently limited by the length of the snow-free growing season during which they need to produce sufficient litters for the population to survive the mortality of the subsequent winter (Ims & Fuglei 2005). The snow-free season on the tundra is definitely lengthening (Derksen & Brown 2012), which may increase the opportunities for voles to move north.

Herbivores can strongly influence the structure and composition of plant communities on which they feed (Post & Pedersen 2008, Ravolainen *et al.* 2011), and may have done so on a massive scale in the Pleistocene (Zimov *et al.* 1995). Such effects need more focused research as herbivore distributions continue to change.

The low Arctic zone, however, is narrow in some regions such as N Norway and N Yukon, and could effectively disappear as it transforms to boreal habitats. These are regions where some herbivores may disappear as their habitats change and key foods disappear, examples being the Norway lemming (Tast 1991) and Nearctic collared lemming. These are also regions where the distributions of some species, such as Arctic ground squirrel and barren-ground shrew, may shrink because they cannot cross ocean channels to reach islands further north (Kerr & Packer 1998, Gilg *et al.* 2012).

> » *Regarding the forest fires, some scientists say it's good for new growth. But do you know what the caribou eat? If the lichen burns, it will take over 100 years for the plants to grow back. Some scientists say these forest fires are good, but it's not like that for us. There never used to be so many forest fires.*
>
> (Dene member Pierre Marlowe, quoted in Parlee *et al.* 2005).

The range shifts and contractions, often seasonal, observed in wide-ranging species such as the migratory tundra caribou appear to result from changing food availability which itself is driven by a complex mix of population abundance, wild fires, weather conditions and, increasingly, human activities. At the timescale of decades, changes in abundance appear to play a strong role, especially in the contraction and relocation of winter ranges. Terrestrial lichens are key winter foods, especially for the migratory tundra ecotype. These grow slowly so can be locally overgrazed forcing high-density caribou herds to relocate winter ranges (Kofinas *et al.* 2002, Miller 2003). The locations and extent of boreal forest fires correlate well with shifts in caribou winter ranges (Schmelzer & Otto 2003). Shrinking winter ranges will likely become food limiting for some herds, if fire frequency and average fire size increase as predicted by climate models (Miller 2003, Zinck *et al.* 2011) and as happens when more people occupy the land and access improves (Sillanpää 2008). This food limitation, and associated density dependent effects on fecundity and recruitment, is likely key to understanding the long-term dynamics of range use and population abundance (Messier *et al.* 1988, Ferguson 1996, Miller 2003).

Populations of high Arctic caribou (and probably other herbivores) occupying the more isolated island groups (e.g. Svalbard, Novaya Zemlya), are the ones most at risk of long-term range loss. Ongoing fluctuations in their inherently small population sizes, coupled with virtually no possibility of natural recolonization and no chance of emigration, increase the risk of extirpation. In the Canadian Arctic Archipelago, interlinked with winter ice, disappearance from one island may not represent extirpation, but simply emigration, though perhaps for a prolonged time.

Tracking the location and intensity of use of calving grounds is crucial for caribou conservation given that: (1) there is controversy over their locations over time, (2) barren cows frequently do not visit the calving grounds, and (3) cow-calf ratios on calving grounds have often been used as a measure of recruitment (Ruttan 2012). However, gaps in monitoring leave uncertainties which cloud our understanding (Gunn *et al.* 2011). For example, in central mainland Canada, the Beverly herd's use of its traditional calving ground markedly declined between 1994 and 2010, perhaps reflecting a decline in herd size (Gunn *et al.* 2011) or an earlier, undocumented, shift to a more coastal calving ground (Nagy *et al.* 2011). We need to better understand how and why caribou shift calving grounds, and it is insightful that timing of snow melt correlates well with such shifts (Griffith *et al.* 2002, McNeill *et al.* 2005).

Human infrastructure and activities, including mineral exploration and development, roads and new settlements, are increasing rapidly on many caribou ranges, and caribou avoid many of these developments (Baskin 2005, Johnson *et al.* 2005, Joly *et al.* 2006). Caribou body condition and herd health need to be monitored to assess ongoing cumulative effects, and calving grounds should be protected from human activity to minimize any risk of reducing calf survival by interfering with suckling behavior (Hummel & Ray 2008).

> » *Elders of the Kolymskaya village, lower Kolyma region, Sakha-Yakutia, Russia, reported in 2006 that willows are moving to tundra and to river banks. They said: "It tells of the changes which are under way. You should graze cows and horses, not reindeer on these spots. All of the tundra is covered with willows and bushes. It grows very fast now. We do not know how we can herd reindeer in the middle of these changes."*
>
> (Mustonen 2007).

Some true Arctic species are likely to lose some of their low Arctic distributions as these tundras change. Low Arctic ranges for reindeer and caribou will contract with the spread of erect shrub tundra. Continental collared lemming distributions may shrink because the dwarf shrub tundras they rely on are at risk of changing to erect shrub tundra or upland graminoid tundra (e.g. Kennedy *et al.* 2001, Myers-Smith *et al.* 2011), and they are poor competitors with at least some other rodents (Ale *et al.* 2011; see also Box 17.5 in Coole, Chapter 17). Where boreal herbivores are expanding their range into low Arctic tundras, they may provide a more abundant and diverse prey base for wide-ranging predators such as red fox and gray wolf. For example, the disappearance of Alaska hares from some regions may be related to the risk of sharing predators with expanding snowshoe hare populations, especially when snowshoe hare abundance drops (Klein 1995).

## 3.3.2. Population sizes and densities

### 3.3.2.1. Status

None of the Arctic terrestrial herbivores is classified as globally Threatened (i.e. Endangered or Vulnerable; IUCN 2011), though some are of conservation concern within regional jurisdictions. The two lemming species limited to Wrangel Island are listed as Data Deficient, meaning that we have insufficient information about likely population size and trend to confirm a listing (IUCN 2001). All other herbivores are listed as Least Concern, meaning they are sufficiently widespread, abundant and stable that current threats do not warrant a Threatened classification. This generally encouraging conservation status of Arctic herbivores reflects the large distributions of most species, often encompassing portions of other biomes, and the relatively low levels of human development and activity in these regions. The latter historical fact is changing quickly, however, catalyzed by climate change.

Arctic herbivore populations often exhibit dramatic population fluctuations through time, independent of human actions. These fluctuations appear cyclic with amplitude of one or two orders of magnitude, and a period of 3-6 years in lemmings, and 40-60 years in caribou (Stenseth & Ims 1993, Gunn 2003, Miller 2003, Bergerud *et al.* 2008).

The variability in period and amplitude of lemming cycles within and among sites indicates that a number of ecological factors influence the pattern. Trophic interactions play a dominant role in driving cyclic dynamics (Ims & Fuglei 2005, Legagneux *et al.* 2012), but the phenomenon requires further investigation (Krebs 2011). In some Nearctic regions (notably the north slope of Alaska's Brooks Range, N Yukon, and parts of the Northwest Territories east of Mackenzie River), lemmings remain at fairly low densities (Batzli & Jung 1980, Pitelka & Batzli 1993, Krebs *et al.* 1995, 2002). In regions where they irrupt cyclically, sympatric lemming and vole species tend to fluctuate synchronously, but not all Arctic regions fluctuate synchronously (Erlinge *et al.* 1999, Krebs *et al.* 2002).

We generally lack abundance estimates for ground squirrels and marmots in Arctic habitats. Similarly, we lack good estimates of population abundance for Arctic pikas. All species are talus-dwelling, and such pika species tend to be long-lived, persist at low densities and have a low reproductive rate (Smith 1988, Smith *et al.* 1990). The northern pika is different in two ways: it may, occasionally, be found at higher density and it may substitute banks of fallen trees or accumulations of driftwood for talus (Smith *et al.* 1990, Sokolov *et al.* 1994).

The population abundance of northern hares is also poorly documented. Hare populations fluctuate widely, the apparent cycles having different periods in different localities (Flux & Angermann 1990, Sokolov *et al.* 1994, Murray 2003). For example, the mountain hare may have

**Table 3.1.** Summary of historical population estimates for 22 circumpolar caribou and wild reindeer herds. Data courtesy of Circum-Arctic Rangifer Monitoring Assessment Network (CARMA) and D.E. Russell & A. Gunn; www.carmanetwork.com/display/public/home. Data vary substantially among herds and over time in accuracy and precision, and represent only general patterns of abundance.

| Year | Western Arctic | Teshekpuk | Central Arctic | Porcupine | Cape Bathurst | Bluenose West | Bluenose East | Bathurst | Dolphin Union | Ahiak | Beverly | Qamanirjuaq | Southampton | George River | Leaf River | Akia-Maniitsoq | Kangerlussuaq-Sisimiut | Taymyr | Lena-Olenyk | Yana Indigurka | Sundrun | Chukotka |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1974 | | | | | | 92,000 | | 251,000 | | | 180,000 | 50,000 | | | | | | | | | | 3,750 |
| 1975 | | | | | | | | | | | | | | 205,000 | 56,000 | | | 449,000 | 49,500 | 109,000 | 21,500 | |
| 1976 | 75,000 | | | | | | | | | | | 44,000 | | 263,000 | | | | | | | | |
| 1977 | | | | 105,000 | | 42,000 | | 160,000 | | | | 44,000 | | | | | | | | | | |
| 1978 | 107,000 | 4,000 | 5,000 | | | 27,000 | | 127,000 | | | 130,000 | | 1,181 | | | | | 475,000 | 52,600 | 86,600 | 27,600 | |
| 1979 | | | | 110,000 | | 35,000 | | | | | | | | | | | | 470,000 | | | | |
| 1980 | 138,000 | | | | | 65,000 | | 140,000 | 3,424 | | 110,000 | | | 390,000 | | | | 485,000 | | | | |
| 1981 | | | 9,000 | | | 46,000 | | | | | | | | | | | | 510,000 | 61,000 | | | |
| 1982 | 172,000 | | | 137,000 | | | | 174,000 | | | 164,338 | | | 360,000 | | | | 525,000 | | 113,000 | 27,000 | |
| 1983 | | | 13,000 | 135,000 | | 65,000 | | | | | | 229,932 | | | 101,000 | | | 540,000 | | | | |
| 1984 | | 11,822 | | | | | | 384,000 | | | 263,691 | | | 586,000 | | | | 575,000 | | | | |
| 1985 | | | | | | | | | | | | 272,032 | | | | | | 590,000 | | 121,000 | | |
| 1986 | 229,000 | | | | 13,476 | 88,369 | | 472,000 | | 30,000 | | | | | 121,000 | | | 595,000 | | | | 32,200 |
| 1987 | | | | 165,000 | 12,517 | 106,887 | | | | | | | 4,033 | | | | | | | 130,400 | 29,100 | |
| 1988 | 343,000 | | | | | | | | | | 189,561 | 220,999 | | | | | | 570,000 | 73,000 | | | |
| 1989 | | 16,686 | | 178,000 | | | | | | | | | | | | | | | | 115,900 | | |
| 1990 | 416,000 | | | | | | | 351,683 | | | | | 9,319 | | | | | 625,000 | 80,900 | | | |
| 1991 | | | | | | | | | | | | | 13,676 | | 276,000 | | | | | 101,400 | | |
| 1992 | | | 23,000 | 160,000 | 19,278 | 112,360 | 15,544 | | | | | | | | | | | | | | | |
| 1993 | 450,000 | 27,686 | | | | | | | | | 87,728 | | | 780,000 | | | | 670,000 | | 85,200 | 39,900 | |
| 1994 | | | | 152,000 | | | | | | | 276,000 | 496,000 | | | | | | | 77,800 | | | |
| 1995 | | 25,076 | 18,000 | | | | | | | | | | | | | | | | | | | |
| 1996 | 463,000 | | | | | | | 349,046 | | 200,000 | | | | | | | | | | | 34,000 | |
| 1997 | | | 20,000 | | | | | | 38,000 | | | | 30,381 | | | | | | | | | |
| 1998 | | | | 129,000 | | | | | | | | | | | | | | | | | | |
| 1999 | | 28,627 | | | | | | | | | | | | | | | | | | | | |
| 2000 | | | 27,000 | | 11,089 | 76,376 | 119,584 | | | | | | | | | | | 1,000,000 | | 42,100 | 29,500 | |
| 2001 | | | | 123,000 | | | | | | | | | | 385,000 | 628,000 | 46,000 | 52,000 | | 90,000 | | | |
| 2002 | | 45,166 | 31,800 | | | | | | | | | | | | | | | | | 34,000 | 28,500 | 125,000 |
| 2003 | 490,000 | | | | | | | 186,005 | | | | | 17,981 | | | | | | | | | |
| 2004 | | | | | | | | | | | | | | | | | | | | | | |
| 2005 | | | | | 2,434 | 20,801 | 70,081 | | | | | | 20,582 | | | 36,000 | 90,500 | | | | | |
| 2006 | | | | | 1,821 | 18,050 | 66,754 | 128,047 | | | | | | | | | | | | | | |
| 2007 | 377,000 | | | | | | | | 27,000 | | | | 15,452 | | | | | | | | | |
| 2008 | | 64,107 | 66,772 | | | | | | | | 5,000 | 345,000 | | | | | | | 80,000 | | | |
| 2009 | 348,000 | | | | 1,934 | 17,897 | | 31,900 | | | | | | | | | | 700,000 | 95,000 | | | |
| 2010 | | | | 169,000 | | | 98,600 | | | | | | | 74,131 | | 31,000 | 98,300 | | | | | 70,000 |

a four-year cycle in Fennoscandia and at least a 10-year cycle in Russia (Flux & Angermann 1990, Prokopjev & Sedalischev 2009), and the Alaska hare a 10-year cycle (Buckley 1954). In the boreal forest of North America, the snowshoe hare cycles with period of 8-11 years (Keith 1981, Murray 2003), but its dynamics in shrub tundra have not been studied. In Sakha-Yakutia, prominent cycles in mountain hares in the mid-20th century have decreased markedly in amplitude, staying at lower densities in recent decades (Prokopjev & Sedalischev 2009). The Arctic hare may move about in large groups of 250-300, while vast areas may have no hares at all (Flux & Angermann 1990). Of these four species, the Alaska hare seems to be the rarest and least likely to reach high densities; it is also the least well-known species.

Caribou abundance is typically assessed at the scale of the herd. Herds are conventionally defined based on the repeated return of cows to the same calving grounds annually. Highs and lows in historical abundance since the 1800s have been reconstructed from the frequency of hoof scars on spruce roots, but only for the Bathurst and George River Herds despite the value of the technique (Morneau & Payette 2000, Zalatan *et al.* 2006). Herd size is often estimated from photographs of calving or summer aggregations. While herd size is fairly often tracked, biologists less frequently monitor rates of birth, recruitment and death, or indices of animal health. Progress needs to be made in relating these indicators to herd size to understand the mechanisms underlying changes in abundance (Boulanger *et al.* 2011).

Caribou herds can vary at least ten-fold through their population cycles. All herds do not fluctuate synchronously, but there can be a strong degree of synchrony among adjacent herds in large regions (e.g. Canadian mainland). The circumpolar caribou population has changed five-fold in historical times with a maximum of about 5.5 million. Currently, the surveyed herds total about 3 million (Tab. 3.1).

Muskox populations can also fluctuate dramatically over time, and appear limited mostly by forage availability as mediated by weather events such as icing and deep hard snow, with predation by gray wolf and brown bear being prominent and increasing in some populations (Reynolds *et al.* 2002, Gunn & Adamczewski 2003, Gunn & Forchhammer 2008, Nagy & Gunn 2009). Most muskoxen reside in Canada (c. 121,000 in 2008). On Greenland there are 9,500-12,500, and re-introduced populations in Alaska total about 3,700 (Gunn & Forchhammer 2008). A general estimate for Russia is 10,000 (Gruzdev 2011).

Sheep populations fluctuate in response to a variety of limiting factors such as winter severity, predation pressure, diseases and parasites. Their ability to access forage in winter is critical, and deep or crusted snow can reduce winter survival and subsequent reproductive output (Krausman & Bowyer 2003).

#### 3.3.2.2. Trends

**Rodents**

Researchers have monitored Arctic lemming and vole population abundance at a variety of low and high Arctic sites (Tab. 3.2). Variability in amplitude of cycles is likely normal, so trends are inherently difficult to demonstrate. There are no consistent trends across all sites, and many time series are too short to derive clear trends. However, some fairly dramatic changes have occurred, especially during the period of recent Arctic climate warming since the early 1970s. Some prominent cyclic patterns have partly collapsed, with a much reduced amplitude and changed periodicity (Traill Island and Zackenberg, Greenland). A prominent cyclic pattern had declined but has recently recovered (north Norway). Some features of the cyclic pattern have changed: lengthening period between outbreaks (Lena River, Wrangel Island, Banks Island) and a less prominent decline phase (Banks Island). Further details are provided in Box 3.1.

**Pikas and hares**

We generally lack quantitative data to assess trend in Arctic pika and hare populations. Reductions of mountain hare populations in Sakha-Yakutia, Russia, are attributed to heavy harvesting by humans (Prokopjev & Sedalischev 2009). General observations indicate that snowshoe hares have increased in abundance north of the Brooks Range and in the Yukon River delta of Alaska, and there may have been a coincident decline in Alaska hares in the Yukon River delta (D. Klein pers. com.).

**Ungulates**

Trends in wild reindeer and caribou numbers must be assessed in the context of natural cycles or fluctuations and the inherent difficulties of counting large numbers of animals over vast areas. In northern Canada, indigenous elders recount stories and recall their own experiences of abundance and scarcity over periods of centuries (Ferguson *et al.* 1998, Legat *et al.* 2002). Methods for estimating population size have only become relatively standardized and rigorous in the past 30 or fewer years (Baskin 2005, Cuyler 2006, Russell & Gunn 2012). Many estimates, especially earlier than the 1980s, may be inaccurate, and gaining sufficient precision remains an issue even with current techniques.

In recent decades, the large majority of migratory tundra caribou herds had been declining at annual rates of 5-17% (Vors & Boyce 2009, Boulanger *et al.* 2011). Between 2000 and 2009, of the 22 migratory tundra herds with fairly substantial monitoring data, 17 herds declined, one was stable and four had increased (Tab. 3.1, some details in Box 3.2). Recent surveys indicate that some herds are now progressing to new phases of a population cycle, somewhat reversing the more general pattern of declines. Considering the herds in Tab. 3.1, 11 are now declining, four are stable, six are increasing and one is not reported by Russell & Gunn (2012).

**Table 3.2.** Summary of major features of small rodent population dynamics at circumpolar monitoring sites with rodent focus. In addition, reports of relative abundance of small rodents in association with breeding bird studies from approximately the last 15 years can be found at the Arctic Birds Breeding Conditions Survey: www.arcticbirds.net

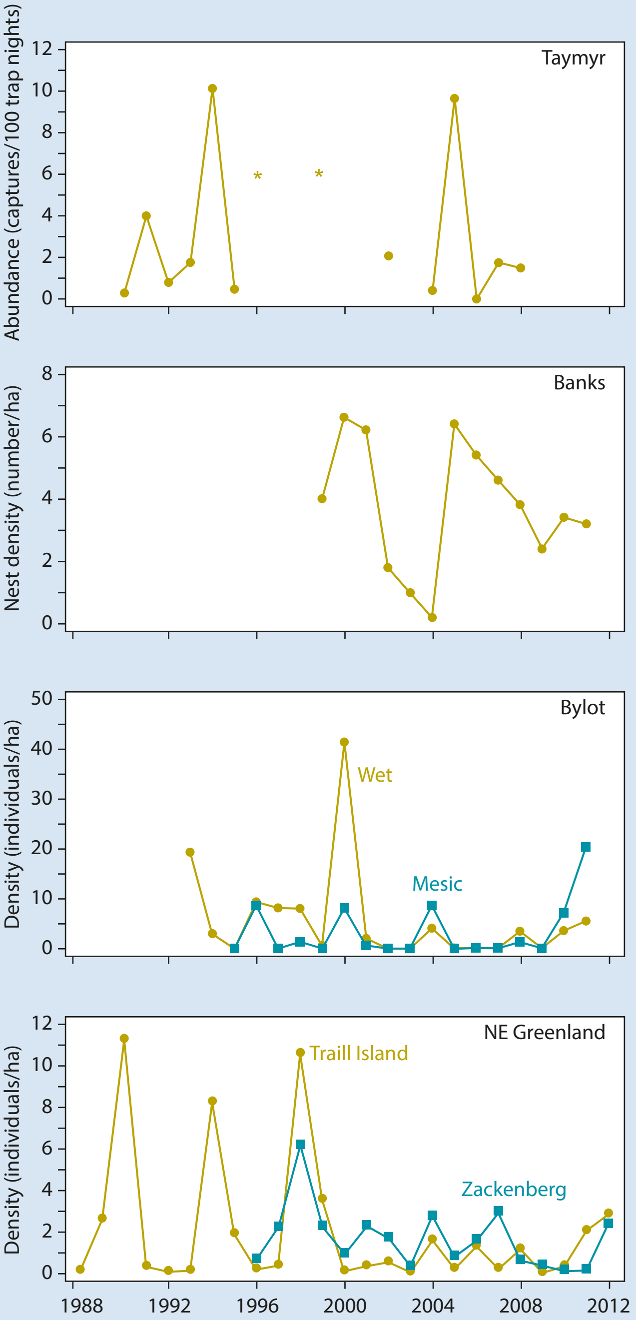
| Site | Species | Features of population dynamics | | Reference |
|---|---|---|---|---|
| Northern Norway | Norway lemming | 1987-2006: | Long period of low abundance with rare outbreak in 1988 | Ims *et al.* 2011,<br>Ims & Yoccoz unpubl. |
| | | 2007-2011: | Moderate outbreaks every 4 years | |
| | Tundra & gray red-sided vole | 1987-2011: | Outbreaks every 5 years with moderate amplitude | |
| Nenetskaya Gryada, Russia | Tundra vole & Palearctic collared lemming | 2004-2010: | Outbreaks in 2004 & 2008 (4 yrs) with low amplitude | Ehrich *et al.* in Reid *et al.* 2011a |
| Southern Yamal Peninsula, Russia | Middendorff & narrow-headed voles; Siberian brown & Palearctic collared lemmings | 1999 -present: | Outbreaks in 1999, 2002, 2005 and 2010 (3 to 5 yr period), and low to moderate amplitude | Sokolov 2002, Sokolov in Reid *et al.* 2011a |
| Taymyr Peninsula, Russia | Siberian brown lemming | 1960-2001: | Outbreaks every 3 to 4 years; lower amplitude in 1990s | Kokorev & Kuksov 2002 |
| | | 1993-2011: | Fluctuations with more variable amplitude since 1990s; outbreaks in 2005 and 2008 | Ebbinge & Masurov 2005, Popov 2009 |
| Lena River Delta, Russia | Siberian brown lemming | 1951-1967: | Outbreaks every 2 to 4 years | Pozdnyakov 2004 and unpubl. data. |
| | | 1980-2011: | Outbreaks every 3 to 5 years and longer period between recent outbreaks | |
| Kolyma River lowlands, Russia | Siberian brown lemming & Palearctic collared lemming | 1980-1984 & 1991-1996: | Synchronous outbreaks every 2 to 4 years | Chernyavsky 2002 |
| Chaunskaya lowland, Russia | Siberian brown lemming & Palearctic collared lemming | 1969-1989: | Synchronous outbreaks every 2 to 4 years | Chernyavsky 2002 |
| Wrangel Island, Russia | Wrangel Island brown lemming & Wrangel Island collared lemming | 1970-2011: | Synchronous, low amplitude, outbreaks with period lengthening from 4-5 years in 1970s to 7 to 8 years in 1990s and 2000s | Chernyavsky & Tkachev 1982,<br>Menyushina *et al.* 2012 |
| Point Barrow, Alaska, USA | Nearctic brown lemming & Nearctic collared lemming | 1955-1973: | Synchronous outbreaks every 4 to 6 years | Pitelka & Batzli 1993 |
| North slope, Yukon, Canada | Nearctic brown lemming & tundra vole | 1989-1998: | No outbreaks. Persistent low densities | Krebs *et al.* 2002, 2011 |
| | | 2006-2010: | No outbreaks. Persistent low densities | |
| Banks Island, Northwest Territories, Canada | Nearctic brown lemming & Nearctic collared lemming | 1993-1996: | Outbreaks separated by 3 years, with different peak densities | Larter 1998 |
| | | 1999-2011: | Low amplitude outbreaks every 4 to 5 years. Less pronounced decline phase recently | Parks Canada 2009,<br>Parks Canada unpubl. data |
| Pearce Point, Northwest Territories, Canada | Nearctic collared lemming & tundra vole | 1987-1992: | No outbreaks. Persistent low densities | Krebs *et al.* 1995,<br>Reid *et al.* 1995 |
| Kent Peninsula region (Hope Bay and Walker Bay), Nunavut, Canada | Nearctic brown lemming, Nearctic collared lemming, Tundra vole & northern red-backed vole | 1984-2000: | Synchronous outbreaks every 4 to 5 years | Krebs *et al.* 2002 |
| Devon Island, Nunavut, Canada | Nearctic collared lemming | 1967-1973: | Outbreaks every 2 or 4 years | Fuller *et al.* 1975 |
| Bylot Island, Nunavut, Canada | Nearctic brown lemming & Nearctic collared lemming | 1994-2011: | Variable amplitude outbreaks every 3 to 4 years. Synchrony variable. | Gruyer *et al.* 2008, G. Gauthier unpubl. data |
| Traill Island, NE Greenland | Nearctic collared lemming | 1988-2000: | High amplitude outbreaks every 4 years | Sittler 1995,<br>Gilg *et al.* 2003,<br>Sittler unpubl. data |
| | | 2000-2011: | Low amplitude fluctuations, higher every 2 to 3 years | |
| Zackenberg, NE Greenland | Nearctic collared lemming | 1996-2000: | High amplitude outbreak in phase with Traill Island | Schmidt *et al.* 2008,<br>Schmidt unpubl. data |
| | | 2000-2007: | Lower amplitude outbreaks every 3 years | |
| | | 2007-2011: | No outbreaks. Persistent low densities | |

## Box 3.1. Lemming abundance trends

Lemming abundance is monitored at Arctic sites using density of winter nests, mark-recapture live trapping, or snap trapping. On the Taymyr Peninsula of Russia, Siberian brown lemming cycled with outbreaks every 3-4 years from the 1960s to 1990s (Kokorev & Kuksov 2002), and now appear to have a more variable period (Box 3.1 Fig. 1) (Ebbinge & Mazurov 2005, Popov 2009). Collared lemmings are less numerous but fluctuate in synchrony. On Wrangel Island, NE Russia, the period between years with peak densities has increased from five years in the 1970s to close to eight years in the 1990s and 2000s, perhaps because snow conditions conducive to winter reproduction are being interrupted more frequently with winter thaws and icing of the ground and snowpack (Menyushina *et al.* 2012).

On southern Banks Island, in the western Canadian Arctic Archipelago, outbreaks of Nearctic collared lemmings and Nearctic brown lemmings occurred every 3-4 years in the 1960s and 1990s (Maher 1967, Larter 1998). Further north on the Island, the cyclic period seems to have increased to five years since the late 1990s (Box 3.1 Fig. 1; Parks Canada 2009 and unpubl. data). On Bylot Island, in the eastern Canadian Arctic Archipelago, Nearctic collared lemmings and Nearctic brown lemmings fluctuate fairly synchronously, with much lower amplitude in the collared lemmings. The brown lemmings exhibit outbreaks with highly variable amplitude, every 3-4 years, in two different habitats (Box 3.1 Fig. 1; Gruyer *et al.* 2008, G. Gauthier unpubl.). However, there is no evidence of substantive shifts in the general pattern during the past two decades, and no trend towards poorer quality winter snow conditions (Bilodeau *et al.* 2012).

Only the Nearctic collared lemming is found on Greenland, and its abundance is tracked using winter nest counts at Traill Island (c. 72° N) and Zackenberg (c. 74° N), both in high Arctic NE Greenland. Until 2000, lemming dynamics on Traill Island were characterized by regular cycles of approximately four years (Box 3.1 Fig. 1; Gilg *et al.* 2003). Given the high degree of correlation in abundance between the two localities (Schmidt *et al.* 2008), the dynamics at Zackenberg were most likely similar to those on Traill Island prior to 1996. Around 2000, the population dynamics changed simultaneously at both localities, and regular cycles were replaced by irregular, lower amplitude fluctuations at low densities, especially at Traill Island (Box 3.1 Fig. 1). The observed decrease in amplitude of population fluctuations corresponds well with population dynamics modelled in climate change scenarios with longer snow-free periods (earlier melt and later onset) and more thaw-freeze events in winter (Gilg *et al.* 2009).



**Box 3.1 Figure 1.** Temporal changes in lemming abundance at various circumpolar sites: A) Taymyr Peninsula, Russia (Siberian brown lemming, stars are years with unquantified high densities; data courtesy of B. Ebbinge & I. Popov); B) Banks Island, Canada (Nearctic collared lemming and Nearctic brown lemming; data courtesy of Parks Canada and L. Nguyen); C) Bylot Island, Canada (Nearctic brown lemming in wet and mesic habitats; data courtesy G. Gauthier); D) NE Greenland (Nearctic collared lemming at Traill Island and Zackenberg; data courtesy of B. Sittler and N.M. Schmidt).

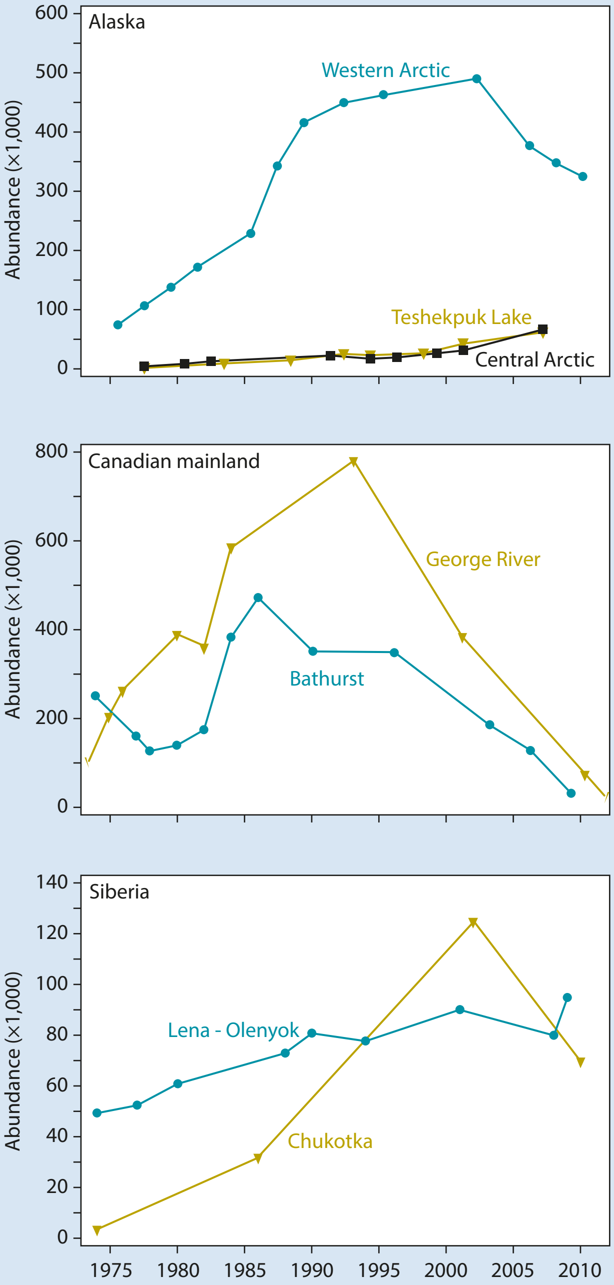
## Box 3.2. Migratory tundra caribou trends

Trends in certain migratory tundra herds illustrate key features of caribou dynamics. Herds fluctuate with wide amplitude over periods of many decades, with a tendency towards synchrony in neighboring herds, but lack of global synchrony. Declines can be associated with reduced food availability on limiting ranges (e.g. reduced availability of winter lichen food after forest fires, icing events and competition with domesticated reindeer), high adult female mortality (not necessarily associated with predation or hunting), and reduced parturition rates. Increases can be associated with improved food availability (including reduced competition with domesticated reindeer) and tight controls on hunting of females.

In Alaska, the Western Arctic herd declined from 1970 to 1976, but, similar to the Canadian herds, increased during the 1980s and 1990s, and reached a peak of 490,000 in 2003 (Box 3.2 Fig. 1). The herd then declined somewhat with high adult female mortality (22-30%) and autumn icing in one year. Herd-wide mortality had increased since the 1980s, averaging 17% (Dau 2009). Harvest levels are quite heavily regulated in Alaska, and the decline of the Western Arctic herd is unlikely to have resulted from hunting and predation mortality alone, and is more likely a result of food limitation. In contrast, both the Teshekpuk and Central Arctic herds have shown a protracted increase since the 1970s. During the Teshekpuk Lake increase, recruitment has been in slow decline but adult survival fairly constant (Parrett 2009). The Central Arctic herd is managed to minimize the effects of the Prudhoe Bay oilfield on its calving and post-calving ranges. The herd has low mortality (1997-2007, 10.5%), with human harvest restricted to < 3%, and also high productivity (Lenart 2009).

The migratory tundra herds in mainland Canada, both west and east of Hudson Bay, have experienced dramatic recent fluctuations in fairly close synchrony. The prolonged decline of the Bathurst herd (Box 3.2 Fig. 1) may reflect delays in implementing harvest restrictions because of controversy over the cause of the decline (Wek'èezhii Renewable Resources Board 2010). East of Hudson Bay, the George River (Box 3.2 Fig. 1) and Leaf River herds have also increased and then declined dramatically over a period of about 40 years. Messier *et al.* (1988) provide evidence that the cyclic dynamic of the George River herd is driven by delayed density dependent food limitation at high abundances.

In Siberia, wild reindeer herds increased synchronously from the 1970s to approximately 2000 (Tab. 3.1, Box 3.2 Fig. 1). Population trends for Chukotka wild reindeer were inversely related to domesticated reindeer abundance, suggesting that competition for forage among herds may affect abundance. Wild reindeer were abundant in the 1890s but then declined, with only a few thousand surviving by the 1970s in small areas not used for reindeer herding (Syroechkovskiy 1995, Klokov 2004). The domestic reindeer industry collapsed from 587,000 in 1971 to about 92,000 by 2001 (Klokov 2004). Coincident with that decline, the wild reindeer recovered to 32,200 individuals by 1986 and 120,000-130,000 in 2002 (Box 3.2 Fig. 1).



**Box 3.2 Figure 1.** Recent time series abundance estimates (figures in thousands of animals) for some migratory tundra caribou and wild reindeer herds (data courtesy of CircumArctic Rangifer Monitoring and Assessment Network (CARMA), and Russell & Gunn 2012).

In Alaska and Yukon, all four migratory tundra caribou herds have been abundant in recent decades. The Porcupine herd has reversed a decline, and the Western Arctic herd is now declining (see Box 3.2). In mainland Canada, caribou numbers were low from the 1950s to the 1970s, when larger herds began to increase to peak sizes in the mid-1980s to late 1990s (Gunn *et al.* 2011). All these herds then declined (e.g. Bathurst herd, Box 3.2), often to historical minimums, though some may now be stable or increasing at low densities. In Ungava Peninsula, the George River and Leaf River herds have experienced dramatic fluctuations (Box 3.2) (Couturier *et al.* 2004).

The status of the 7-10 smaller herds on the northeast mainland, Baffin Island and smaller islands in Hudson Bay is currently unknown, as their abundance is rarely monitored. The exception is Southampton Island, where following the reintroduction in 1967, the herd grew to peak population in the 1990s, and has since declined to about 7,800 (Heard & Ouellet 1994, Russell & Gunn 2012).

W Greenland has a long history of cyclic fluctuations, with high numbers lasting 10-25 years and periods of low numbers of 35-70 years (Meldgaard 1986). Total abundance was about 100,000 in 1970, declining substantially but to uncertain levels by the late 1970s, and recovering to about 140,000 in 2001 (Cuyler 2006, Cuyler *et al.* 2007).

In Russia, wild reindeer have also been through declines and increases, most often in opposite trend to domesticated reindeer herds in the same regions, and sometimes strongly influenced by commercial hunting (Syroechkovskiy 2000, Baskin 2005) (Box 3.2). In 1999, wild reindeer were estimated at 1.3 million compared with the estimated 1.5 million domesticated reindeer, and an estimated carrying capacity for the entire range of about 5 million (Syroechkovskiy 2000). On the Yamal Peninsula, wild reindeer declined during the extensive development of the domesticated reindeer industry in the mid-20th century (Syroechkovskiy 1995), but have recently rebounded (Klokov 2004). The Taymyr herd, one of the largest in the world, increased in the mid-20th century, until commercial hunting held the herd at about 600,000. Following removal of subsidies to commercial hunters in the 1990s, the herd grew rapidly (Kolpashchikov *et al.* 2003), but is now assumed to be declining (Klokov 2004). In Sakha-Yakutia (central Siberia) wild reindeer recovered from the 1950s to 1980s, coincident with a steep decline in domesticated reindeer numbers, but then declined with illegal hunting being partly to blame (Klokov 2004). In Chukotka, wild reindeer numbers have also fluctuated in the opposite trend to numbers of domesticated reindeer (Syroechkovskiy 2000). Numerous small wild reindeer herds remain at low numbers and require particular protection from the risk of overharvest (Syroechkovskiy 2000).

Considering Arctic island caribou, recent trends show Palearctic herds increasing while Nearctic herds mostly declined. On Svalbard, a decline was reversed when hunting was stopped in 1928. Numbers have since increased, with setbacks when icing restricted access to forage. Novozemel'sk reindeer declined in the early 20th century, but hunting was banned in 1934, and numbers recovered, despite setbacks from icing. Across the larger land mass of the Canadian Arctic islands, Peary caribou have declined dramatically in the last 50 years, largely because of severe winters (Miller & Gunn 2003).

Muskox populations grew in Canada in the late 20th century, concurrent with range expansion, and especially on the southern Canadian Arctic Archipelago, reaching about 121,000 by 2008 (Fournier & Gunn 1998, Gunn & Forchhammer 2008). Re-introduced populations in Alaska have generally grown quite rapidly since the 1970s (Reynolds 1998), then stabilized or fluctuated in the past decade (Alaska Department of Fish and Game 2012). Native populations in NE Greenland have experienced large fluctuations historically, recently rebounding from major declines following severe winters in the period 1940-1960 and in the early 1980s (Forchhammer & Boertmann 2006). They may fluctuate over fairly long time spans (> 5 years), and have recently increased in the Zackenberg area (Forchhammer *et al.* 2002, 2008). Introduced populations in Russia, particularly on the Taymyr Peninsula and Wrangel Island, have grown substantially (Gruzdev & Sipko 2007a, Sipko 2009), and introduced populations in W Greenland generally prospered in the first decades (Boertmann *et al.* 1991).

Some populations of Eurasian elk have grown in size, in conjunction with their increased summer use of low Arctic habitats. In Finnmark county, north Norway, only 15 Eurasian elk were hunted in 1961, but the harvest increased to over 800 by 2007, and the population now appears stable (Fjellaksel 2010). The same general situation appears true in western Russia (Lomanova 2007).

Populations of moose in the Yukon-Kuskokwim deltas of western Alaska have increased in recent years following a reduction in the number of illegal kills and reflecting the fact that moose are below carrying capacity in the region (Alaska Department of Fish and Game 2011, Herman-Mercer *et al.* 2011). Populations on the north slope of the Brooks Range have been gradually increasing from the 1990s to present, perhaps reflecting the relatively favorable winters and improving availability of foods, but here and on the Seward Peninsula moose numbers can be dramatically affected by hard winters and disease (Alaska Department of Fish and Game 2011). Similar increases in abundance have been reported by Inuvialuit harvesters on the north slope of the British Mountains in Yukon, Canada (Aklavik Hunters and Trappers Committee 2003).

Populations of snow sheep are quite disjunct and not well studied. The protected population on the Putorana Plateau increased through the 1980s and 1990s to approximately 5,500 individuals (Sipko & Larin 1999), but the populations in Chukotka are subject to hunting and may total only 1,500 (Harris & Tsytsulina 2008). Dall's sheep populations in Arctic North America are generally believed to be stable, with adequate management of hunting (Alaska Department of Fish and Game 2012).

### 3.3.2.3. Causes and prospects

Arctic rodent population cycles, where they occur, seem to have become more variable in period and amplitude in recent decades. However, we lack long-term time series in most regions, so do not know whether changes are part of the general instability of these populations or a definite response to changing climate. Snow quality and quantity likely play a prominent role in population dynamics (Bilodeau *et al.* 2012), and are changing in a warming climate. Snow is tending to accumulate later and melt earlier (Dye 2002, Brown & Robinson 2011), and winter rain and thaws make it less insulative. A lemming outbreak depends, at least in part, on winter and spring reproduction under the snow (Stenseth & Ims 1993), so winter food availability and thermal conditions are crucial. In regions with low total snow fall but consistently cold temperatures (e.g. semi-desert of much of Arctic North America and Siberia), lemmings and voles select habitats with deeper snow (ideally > 60 cm deep), and their populations are more likely to grow in winter when snow comes early and deep in the autumn (Reid & Krebs 1996, Duchesne *et al.* 2011, Reid *et al.* 2011b). Using models, Gilg *et al.* (2009) found that the reduced amplitude of fluctuations in E Greenland could result from decreases in the duration of annual snow cover and increases in the frequency of thaw-refreeze events during winter. These factors are implicated in the lengthening of the cycle period on Wrangel Island (Menyushina *et al.* 2012). In regions with strong maritime influence, snow fall tends to be deeper but frequently influenced by melting temperatures that compact the snow pack and create ice layers within it and on the ground. Under such conditions, small rodents have difficulty creating and maintaining tunnels to access food, and experience reduced survival, reduced winter reproduction and a dampening of population fluctuations (Aars & Ims 2002, Korslund & Steen 2006, Kausrud *et al.* 2008). The recent recovery of high amplitude irruptions in Norway lemmings may result from more persistently cold winters with a snow pack more conducive to breeding (Ims *et al.* 2011).

Small rodent abundance, at least in summer, is heavily influenced by predation (Krebs *et al.* 2003, Legagneux *et al.* 2012), and removal of most of this predation pressure is a necessary condition for population growth (Reid *et al.* 1995, Wilson *et al.* 1999). The strength of an outbreak may increase when multiple small rodent species, with shared predators, are fluctuating synchronously (Ims *et al.* 2011). However, the presence of medium-sized herbivores in the food web allows predators to dampen cycles and keep rodents at low densities (Reid *et al.* 1997). Increasing diversity of herbivore species in the low Arctic food web could have divergent impacts on lemming and vole abundance, depending on which species are involved and how predators are able to respond. Some Arctic rodent species have low pathogen and parasite loads (e.g. Norway lemming; Laakkonen *et al.* 2001), and parasites have not yet been implicated as a strong factor in their population dynamics. This is an understudied topic, and a warming climate may well influence the life-cycle dynamics, transmission rates and geographic distributions of pathogens that have free-living, intermediate or vector-borne hosts (Harvell *et al.* 2002).

The Arctic ground squirrel experiences temperatures in hibernacula far below freezing, and has evolved a particular mechanism of androgen-driven muscle accumulation in summer to fuel winter energy needs (Boonstra *et al.* 2011). Decreases in duration and depth of insulative snow may put this species at greater risk of lethal freezing in winter.

Populations of collared pika and American pika *O. princeps* living outside the Arctic respond demographically to changes in the quality and quantity of their foods, or in the temperature regime to which they are adapted, and patterns of snow accumulation and melt affect both their foods and sub-nivean temperatures (Li & Smith 2005, Morrison & Hik 2007, Beever *et al.* 2011). Arctic pika populations may respond in similar ways. Increased growth of foods and improved winter insulation with deeper snow could enhance populations. However, late snowmelt and winter icing could have the opposite effect.

The potential direct and indirect effects of a warming climate on hares include improved food quantity with increasing primary production and proliferation of willows, reduced access to winter foods with deeper and harder tundra snow packs, and increased predation pressure with an expanding diversity and abundance of other herbivores including other hare species and ungulates (Klein 1995, Murray 2003). Mech (2000) noted reduced reproduction and a summer decline in Arctic hares on Ellesmere Island, Canada, apparently because of energy deficit following an early snow fall the year before. Mech (2007) also found a strong correlation between gray wolf numbers and an index of Arctic hare density. We need standardized long-term censuses, coupled with hypothesis-driven measures of causal factors, to allow firm inferences about the relative effects of these factors in the future.

Considering caribou and wild reindeer, recent declines and current low numbers in many herds are likely part of long-term natural cycles. The demographic parameters most strongly correlated with abundance trends are adult female and calf survival (Boulanger *et al.* 2011). Survival is a complex outcome of the effects of various causes of death, forage availability and parasite load, perhaps integrated through stress levels. All these factors need to be considered and likely vary in strength at different times in the cycles. A widespread concern has been that the changing climate, with extreme weather events such as deeper or harder snow cover, was driving the synchronous declines in so many herds (Vors & Boyce 2009).

Recent reversals in some of the declines, and the inability to relate all declines to weather patterns, suggest that fluctuations may be part of longer term cycles and their underlying causes (Russell & Gunn 2012).

Population trends can be influenced by human harvest. Indigenous elders emphasize the need to show strong respect for caribou and limit harvest when numbers are low (Legat *et al.* 2002), and a mix of voluntary and mandatory harvest restrictions has been established within communities (e.g. PCMB 2010). Hunter behavior and lags in application of management actions (principally harvest restrictions) likely contribute to population fluctuations (Fryxell *et al.* 2010), especially by accelerating declines or prolonging the low phase. In some Canadian migratory herds, for which abundance is not monitored very frequently, declines were well underway before hunting levels were reduced to take a smaller proportion of the herd (Gunn *et al.* 2011).

In Russia, historical commercial hunting has taken large proportions of some herds and has even caused declines when population levels were quite high (Klokov 2004, Baskin 2005). In Greenland, failure to detect increasing numbers may have contributed to conservative harvest management at a time when the herds were likely increasing (Cuyler *et al.* 2007).

Maximum caribou abundance is likely limited by food availability, with some herds exceeding carrying capacity at high densities (Messier *et al.* 1988, Klein 1999, Miller 2003). In herds with relatively small Arctic tundra range as a proportion of the annual range (e.g. George and Leaf River herds), caribou may more readily exceed the carrying capacity of their tundra calving and summer ranges (Messier *et al.* 1988, Couturier *et al.* 1990). In many other herds, the tundra range is very extensive, and the forested winter range is a relatively small proportion of the annual range. These herds may more readily exceed the carrying capacity of these forested winter ranges, where ground lichen cover is the dominant winter food (Miller 2003). Declines from peak numbers in Russian wild reindeer often appear to result from herds exceeding the carrying capacity of their ranges (Syroechkovskiy 2000, Baskin 2005).

Weather patterns and events affect caribou in diverse ways. Warmer weather conditions in June can significantly enhance the survival of calves by increasing the green-up of vegetation with its associated pulse of nutrients coincident with peak lactation (Griffith *et al.* 2002). Deep snow reduces access to winter foods and reduces survival (Kumpula & Colpaert 2003). Icing of the ground or the snowpack, following winter rain or melting, is strongly correlated with starvation-induced die-offs of Peary caribou (Miller & Barry 2009) and population declines in Svalbard and Wrangel reindeer (Kohler & Aanes 2004, Gruzdev & Sipko 2007b). However, the adverse effects of reduced access to food in winter are more pronounced when caribou are already close to, or exceeding, the carrying capacity of their range, and herds can often cope with difficult winters when food is still plentiful and therefore likely available in some habitats (Ferguson 1996, Tyler 2010). The negative effects of difficult snow conditions may be partially offset by projected increases in food abundance with warmer summers (Tews *et al.* 2007).

At a regional scale, long-term switches in climate regime, such as the North Atlantic or Arctic Oscillations (NAO or AO), may affect abundance of some herds through changes in productivity or quality of key foods and also weather events (snowfall, icing) affecting access to foods and ultimately survival (Griffith *et al.* 2002, Post & Forchhammer 2002, Forchhammer *et al.* 2005, Joly *et al.* 2011). These patterns may synchronize cycles across wide regions and influence the timing of declines through their influence on carrying capacity.

» *Grigory Ivanovich Rynavryntyn was born in the village of Ilirnei in the Bilibinsky district into a family of reindeer herders, and talks of the active mining industry in the Bering region of Siberia. "It had done a lot of harm to reindeer husbandry by destroying vast areas of their pasture lands."*

(Bat'yanova 2008).

Human activity and infrastructure, most often resulting from exploration and development of mineral and hydrocarbon resources, can destroy tundra habitats if poorly managed, can facilitate heavy hunting and have significantly contributed to declines of some Russia herds (Baskin 2005). However, the demographic consequences are not necessarily detrimental and probably depend on how well the infrastructure is planned and developed to minimize its footprint, the availability of alternative range and the management of mortality factors. The Central Arctic herd in Alaska shifted its calving away from the vicinity of oilfield infrastructure, with a consequent reduction in nutrition for cows and reduced calf growth (Arthur & Del Vecchio 2009), but the herd has continued to increase since the 1970s. Pavlov *et al.* (1996) suggested that the combined effects of gas pipelines, railway roads and river traffic keeping the Yenisey River open may have reduced access for the Taymyr herd to its southwestern winter ranges in the 1970s and early 1980s, but the herd continued to increase while using other winter ranges to the east. Animals in the Bathurst herd avoided an area of 10-15 km around two open-pit diamond mines (Boulanger *et al.* 2012), the development of which coincided with, but cannot be directly implicated in, the herd's decline to a historic minimum in 2006.

The shift in Russian political economy from collective to private ownership of domesticated reindeer in the 1990s resulted in a decline in domesticated reindeer and an expansion of some wild reindeer herds, which gained access to more range (Syroechkovskiy 2000).

Human presence is increasing across most caribou and wild reindeer ranges. In Greenland, hunting of caribou and muskoxen has increased with more people, stronger boats and a market economy for wild meat (Landa 2002). In Alaska, oil and coal reserves lie under the Western Arctic herd's calving ground: six roads and five mines are being planned (Dau 2009). Human activity on the calving grounds is probably the most risky, because calf survival depends heavily on a focused and strong bond with the mother (Miller 2003).

Trends in climate are now interacting with factors driving long-term caribou population fluctuations, with complex and uncertain outcomes. Warmer winter temperatures and a shorter snow season could reduce energetic costs of foraging and migrating, or increase them if warmer temperatures bring more extreme rain and icing events (Vors & Boyce 2009). Earlier snow melt makes the pulse of nutrient-rich new plant growth earlier, but pregnant cows risk falling behind and missing this generally advancing but crucial period of green-up (Post & Forchhammer 2008). They would have to migrate and give birth earlier to still benefit from this pulse, but it is unknown whether they can adapt by advancing the rut and changing the timing of migration. Although the trend is to earlier spring melt, variability is high, and no single set of behaviors will be adaptive in all situations. Migratory caribou will continue to face late melts and difficulties in traversing snow, or early and fast melts when some streams and rivers may become impassable. Warmer summers might increase levels of harassment by warble *Hypoderma tarandi* and nose-bot flies *Cephenemyia trompe*, leading to less time spent feeding, but drier conditions might reduce mosquito populations (Vors & Boyce 2009). The frequency and severity of forest fires are predicted to increase (Zinck *et al.* 2011), potentially reducing the carrying capacity, and therefore peak herd size, of mature forest winter range for migratory tundra herds.

The cumulative effects of development and a warming climate increase the risks. The Dolphin and Union herd crosses 20-50 km of sea ice from summer range on Victoria Island to winter on the mainland (Poole *et al.* 2010). Rising November temperatures have delayed ice formation on average by 10 days from 1982 to 2008, delaying caribou migration and increasing the risk of deaths from falling through weak ice. These risks will be compounded by an increase in commercial shipping (Poole *et al.* 2010).

> » *In recent years, all kinds of cruise ships are coming in to our area. Last year alone, there were maybe five or six cruise ships that came into town. More are coming every year. ... But hunters have been complaining about those ships because they go all over Cumberland Sound, even to the campsites. People are saying they are scaring away the animals, the mammals and whales.*
>
> (Community member quoted in Inuit Circumpolar Council 2008).

Although there is little evidence of a strong effect of pathogens and parasites on Arctic ungulate populations, these are emerging as a higher risk in a warming climate (Hoberg *et al.* 2003). Empirical prevalence and modelled dynamics of a protostrongylid nematode *Umingmakstrongylus pallikuukensis* in muskoxen reveal broadened seasonal windows for transmission and reduced generation times in the parasite, likely leading to higher infection rates which predispose the hosts to predation (Kutz *et al.* 2001, 2005). A mosquito-borne filarioid nematode, *Setaria tundra*, is associated with die-offs of reindeer and Eurasian elk in Fennoscandia (Laaksonen *et al.* 2010).

Muskox populations are susceptible to starvation when ice encrusts the ground and prevents good access to food (Nagy & Gunn 2009), and deeper snow packs appear to inhibit population growth through starvation mortality or reduced subsequent productivity (Forchhammer *et al.* 2008). Some muskox populations are increasingly affected by predation from brown bears (Reynolds *et al.* 2002) and by extreme weather related accidents such as a storm surge trapping animals in ice (National Park Service 2011). Hunting is an important management tool in Alaska, especially for island populations without wild predators (Alaska Department of Fish and Game 2012).

## 3.4. TERRESTRIAL INSECTIVOROUS MAMMALS

> » *When people lived in cabins made from logs, they saw shrews more often, as the shrews could get in more easily and run around. Unless they see the smaller size and pointy nose, they do not think 'shrew'.*
>
> (Aklavik Hunters and Trappers Committee 2003).

One group of insectivorous mammals, the shrews (Soricidae), has colonized Arctic habitats. These small-bodied mammals (2-12 g) require snow cover as insulation from the winter cold and a steady ingestion of food to fuel their relatively high metabolic rates (Churchfield 1990, 2002). Shrews feed on a wide diversity of Arctic invertebrates and nutrient-rich seeds and also scavenge carcasses (Dokuchaev 1989, Churchfield 1990). In summer, the pulse of invertebrate reproduction and activity probably provides abundant food. In winter, most invertebrates are relatively inactive and hidden in soil or vegetation (Bale *et al.* 1997), so shrew survival decreases and appears strongly affected by food availability (Churchfield 1990, 2002). To deal with this winter shortage of energy and nutrients, individual shrews can increase the thickness of their fur, reduce their body size (Dehnel's phenomenon) and reduce their metabolic rate (Mezhzherin 1964, Merritt 1995, Churchfield 2002). Also, within a species, they are generally smaller at colder northern latitudes than further south, in contrast to Bergmann's rule (Ochocinska & Taylor 2003, Yom-Tov & Yom-Tov 2005).

## 3.4.1. Species richness and distribution

### 3.4.1.1. Status

In the Arctic we find representatives from only one genus (*Sorex*) of the large global diversity of shrews. The distributions of 14 *Sorex* species recognized by Wilson & Reeder (2005) overlap the Arctic biome, however, the exact number of species is still in question. Some consider St. Lawrence Island shrew *Sorex jacksoni*, Portenkoi's shrew *Sorex portenkoi* and the barren-ground shrew *Sorex ugyunak* to be conspecific (Dokuchaev 1999, Andreev *et al.* 2006). Many of the Siberian and North American species are closely related to the cinereus shrew *Sorex cinereus* and show little genetic differentiation from each other (Demboski & Cook 2003). Recent genetic evidence suggests that the Alaska tiny shrew *Sorex yukonicus* is the same species as at least the Siberian populations of the Eurasian tiny shrew *Sorex minutissimus* (Hope *et al.* 2010).

No shrew species inhabits the high Arctic, and nine species are primarily boreal in distribution, with small extensions into the low Arctic (Appendix 3.1). The tundra shrew and the tiny shrew species complex are the only shrews to claim a circumpolar distribution (Hope *et al.* 2010). Five shrew species can be considered truly Arctic, being distributed exclusively in the Arctic (four species) or having an extensive Arctic tundra distribution far from treeline (tundra shrew) (Appendix 3.1).

The Siberian and Alaska/Yukon regions have the highest diversity of shrews today, likely reflecting their ability to support some species during the last ice age, their direct connections to extensive boreal regions and isolation of the Pribilof and Saint Lawrence Island shrews with Holocene sea level rise. Shrews are absent today from land masses that were both largely ice-covered and subsequently isolated from mainland refugia by wide ocean passages (Canadian Arctic Archipelago, Greenland, Ungava, Iceland). This is despite the colonization of the Canadian Arctic mainland by the barren-ground shrew, likely from Beringia (Demboski & Cook 2003). These patterns suggest that the refugium on the Canadian Arctic Archipelago did not support shrews, and that shrews have been unable to traverse ocean passages more than a few kilometers wide even when ice covered.

### 3.4.1.2. Trends

We have no information on changes in shrew distributions in recent history. Genetic analyses of the circumpolar tundra shrew demonstrate population divisions coincident with late Pleistocene refugia and an ability of various lineages of this widespread species to persist through dramatic climate change in the Pleistocene probably because it occupied a variety of habitats (Bannikova *et al.* 2010, Hope *et al.* 2011).

### 3.4.1.3. Causes and prospects

Given relatively high metabolism and small body size, shrew survival is very likely affected by energy availability in winter, as determined by food and thermal cover of snow (Mezhzherin 1964, Churchfield 2002, Yom-Tov & Yom-Tov 2005). A warming climate may expand the niche for shrews by enhancing invertebrate production which is temperature dependent (Bale *et al.* 1997). The proliferation of erect shrub growth in some regions may increase local snow accumulations (Callaghan *et al.* 2005), expanding the geographic extent of their thermal niche. The relaxation of energetic constraints in a warming climate has a quick effect on body size, which in the cinereus shrew has increased in Alaska over the second half of the twentieth century (Yom-Tov & Yom-Tov 2005). Interference competition among shrew species appears to affect spacing behavior (Dokuchaev 1989) and may influence distribution patterns.

The Arctic Ocean and associated inter-island channels appear to form an absolute barrier to northward expansion of shrew distributions. As mainland habitat conditions change, the truly Arctic species may lose some of their distributions, but we do not know what habitat or competitive factors currently define those distributions, so any thoughts are speculative.

## 3.4.2. Population sizes and densities

### 3.4.2.1. Status

The global status ranking is Least Concern for 12 of 14 shrew species (IUCN 2011), meaning their population and distribution characteristics reveal no strong risks at present. Portenkoi's shrew is Data Deficient (Tsytsulina 2008b). The Pribilof Island shrew *Sorex pribilofensis* is Endangered, because it is only found on one island (St. Paul) which is relatively small (< 500 km$^2$) with limited known habitat and uncertain population abundance (Woodman *et al.* 2008).

### 3.4.2.2. Trends

> » *Fish is a common bait in traps and shrews eat this bait to the bone. Trappers understood that this activity was related to the abundance of shrews.*
>
> (Aklavik Hunters and Trappers Committee 2003).

Shrews are the least-studied terrestrial mammals in the Arctic, and we lack data on population abundance. Studies of north boreal shrews indicate that abundance follows an annual cycle with winter declines strongly influenced by food availability, and summer increases fuelled by reproduction (Henttonen 1985, Dokuchaev 1989). In boreal Siberia, with abundant snow, shrews follow a four-year cycle, coincident with the cycle in lemming and vole abundance (Sheftel 1989). Such cycles might be fairly widespread (Henttonen 1985, Dokuchaev 1989), though less evident in regions of poor winter snow cover (Sheftel 1989). Shrews and rodents share the same suite of predators, but shrews are generally less palatable, so may experience heavier predation after the rodents have crashed (Henttonen 1985).

### 3.4.2.3. Causes and prospects

Arctic shrew populations may benefit from increasing invertebrate productivity and deeper snow packs. They might suffer from increased frequency of icing events and any increases in predation pressure (Aitchison 1987). Prospects are hypothetical, and point to the need for long-term monitoring of population abundance and demographic parameters in key regions.

## 3.5. TERRESTRIAL CARNIVOROUS MAMMALS

Plant growth and thus herbivore biomass are low in the tundra, therefore terrestrial carnivores are usually rare, highly mobile and mostly solitary. Yet they are present throughout the Arctic tundra, and most of them are active year-round. Their diet is highly diverse, varying from strictly carnivorous to largely vegetarian. They sometimes influence the size and distribution of other vertebrate populations by top-down effects through the Arctic food web (Berteaux 2005, Legagneux *et al.* 2012).

Carnivores can be prey, predators and competitors for humans (Fig. 3.3). People have thus evolved a long, varied and complex relationship with them, ranging from persecution to exploitation to veneration. For most of the 20th century, fur trading (mostly Arctic fox) was a critical economic activity for many Arctic communities, until the fur market largely collapsed in the 1980s (Robinson 2005). Veneration for some of the most charismatic terrestrial carnivore species has developed in many places. Today, many people give the largest carnivore species a high existence value rooted in their power, mystique and beauty (Dickman *et al.* 2011). The following stories show very well how humans and carnivores have built this rich and varied relationship.

> *Early 60s, they were poisoning wolf, at the same time I guess, wolverine and foxes and that go with it as well, and the population went really, really down to about nothing.*
>
> (Participant #401 from Arviat, Nunavut; Cardinal 2004).

> *We know that the bear is a sacred animal. That is why we do not shoot the bear; we do not eat its meat.*
>
> (Alexei Gavrilovich Tretyakov, a retired reindeer herder from Andreyushkino in the Lower Kolyma, Russia; Mustonen 2009).

> *After the war there were many wolves here, none really counted them though. But there were several packs plus some couples to add up with few lonely ones too. We had to herd the reindeer constantly because of these predators. If a pack of say, ten wolves would come hunting, with one single attack they could take ten reindeer. Another attack or another pack, and it would be another ten reindeer!. Since then few wolves have appeared in the region.*
>
> (Late Saami Elder Niillas Vuolab, a reindeer herder from the Kaldoaivi region of Sápmi, Finland; Helander *et al.* 2004).

> *I was tracking a wolverine one time, and all of a sudden it turned towards the wind and it went for about a mile, and it dug into the snow and it retrieved a whole, you know weathered bone – caribou. Completely white, and yet a mile away.*
>
> (Participant #401, Arviat, Nunavut; Cardinal 2004).

> *There used to be less wolverines. Now there is a massive number of them. They have increased in numbers and should be harvested. They kill a lot of reindeer. No difference to them, old and young alike are killed. Wolves tear and attack the reindeer as well. I think they are increasing as well. Before, when the price of the gasoline was lower, we used to shoot them from helicopters but no longer. Then we killed wolves from ski-doos. That no longer happens either. I cannot say exactly how many, but the numbers were great. Mostly reindeer are killed by humans though. A human kills everything in front of him.*
>
> (Saami reindeer herder Philippov from the community of Lovozero, Kola Peninsula, Russia; Snowchange Luujäu'rr (Lovozero) Oral History Archive 2002-06).

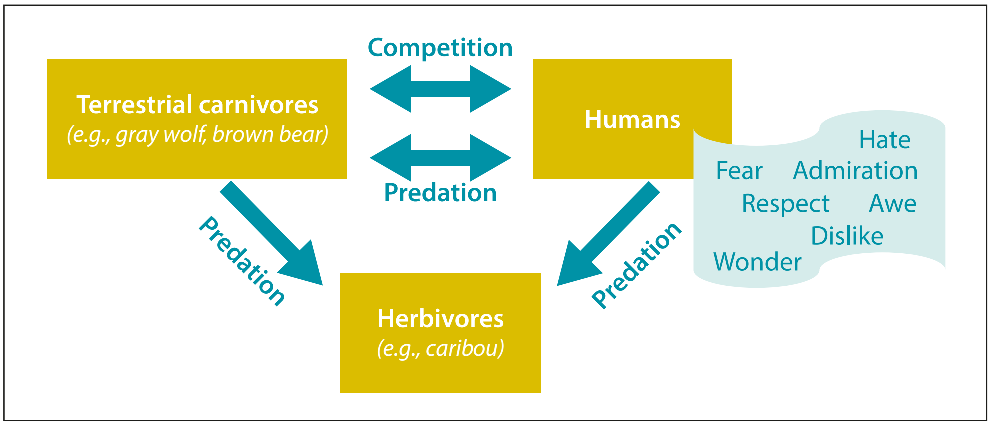


**Figure 3.3.** Main ecological relationships linking humans, terrestrial carnivorous mammals and their shared prey, as well as some of the emotions felt by humans towards carnivores.

The fates of species such as the gray wolf, Arctic fox, brown bear and wolverine now get worldwide attention because these charismatic animals symbolize the last remaining wildernesses of the world. In addition, past and current exploitation for their valuable fur and competition with humans for some herbivores have generated strong interest in learning about these carnivores (Gagnon & Berteaux 2009). However, assessing the status and trends of carnivore populations is often difficult because of their secretive nature, large home ranges and the vast expanses of land that need to be covered during surveys. This results in numerous data gaps even for basic population sizes, densities and distributions.

## 3.5.1. Species richness and distribution

### 3.5.1.1. Status

There are 13 species of terrestrial carnivorous mammals in the Arctic (Appendix 3.1). This represents about 10% of the 128 species (Wilson & Mittermeier 2009) belonging to the order Carnivora worldwide. Among the Arctic species are four species of canids (red fox, Arctic fox, gray wolf and coyote *Canis latrans*). All have a circumpolar distribution and inhabit the high Arctic, except for the coyote which only occurs in the western North American low Arctic where it is very sporadic (Slough & Jung 2007). The two felids (Eurasian and Canadian lynx, *Lynx lynx* and *L. canadensis*) and two bears (brown or grizzly bear, and black bear) are mostly confined to the low Arctic. Lynx actually rarely go north of the treeline. The five mustelids (weasels and relatives) have various distributions, ranging from the circumpolar distributions of the wolverine, stoat (or short-tailed weasel or ermine) and weasel (or least weasel, *Mustela nivalis*) to the more restricted distributions of the American mink and North American river otter *Lontra canadensis*, which just reach the southern margin of the low Arctic.

Of the 13 species of terrestrial carnivorous mammals occurring in the Arctic, six occur in the high Arctic, but none is confined to the high Arctic. Overall diversity is highest in low Arctic areas such as the Alaska to Mackenzie River region, with 11 of the 13 species present (Fig. 3.4). In sharp contrast, the Arctic fox is the only terrestrial carnivore on some islands such as Svalbard. Most other Arctic regions have between four and nine species of terrestrial carnivores. Species of terrestrial carnivorous mammals that occur in the Arctic all have a distribution that is restricted to the northern hemisphere, except for the red fox which was introduced to Australia. No species is endemic to the Arctic, and the Arctic fox is the only species that can be considered an Arctic specialist, the few populations living south of the Arctic being restricted to tundra habitats. The Arctic fox may be the only terrestrial mammal to have been observed on the sea ice up to the North Pole (Angerbjörn *et al.* 2008a).

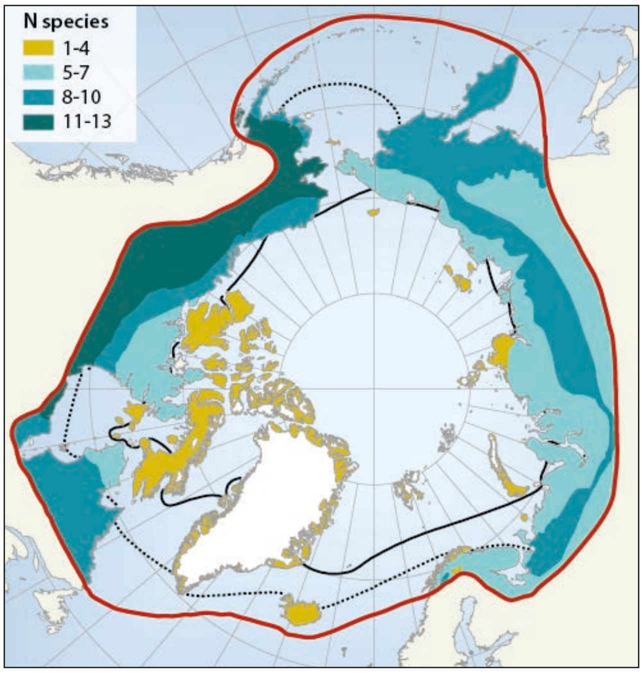


**Figure 3.4.** Diversity of terrestrial carnivorous mammals across the circumpolar Arctic and sub-Arctic (based on IUCN distribution maps www.iucnredlist.org/initiatives/mammals).

The species richness of terrestrial Arctic carnivores is relatively similar in the Palearctic and Nearctic, with about 10 species in each (Appendix 3.1, Fig. 3.4). However, there are twice as many species in the low Arctic as in the high Arctic, probably reflecting the higher diversity of prey and the higher productivity found at lower latitudes (Krebs *et al.* 2003).

The taxonomy of this group is now well established at the genus and species levels, although the status of the Arctic fox genus is still debated. Some place the species in the genus *Vulpes* (Wilson & Reeder 2005) and others in the genus *Alopex* (Wilson & Mittermeier 2009). There is more taxonomic debate at the level of the subspecies with concerns that the currently recognized subspecies do not always match the genetic data (Wilson & Mittermeier 2009). Wilson & Mittermeier (2009) recognized 106 subspecies in the 13 species of terrestrial carnivorous mammals found in the Arctic, but most subspecies do not belong to the region. The diversity found at the sub-species level is highly variable (the wolverine has only two subspecies whereas the stoat has 34) and may correlate with the dispersal abilities of the species.

### 3.5.1.2. Trends

> » *I haven't seen the Arctic fox in a long time.*

(Much-respected Saami hunter Heikki Länsman spoke of the last observation of an Arctic fox in the Kaldoaivi region (Finland) and said that it was some 10 to 15 years ago; Helander *et al.* 2004).

> » *They [wolverine] seem to be moving north, northward a little bit. Starting to see them on Victoria Island, compared to the past there were not as much down there.*
>
> (A. Niptanatiak, Kugluktuk NU; Cardinal 2004).

There are many documented examples of changes in distribution of terrestrial mammalian carnivores, but trends vary widely among species, populations and regions, ranging from clear expansion to local extirpation. Generalizations are thus difficult. Lack of precise data at the scale of most populations also complicates a global analysis. In addition, carnivores often compete with each other for the same resources so that negative trends in one species often result in positive trends in another. For example, gray wolf and coyote densities have been found to be negatively correlated (Berger & Gese 2007), whereas red foxes may exclude Arctic foxes from newly colonized areas (Tannerfeldt *et al.* 2002). The following examples (summarized in Tab. 3.3 or described at length in the text below) illustrate some of the best documented changes in distributions of species or populations. However this is by no means an exhaustive list of observed changes throughout the circumpolar Arctic.

In 1966, the gray wolf was regarded as functionally extinct in Norway and Sweden (Wabakken *et al.* 2001). In 1978 the first confirmed reproduction on the peninsula in 14 years was recorded, and a small population now resides in Sweden and Norway (Vilà *et al.* 2003), although this is in the boreal region. Similarly, the wolf population in Finland was almost extirpated before the end of the 19th century (Aspi *et al.* 2006). Since then, the wolf population in Finland has increased and expanded its range as a result of conservation strategies and hunting control (Kojola *et al.* 2006), but also remains in the boreal. There are thus still no wolves in the Arctic or sub-Arctic areas of Fennoscandia. After being exterminated from E Greenland in the 1930s, the gray wolf has recolonized and established a new population in this area during the last thirty years (Marquard-Petersen 2011). Interestingly, whereas humans had exterminated the local population, they may also have unintentionally favored their come-back as lone wolf immigrants may have followed military sled patrols from northern Greenland (Marquard-Petersen 2011).

The historical distribution of the coyote was restricted to the plains and deserts of central North America (Gier 1975, Bekoff & Wells 1986). However, its range has expanded to include Alaska and northwest Canada, coinciding with the removal of wolves. Some may now be found on the northern shores of Alaska and Yukon (Gese *et al.* 2008), although the evidence is controversial.

The Arctic fox has expanded its distribution in some parts of its range while retreating in other parts. The species was introduced to isolated islands in the Aleutian chain at the end of the 19th century by the fur industry (Bailey 1992), while the southern edge of the species' range may have moved northward during the 20th century resulting in a smaller total range (Hersteinsson & Macdonald 1992) both in North America and Eurasia. In parallel, the northern range of the red fox has shifted northward to include the tundra zones of Fennoscandia and Russia (Skrobov 1960 and Chirkova 1968 in Hersteinsson & Macdonald 1992, Killengreen *et al.* 2007, Rodnikova *et al.* 2011). Similarly, the distribution of the red fox has spread northwards into Canada's tundra during the last century (Macpherson 1964), and Pamperin *et al.* (2006) indicate that there is evidence for a similar range expansion of red foxes in Alaska. The timing of range expansion in the Canadian red fox population can be detected by a review of harvest and trading figures, and Macpherson (1964) reported the presence of red foxes on Baffin Island starting around 1918/1919 and north Baffin Island around 1947. Some residents of Pond Inlet, Nunavut, recall their first sightings of red

**Table 3.3.** Examples of historical and recent distribution changes observed in terrestrial carnivorous mammals in the Arctic.

| Species | Observed change | Dates | Reference |
|---|---|---|---|
| Coyote | Northward range expansion in the Northwest Territories and Labrador, Canada | 1990s | Chubbs & Phillips 2002,<br>Cluff 2006 |
| Arctic fox | Introduced to the Aleutian chain by the fur industry | Late 19th century | Bailey 1992 |
| Arctic fox | Disappearance from Finland | Late 20th century | Henttonen *et al.* 2007 |
| Red fox | Northward spread into eastern Canadian Arctic, Siberia and Fennoscandia | 1920-1960 | MacPherson 1964, Hersteinsson and Macdonald 1992 |
| Brown bear | Northern range expansion onto King William Island | Late 20th century | Keith & Arqviq 2006 |
| Brown bear | Northward expansion to the eastern bank of the Kolyma Delta, Russia | Late 20th century | Mustonen 2009 |
| Wolverine | Extirpation from the Cape Henrietta Maria region, James Bay, Canada | 1970s | Dawson 2000 |
| American mink | Introduced to Iceland in 1931 for fur-farming purposes; now present throughout most of the country | First half of 20th century | Hersteinsson 1992 |

fox in 1947-1948 or during the 1950s near Pond Inlet (Gagnon & Berteaux 2009). A static relationship between Arctic fox and red fox in the western Canadian Arctic during the last four decades suggests that the red fox expansion may have met its limit in some places (Gallant *et al.* 2012).

The brown bear occupies most of Alaska (Miller *et al.* 1997) and mainland Nunavut (Ross 2002). Traditional ecological knowledge suggests that its range in Nunavut is expanding eastwards (McLoughlin & Messier 2001). Hunters and residents of Gjoa Haven (Nunavut) confirmed the northern range expansion of bears onto King William Island (Keith & Arqviq 2006). Chestin (1997) found no evidence of any changes in the historical northern distribution limit of brown bear in European Russia and W Siberia. Chestin *et al.* (1992) suggested that brown bears were never found on the Russian tundra, except in the Chukotka Peninsula. However, the situation appears to have changed. From Nenetsky district to Yamal Peninsula, brown bears are sometimes observed into the tundra by Nenets and scientists (N. Lecomte, unpubl.). Chukchi elders from the Kolyma delta region of Siberia now report many tundra brown bears that have come from the forest zone (Mustonen 2009).

Community fur returns and local knowledge suggest that there have been no change of the northern range of Canadian lynx in the Northwest Territories, Yukon or Alaska through the 1980s and 1990s (Poole 2003). The world's northernmost lynx population is found in Scandinavia (Odden *et al.* 2009). In this area, Eurasian lynx are becoming increasingly common (Hellborg *et al.* 2002).

There have been few studies of wolverines in North America, and the historical distribution remains unknown (COSEWIC 2003). However, Dawson (2000) reports that a small population on the coast of James Bay, in the Cape Henrietta Maria region, may have been extirpated during the 1970s, but that the species appears to be recolonizing some areas in NW Ontario. There have been no verified reports of wolverine in Quebec or Labrador for about 25 years (COSEWIC 2003). Wolverines were numerous and widely distributed in Fennoscandia up to the 19th century. Following intense persecution, their distribution and population size declined markedly during the 1900s (Landa *et al.* 2000, Flagstad *et al.* 2004). Landa *et al.* (2000) suggested that current distribution is restricted to the central and northern parts of Norway, Sweden, Finland and Russia.

The American mink was introduced to many parts of Europe in the 1920s and 1930s, mainly for fur-farming (Wildhagen 1956, Hersteinsson 1992, Bevanger & Henriksen 1995). Some introductions occurred in sub-Arctic areas such as near Murmansk in NW Russia (Lever 1985). Bonesi & Palazon (2007) report their presence in the low Arctic areas of Iceland, and they have been observed in the low Arctic of mainland Norway (N.G. Yoccoz, unpubl.).

#### 3.5.1.3. Causes and prospects

Distributions of terrestrial carnivorous mammals have changed in the past century under both direct and indirect human influences. Direct human influences include overharvesting or persecution and introductions to previously unoccupied areas, both in direct relation to the economic incentives generated by the fur market (Robinson 2005). Indirect human influences probably include effects of climate change (Gilg *et al.* 2012), removal of competitors (usually other carnivores) and manipulation of herbivore population densities. Delivery of food subsidies, in the form of carcasses of semi-domesticated reindeer or simply human waste, has also influenced the distribution of terrestrial carnivorous mammals in the Arctic (Killengreen *et al.* 2011). Direct human influences may have been the most important drivers of change in the first half of the 20th century, whereas indirect human influences may have become more prevalent in the second half.

A rebirth of the fur market is possible if emerging economies resuscitate a high demand for fur products (Robinson 2005). However, climate change, industrialization of the Arctic and increased wildlife-human conflicts due to colonization by humans of new areas are more likely to influence populations of terrestrial carnivorous mammals in the decades to come.

These causal factors influencing past or future status and trends in species distributions are all mediated through changes in population abundance. We will therefore explore these causes and prospects in more detail in the next section.

### 3.5.2. Population sizes and densities

#### 3.5.2.1. Status

Most of the 13 species of terrestrial carnivorous mammals covered here are socially solitary and maintain territories, which may limit their density and thus population size. Yet total population sizes of all species probably range at least in the tens of thousands given their wide geographical range. Global, and specifically Arctic, population size and density estimates exist for very few mammalian carnivore species (Tab. 3.4). In some species, most individuals live in the Arctic (e.g. Arctic fox) whereas in others only a very small (e.g. Eurasian lynx) or even insignificant (e.g. coyote) proportion of the global population is found there. It is often not possible to split populations between their Arctic and boreal components as individuals freely move across biome boundaries. For example, gray wolves can follow caribou during their seasonal migrations from tundra breeding grounds to boreal wintering areas (Walton *et al.* 2001).

None of the terrestrial carnivorous mammals included in this chapter is threatened at the global scale (Tab. 3.4). At the scale of individual jurisdictions, in many cases no

**Table 3.4.** Status and trends of Arctic terrestrial mammalian carnivores. Status and trends were assessed within political boundaries and thus refer to populations that often extend beyond the Arctic region.

<table>
<tr><th rowspan="2"></th><th rowspan="2">World IUCN</th><th rowspan="2">Alaska, USA</th><th colspan="5">Canada</th><th rowspan="2">Green-land</th><th rowspan="2">Ice-land</th><th colspan="2">Norway</th><th rowspan="2">Swe-den</th><th rowspan="2">Fin-land</th><th colspan="3">Russia</th></tr>
<tr><th>All</th><th>Yukon</th><th>NWT</th><th>NU</th><th>Quebec, Labrador</th><th>Main-land</th><th>Sval-bard</th><th>All</th><th>East</th><th>West</th></tr>
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<tr><td>American river otter</td><td>🟩 →</td><td>▒</td><td>▒</td><td>▒</td><td>🟩 ∴</td><td>▒</td><td>▒</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
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| **Population Trends**<br>Dashed: based on expert opinion | |
|---|---|
| → | Stable trend |
| ↓ ↑ | Decreasing or increasing trend |
| **Population Size (survey based)**<br>Grey: based on expert opinion | |
| • | < 100 individuals |
| •• | 101 to 1,000 individuals |
| ∴ | 1,001 to 10,000 individuals |
| ⁘ | 10,001 to 50,000 individuals |
| ⁙ | 50,000+ individuals |

| **Population Status** | |
|---|---|
| 🟥 | Critically Endangered |
| 🟧 | Endangered |
| 🟨 | Vulnerable / Threatened |
| ▤ | Near Threatened / Special Concern |
| 🟩 | Least Concern / Non-Endangered / Not at Risk |
| ▒ | Data Deficient / No Information<br>Not Evaluated / No Information on species status found |
|  | Not present in country/region |

References:
Gray wolf: COSEWIC 1999a, Sillero-Zubiri *et al.* 2004, Cluff 2005, Gärdenfors 2005, Norwegian Red List 2006, Mech & Boitani 2008.
Coyote: NWT 2004.
Arctic fox: NWT 2004, Sillero-Zubiri *et al.* 2004, Gärdenfors 2005, Norwegian Red List 2006, Fuglei 2007, Angerbjörn *et al.* 2008a.
Red fox: Voigt 1987, NWT 2004, Norwegian Red List 2006, Macdonald & Reynolds 2008.
Brown bear: Miller *et al.* 1997, Gau & Veitch 1999, Rassi *et al.* 2001, COSEWIC 2002, Kindberg *et al.* 2004, Gau 2001, Norwegian Red List 2006, McLellan *et al.* 2008.
American black bear: COSEWIC 1999b, NWT 2004, Garshelis *et al.* 2008.
Canadian lynx: COSEWIC 2001, NWT 2004, Nowell 2008.
Eurasian lynx: von Arx *et al.* 2004, Breitenmoser *et al.* 2008.
Least weasel: NWT 2004, Hellstedt *et al.* 2006, Norwegian Red List 2006, Tikhonov *et al.* 2008.
Stoat: NWT 2004, Hellstedt *et al.* 2006, Norwegian Red List 2006, Reid & Helgen 2008.
Wolverine: Landa *et al.* 2001, Rassi *et al.* 2001, Gau and Mulders 2001, COSEWIC 2003, Novikov 2005, Abramov *et al.* 2009, Brøseth *et al.* 2009.
American mink: NWT 2006.
American river otter: NWT 2004, Serfass & Polechla 2008.

information exists on status of populations, as shown by the many gray cells in Tab. 3.4. For example, only the status of gray wolf and Arctic fox has been assessed in Alaska, whereas only the status of gray wolf has been assessed in Russia. At a regional scale, many populations are vulnerable, endangered and possibly extirpated (see Tab. 3.4 for individual species references). Several primarily boreal species are endangered or threatened in Fennoscandia, including gray wolf and wolverine in mainland Norway, Sweden and Finland, and brown bear in Norway. Arctic fox, the only truly Arctic carnivore in this region, is now one of the most endangered mammal species in Europe. The wolverine population in Quebec and Labrador may be locally extirpated (Fortin *et al.* 2005). The gray wolf subspecies *C. l. arctos*, found in the Northwest Territories and Nunavut was considered for protected status in 1999 but was not listed due to insufficient data (Van Zyll de Jong & Carbyn 1999).

#### 3.5.2.2. Trends

The behavioral adaptations that make these species effective predators also make them elusive to researchers, so that detailed estimates of trends in population size are rare. In the smallest species (least weasel, stoat and American mink), such data are completely absent. Most species for which information exists are considered to be stable in terms of global population size (Tab. 3.4), with coyote and American black bear even increasing. One exception is the wolverine, which is considered as declining on a global scale.

This general stability of nothern populations of terrestrial carnivores fits the trend of the Arctic Species Trends Index during the period 1970-2004, which was calculated from 306 species (965 populations) of vertebrates (McRae *et al.* 2010). Here we summarize some trends documented in a few species or populations to show the diversity of trends observed among populations and the nature of the evidence that exists regarding changes in size and density of populations. Some of the reported trends are for populations that largely spread south of the Arctic.

In NE Greenland, Dawes *et al.* (1985) report a decline in the wolf population during the 1930s, and by the early 1940s the species was most likely extirpated. However, the species came back after the cessation of fur trapping activities, and Marquard-Petersen (2009) found evidence that between 1978 and 1998 the wolf population of N and E Greenland consisted of up to 55 wolves in favorable times and maximum wolf density was estimated at 0.03 wolves/100 km$^2$ in this very alpine area. The gray wolf population in Scandinavia during the winter season of 2008-2009 was estimated between 213-252 individuals (Wabakken *et al.* 2009). Russia's total population is estimated to be about 70,000 and is fully viable (Mech & Boitani 2008). However, the population and density estimates specifically for Arctic Russia are not known. Indigenous communities of the Lower Kolyma region, in northeast Russia, report that the regional wolf population is stable and healthy (Mustonen 2007). No information is available for coyote population estimates or densities within its northern range.

The Fennoscandian Arctic fox population declined between 1983 and 2000 (Angerbjörn *et al.* 1995) and was close to extinction around the year 2000. Numbers have increased since in response to intensive actions (Angerbjörn *et al.* 2008b), and today there are about 0-250 individuals distributed in four geographically separate areas (Dalén *et al.* 2006, Angerbjörn *et al.* 2008b). The number of Arctic foxes estimated in Norway (mainland) and Sweden is 150 and 80, respectively (Angerbjörn *et al.* 2008b). However, there have not been any confirmed litters born in Finland since 1996 (Kaikusalo *et al.* 2000, Dalén *et al.* 2006). The red fox has been reported to be increasing in numbers within the Fennoscandian mountain tundra (Østbye *et al.* 1978, Kaikusalo & Angerbjörn 1995, Tannerfeldt *et al.* 2002).

According to McLellan (1994), populations of brown bears in tundra habitat exist at the lowest recorded densities of all North American brown bears. Reynolds (1982) reported for Alaska North Slope populations that high bear densities in optimum habitat approached 2 bears/100 km$^2$, and densities in lower quality habitats were about 0.5 bears/100 km$^2$. Similarly, the density for bears of all ages in NW Alaska was estimated to be 2/100 km$^2$ (Ballard *et al.* 1990). Local hunters in NW Alaska believed brown bears were numerous and more abundant than observed historically (Loon & Georgette 1989). Brown bear population estimates for NE Europe suggest that there are about 37,500 bears (for the area including the Ural Mountains to the Finnish west coast, 53° to 69° N; Swenson 2000). Between 1998 and 2002 the number of adult female brown bears in Norway was estimated to be 6-12, with the highest density above the Arctic Circle (Swenson *et al.* 2003). This population does not meet the requirements to qualify as a viable population (Sæther *et al.* 1998) and is therefore dependent on the management of bear populations in Sweden and Finland (Norwegian Red List 2006). In Sweden, there were 1,635-2,840 bears in 2004, with a yearly growth rate of 4.7% (Gärdenfors 2005), rising to 3,000-3,700 in 2010 (Kindberg *et al. 2011).* Risk analysis of population demographic data from bear research in Scandinavia shows that today's Swedish bear population is viable (Gärdenfors 2005). The brown bear population size in Finland is estimated to be 810 (Kojola *et al.* 2006), and there are conflicting reports as to whether this population is increasing or decreasing (Kojola *et al. 2006*). Chestin *et al.* (1992) suggested a density of $< 0.2$ individuals/100 km$^2$ on the Russian tundra.

The total population of American black bears is believed to be increasing (Garshelis *et al.* 2008), but there are limited data to support this (Garshelis & Hristienko 2006). During the past two decades, most American black bear populations have grown both numerically and geographically (Williamson 2002). However, in northern latitudes few studies of black bears have been conducted to confirm this (Miller *et al.* 1997, Bertram & Vivion 2002).

The Eurasian lynx population (excluding Russia) is currently estimated to be 8,000 individuals, and the whole population (including Russia) is believed to be stable (Breitenmoser *et al.* 2008).

Wolverines are among the rarest and least studied mammalian carnivores in North America (Ruggiero *et al.* 1994, Copeland & Whitman 2003). Wolverines in Nunavut are believed to be stable, but sensitive to harvest pressures (COSEWIC 2003). In an indigenous traditional knowledge study of wolverines in N Canada, the majority of participants reported that wolverines were at low densities and rarely seen (Cardinal 2004). Most interviewees reported that populations were either stable or increasing, except near Yellowknife, Northwest Territories where the population might be decreasing. The wolverine population in N Yukon was thought to be increasing, due to less local trapping, and in the Kivalliq region, Nunavut, to have increased over the past 20-30 years (Cardinal 2004). The current population estimate of wolverines in the central to northern parts of Norway, Sweden, Finland and Russia is around 2,000 individuals (Landa *et al.* 2000), having increased since a period of persecution during the 1900s (Flagstad *et al.* 2004). The number of wolverines in the Murmansk, Kola Peninsula region of Russia is estimated to be 200-330 in 2004 (Makarova 2005), with Saami reporting increasing numbers (Mustonen & Mustonen 2011). Across Russia, an overall decrease in numbers seems to have taken place in the late 20th century (Landa *et al.* 2000).

American mink population densities and trends are unknown for most Arctic regions. Population numbers are reported as stable in the Northwest Territories (NWT 2006), but most data may come from non-Arctic areas. In Europe and Iceland, population estimates and trends are based on hunting records and largely show some stability in recent years. However, figures are again largely influenced by data coming from non-Arctic areas.

Limited information is available for North American river otter, although overall the population trend is believed to be stable (Serfass & Polechla 2008).

### 3.5.2.3. Causes and prospects

Many factors influence population numbers of Arctic carnivores and influencing factors rarely occur singly. Historically, population sizes were likely altered by hunting and trapping in some populations. While hunting and trapping have decreased for some of these species, they continue for others, some of which remain under high harvest pressure. Contaminants have been found in Arctic carnivores, but unfortunately, as with many other Arctic species, their sensitivities to contaminants and pollutants are largely unknown. Changes in climate, including temperature, snowfall and ice cover, have been shown to influence population densities. However, complex interactions between climate change and other factors can magnify impacts on biodiversity (CAFF 2010). Land-use changes have altered species distributions, migration routes and home ranges. Carnivorous species depend on other animals as targeted prey or via scavenging, so that changes in other species' populations often alter the demography of Arctic carnivores. There is limited information regarding effects of disease and parasites on Arctic terrestrial mammal carnivores. We now detail these causes and prospects.

#### Hunting and trapping

Current population sizes are commonly affected by hunting and trapping because fur-bearing mammals have experienced heavy harvest rates in some regions. For many mammalian carnivore populations, hunting and trapping pressure has decreased with declining fur prices (e.g. Arctic fox; Angerbjörn *et al.* 2004), yet for others it is still a concern. Increased access to northern regions via roads, all-terrain vehicles and snowmobiles has allowed hunters to cover more area, travel longer distances and visit more remote locations. This modernization of hunting has impacted all harvested species. In addition to legal harvesting, poaching is also an issue for some species.

In some regions of Canada's North, gray wolves were trapped and poisoned during the 1950s until they were extirpated. Poisoning, now illegal, has mostly been discontinued. Gray wolves are currently harvested for both commercial and subsistence use (Van Zyll de Jong & Carbyn 1999). On some Arctic islands, the annual harvest may be as high as 25% of the total population (Carmichael *et al.* 2001). In E Greenland, wolves were exterminated by commercial hunters in the 1930s, but recolonization has occurred due to migrating wolves from Canada (Marquard-Petersen 2009, 2011). Currently, wolverines are also harvested in some regions.

The Arctic fox in Scandinavia is classified as critically endangered after having experienced intensive hunting in the early 20th century, resulting in the population declining to a few hundred individuals (Lönnberg 1972 in Dalén *et al.* 2006); this population has failed to recover despite more than 65 years of protection (Dalén *et al.* 2006). However, Arctic foxes are sustainably hunted in Iceland, where red foxes are absent (Hersteinsson 2010).

Persson *et al.* (2009) suggest that poaching affects wolverine population dynamics in northern Scandinavia, causing up to 60% of adult mortality. In the forest and tundra areas of western Russia (specifically the Archangelsk Oblast region), the wolverine population is believed to be limited by motorized hunting (Landa *et al.* 2000). Wolverines in Canada's low Arctic tundra are likely to experience an increase in mortality due to increasing levels of resident and sport hunting, as well as resource development activity (Mulders *et al.* 2007), but possible effects on their population are not known. Although the Norwegian wolverine population is considered endangered, regular harvest or killing of litters has become an important tool in wolverine population management (Sæther *et al.* 2005). However, current management quotas may be too high to maintain a viable wolverine population and, if continued, are likely to lead to extinction over large parts of Norway within a relatively short period (Sæther *et al.* 2005).

### Pollution

The sensitivities of most Arctic species to many contaminants are unknown (Brunström & Halldin 2000, Hoekstra *et al.* 2003), limiting the ability to determine the risk for future adverse health effects (Brunström & Halldin 2000). Top-level carnivores accumulate organochlorine contaminants (e.g. PCBs) to relatively high concentrations compared with other terrestrial mammals due to biomagnification (Hoekstra *et al.* 2003). Canadian data indicate that Arctic terrestrial mammals have lower organochlorine contaminant concentrations than marine mammals, but terrestrial mammals (e.g. Arctic fox, wolverine) that feed or scavenge on marine animals tend to have relatively high concentrations (Hoekstra *et al.* 2003, Fisk *et al.* 2005). Therefore, coastal populations could have higher organochlorine concentrations due to the increased contribution of marine biota to their overall diet. Conversely, heavy metal contaminant levels in Canadian terrestrial mammals are similar or greater than those seen in marine mammals (Fisk *et al.* 2005).

### Climate change

Changes in climate may be providing new habitats for southern species to extend their northern range limits. The current number of brown bears may be increasing due to the appearance of new ecological niches because of rising air temperatures in sub-Arctic regions (Mineev 2007). Similarly, North American river otters may prosper in previously marginal northern areas in Alaska (Feldhamer *et al.* 2003) and potentially other regions. More extensive research has been conducted on the range expansion of red fox. Hersteinsson & Macdonald (1992) analyzed factors limiting the distribution of red foxes at their northern limit and found that summer temperature limited fox distribution. However, variables related to winter conditions (minimum temperature, maximum snow depth and duration of snow cover) may also have a significant effect (Hersteinsson & Macdonald 1992, Barton & Zalewski 2007, Gallant *et al.* 2012). On Iceland red fox are absent, providing an important opportunity to study the Arctic fox's response to climate change.

Decreased amounts of snow may be considered as habitat loss in some species. Brodie & Post (2010) argue that wolverine population declines may in part result from declining snowpacks, with snow accumulations being reduced by warmer winters. Declining snowpack could affect demographics of carnivores by reducing reproductive success due to decreased availability of den sites that require snow for den structure and insulation (Magoun & Copeland 1998, Aubry *et al.* 2007), decreased juvenile survival due to altered thermal regimes (Pulliainen 1968 and Bjärvall *et al.* 1978 in Copeland *et al.* 2010), altered availability of food in winter and early spring (Persson 2005, Lofroth *et al.* 2007), and reduced density of ungulate carcasses through increased ungulate survival (Wilmers & Post 2006).

In some regions, prolonged snow cover during summer is also possible due to climate change (via increased precipitation and decreased summer temperatures). It has been suggested that snow-covered vegetation may increase herbivore mortality and as a result augment wolf reproduction on Ellesmere Island, Canada (Mech 2004).

Several Arctic mammals use sea ice for travel, and ongoing decreases in the extent or duration of sea ice may impact genetic diversity of these species. For example, sea ice is necessary for the dispersal of Arctic fox between island populations, and if seasonal ice connections between Arctic islands are lost, small isolated populations of foxes will lose genetic diversity and have higher levels of inbreeding and genetic divergence (Geffen *et al.* 2007). The two wolf populations on Banks Island and the high Arctic (Ellesmere and Devon Islands) show genetic signatures of recent population declines, suggesting that their recovery is a result of recolonization from other islands; therefore these wolves may function as a metapopulation, where migration is occurring primarily through two sea ice corridors from Baffin Island and Victoria Island, respectively (Carmichael *et al.* 2008).

### Industrial development and land-use changes

Industrial developments and landscape alterations affect species by fragmenting habitat, altering migration corridors and increasing human access. An increase in barriers due to habitat loss between populations causes decreases in immigration and potentially reduced gene flow (see Linnell *et al.* 2005 and Aspi *et al.* 2009 for discussion on gray wolves).

Mineral exploration and developments in Canada's central Arctic has led to increased human presence in this region. Johnson *et al.* (2005) examined factors that influenced the distribution of gray wolves, brown bears, wolverines and barren-ground caribou. They found that mines and other major developments had the largest negative effect on species' occurrence, followed by exploration activities and outfitter camps. Wolves and bears had the strongest negative response to human disturbances (Johnson *et al.* 2005).

Migration of brown bears from Russia to Finland has provided a stable source of immigrants to repopulate Finland and maintain a high genetic diversity within the re-established region (Saarma & Kojola 2007), but increased fragmentation or barriers could limit this migration.

Human actions likely will be a controlling factor in the success and persistence of wolverine populations. Increasing levels of human development and harvesting pressures may cause further habitat loss and fragmentation for the wolverine populations across the Northwest Territories (COSEWIC 2003). Although the cumulative effects of habitat alteration, increased road building and traffic are not fully understood, developments in the Arctic tundra frequently attract wolverines, which may be killed as nuisance animals (COSEWIC 2003). Potential cumulative impacts of habitat loss, disturbance and increasing mortality pressures may lead to a decline in wolverine abundance (Mulders *et al.* 2007). Increased road access usually results in greater hunting and trapping pressure, which is a primary mortality factor for wolverines (Hornocker & Hash 1981, Magoun 1985). Wolverines may be especially vulnerable on the Arctic tundra, where visibility and snowmobile access are good (COSEWIC 2003). A hunter from Inuvik, Northwest Territories, noted that seismic lines cut for oil and gas exploration are a threat to wolverine habitat (Cardinal 2004), and others noted that new roads would allow hunters greater access (Cardinal 2004).

In Canada's central Arctic, brown bears could be in danger of population decline if human activity proceeds at an increasing rate (McLoughlin *et al.* 2003). The barren-ground brown bear might be more susceptible to human activity due to their large spatial requirements compared with other brown bears in North America (McLoughlin *et al.* 1999). Similarly, disturbance from diamond mining and road construction near wolf dens has a negative effect on their reproductive success directly or, indirectly, by altering the distribution or timing of movements of caribou, their main prey (Walton *et al.* 2001).

**Parasites and diseases**

Due to the distances these species travel, diseases may be transmitted over long distances. However, the low population densities of these species also act to reduce disease transmission. An outbreak of sarcoptic mange *Sarcoptes scabiei* occurred in Scandinavian red foxes during the late 1970s and 1980s (Lindström *et al.* 1994). Within eight years, the sarcoptic mange had spread over mainland Sweden and killed approximately 50% of the red fox population (Lindström & Mörner 1985), with as much as 90% mortality reported in some regions (Mörner 1992). The Scandinavian red fox population began to recover in the late 1980s (Lindström *et al.* 1994). Encephalitozoonosis *Encephalitozoon cuniculi* is thought to influence Arctic fox population dynamics in Iceland (Hersteinsson *et al.* 1993). Currently, rabies is regarded as endemic among Arctic and red fox in northern and western regions of Alaska, with a 3-4 year cyclic epidemic occurrence (Ritter 1981 and Follmann 1990 in Mørk & Prestrud 2004), and in Svalbard and NW Russia (Mørk *et al.* 2011).

It is currently unknown what parasites and diseases may threaten Arctic carnivores in the future. A number of diseases and parasites of domestic species could be detrimental. Also, some previously recorded diseases, including those from temperate latitude populations, could be devastating if outbreaks were to occur. An example is sarcoptic mange in isolated fox populations such as those on islands (Henriksen *et al.* 1993).

## 3.6. MARINE MAMMALS

The world's marine mammals were recently classified as disproportionately threatened and data poor compared with their terrestrial counterparts. Their status was noted of particular concern, and several reviews have outlined global conservation issues (Schipper *et al.* 2008, Kovacs *et al.* 2012). Several species inhabit the Arctic marine biome exclusively and are specially adapted to the dynamic and extreme environment (Laidre *et al.* 2008a). Arctic marine mammals are highly associated with sea ice or are sea ice obligates – meaning their life history events (reproduction, molting, resting) and feeding behavior are closely linked to sea ice dynamics. With some exceptions, these species range widely and undergo large seasonal migrations, covering thousands of kilometers in a single year. Most species of endemic Arctic marine mammals are also important cultural and food resources for indigenous peoples.

Assessing the status and trends of marine mammal populations in the Arctic is difficult because of the elusive nature of many species and their large ranges. Further, there are logistical challenges associated with surveying vast remote marine areas. Therefore, there are numerous data gaps even for basic information such as population sizes, trends and distributions. Here we summarize what is known about these parameters for marine mammals that inhabit low and high Arctic waters and we discuss implications of data gaps given predictions of sea ice loss and climate warming (e.g. IPCC 2007).

### 3.6.1. Species richness and distribution

#### 3.6.1.1. Status

There are 35 species of marine mammals that inhabit or seasonally use Arctic waters. In this review, we discuss these species in the context of 12 regions in low or high Arctic waters (Appendix 3.2, Fig. 3.5). Of these species, seven are endemic to the Arctic and are dependent on, or highly associated with, sea ice for all or parts of the year. We refer to these as the core Arctic species, and they are the narwhal, beluga *Delphinapterus leucas*, bowhead whale, ringed seal *Pusa hispida*, bearded seal *Erignathus barbatus*, walrus and polar bear. In addition, four other ice seal species are highly dependent on sea ice for pupping in the low Arctic in spring, but are generally pelagic or use sub-Arctic waters for the rest of the year. We include these in this assessment, and they are the spotted seal *Phoca largha*, ribbon seal *Phoca fasciata*, harp seal *Pagophilus groenlandicus* and hooded seal *Cystophora cristata*.

The three species of Arctic cetaceans have different patterns of distribution and population structure. The beluga has a circumpolar Arctic distribution and is found in discrete subpopulations in the high and low Arctic, generally defined by summering areas (O'Corry-Crowe *et al.* 1997, Richard *et al.* 2001, Innes *et al.* 2002, Palsbøll *et al.* 2002). The narwhal is confined to the Atlantic Arctic in the eastern Canadian high Arctic and in waters around W and E Greenland, Svalbard and Franz Joseph Land (Gjertz 1991, Koski & Davis 1994, Dietz *et al.*

**Figure 3.5.** Regions used to enumerate Arctic marine mammal species. High Arctic and low Arctic marine boundaries are shown with solid and dashed lines, respectively. These were used to define areas in Appendix 3.2. We do not include species that only use sub-Arctic waters, except for the seasonally ice covered Sea of Okhotsk, entirely within the sub-Arctic, where several populations of core Arctic marine mammals occur. Note that while populations and species are enumerated within regions, individuals frequently cross several regional boundaries.

2001, Heide-Jørgensen & Aquarone 2002, Innes *et al.* 2002). Narwhals sporadically move into Russian and occasionally Alaska Arctic waters from the Barents Sea through to the Chukchi Sea (Burdin *et al.* 2009, Allen & Angliss 2011). The bowhead whale, the only mysticete to inhabit the Arctic year round, has a circumpolar distribution with most populations moving between high Arctic waters in summer and low Arctic waters in winter (Braham *et al.* 1980, Ellison *et al.* 1987, George *et al.* 1989, Moore & Reeves 1993, Heide-Jørgensen *et al.* 2006, Citta *et al.* 2012). However, individuals of the Svalbard-Barents Sea stock overwinter in the high Arctic (Lydersen *et al.* 2012, Stafford *et al.* 2012).

Of the true Arctic pinnipeds, ringed seals have a circumpolar distribution, inhabiting permanently or seasonally ice-covered areas from the North Pole to the low Arctic with their distribution extending into some lake and river systems in northern Canada (Kovacs *et al.* 2008). Bearded seals also have a circumpolar distribution in the Arctic.

Polar bears have a circumpolar distribution. They occur throughout ice-covered Arctic regions, especially in areas of annual ice cover over the continental shelf and the inter-island channels of various archipelagos. Their distribution is not uniform, and the global population is divided into 19 recognized sub-populations (Paetkau *et al.* 1999, Obbard *et al.* 2010).

Walruses have a discontinuous circumpolar distribution with two recognized subspecies: the Atlantic walrus *Odobenus rosmarus rosmarus* distributed from the eastern Canadian Arctic to the Kara Sea, and the Pacific walrus distributed in the Pacific Arctic from Mys Shelagskyi in Siberia to Barter Island in Alaska and in the Bering and Chukchi Seas. A third subspecies, the Laptev walrus *O. r. laptevi*, confined to the Laptev Sea region was suggested (Chapskii 1940) based on a limited sample (Fay 1985), but recent molecular genetics studies concluded that the Laptev walrus belongs with the Pacific subspecies (Lindqvist *et al.* 2009).

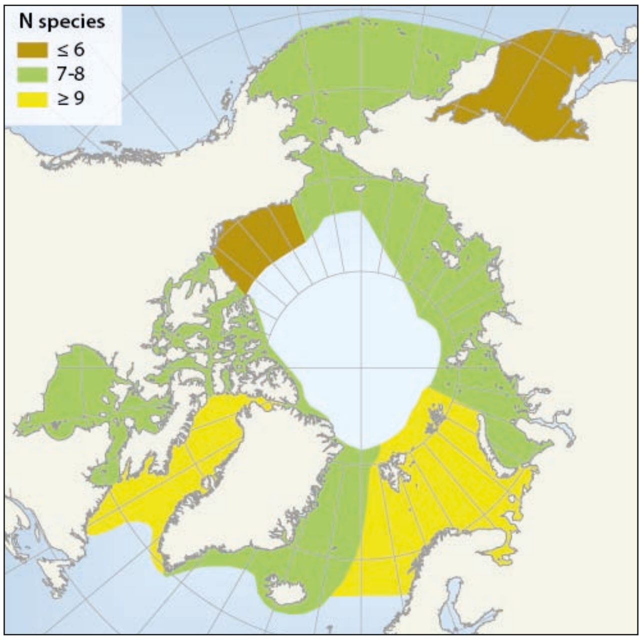

**Figure 3.6.** Species richness of marine mammals (n = 11 core Arctic marine mammals only) in high and low Arctic waters.

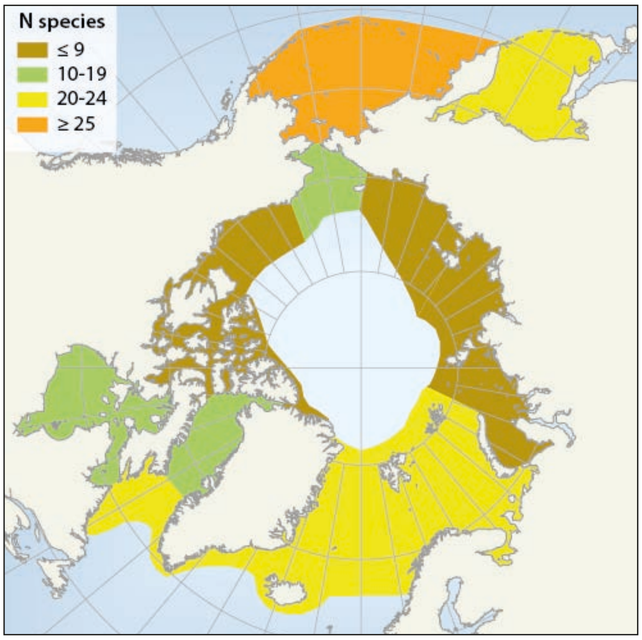

**Figure 3.7.** Species richness map of marine mammal that are present or seasonally occur in low and high Arctic waters at any time of the year (n = 35).

Of the four sub-Arctic ice seal species, the spotted seal and ribbon seal are found in the Pacific Arctic and peripheral seas (Burns 1981, Boveng *et al.* 2008, Boveng *et al.* 2009). Conversely, the harp seal and hooded seal are confined to the Atlantic Arctic, and are widely distributed throughout the North Atlantic and Arctic Ocean shelf and seas (Lavigne & Kovacs 1988, Kovacs 2008a, 2008b).

Species richness for the resident Arctic marine mammals (n = 11) is highest in three regions: Baffin Bay, Davis Strait and the Barents Sea, where nine of 11 species are present (Fig. 3.6). Most other regions have seven or eight Arctic species present. The Beaufort Sea and the Sea of Okhotsk regions have six species.

In addition to the 11 Arctic ice-dependent species discussed above, there are 24 other marine mammal species that occur in low Arctic waters or migrate to the high and low Arctic seasonally, from tropical and temperate waters, to feed (Appendix 3.2). These species do not depend on the Arctic ecosystem year-round. They include four species of pinnipeds: the northern fur seal *Callorhinus ursinus* and the Steller sea lion *Eumetopias jubatus* found in the Pacific low Arctic within the Okhotsk and Bering Seas (Pribilof Islands); the gray seal *Halichoerus grypus* found in the Atlantic Arctic, and the harbor seal *Phoca vitulina* which occurs in low Arctic waters of the Atlantic and Pacific, with one population living in the high Arctic in Svalbard.

Nineteen species of cetaceans seasonally use low or high Arctic waters. The North Pacific right whale *Eubalaena japonica* and the gray whale *Eschrichtius robustus* are confined to the Pacific low and high Arctic. The North Atlantic right whale uses low Arctic waters of E Greenland. The blue whale *Baleanoptera musculus*, fin whale *Balaenoptera physalus*, sei whale *Balaenoptera borealis*, minke whale *Balaenoptera acutorostrata* and humpback whale *Megaptera novaeangliae* are found in both low and high Arctic waters in summer in both the Atlantic and Pacific. The sperm whale *Physeter macrocephalus* can also be found in the low Arctic waters of both the Atlantic and Pacific. Baird's beaked whale *Berardius bairdii*, Stejneger's beaked whale *Berardius stejnegeri* and Cuvier's beaked whale *Ziphius cavirostris* are all found in the low Arctic waters of the Pacific Arctic, specifically in the Okhotsk and the Bering Seas. The northern bottlenose whale *Hyperoodon ampullatus* is found in the low Arctic waters of the Atlantic, including Davis Strait, Baffin Bay, E Greenland and the Barents Sea.

Among the delphinids and porpoises, the killer whale *Orcinus orca* visits circumpolar Arctic waters during the ice-free season in nearly all regions. The white-beaked dolphin *Lagenorhynchus albirostris*, long-finned pilot whale *Globicephala melas* and Atlantic white-sided dolphin *Lagenorhynchus acutis* are all found in the Atlantic low Arctic during summer. Dall's porpoise *Phocoenoides dalli* occurs in low Arctic waters of the Pacific, while harbor porpoise *Phocoena phocoena* are found in low Arctic waters of both the Atlantic and Pacific.

Finally, the sea otter *Enhydra lutris* extends peripherally into low Arctic waters in the southern Bering Sea. For this species, sea ice is a serious impediment, causing animals to die or abandon areas when coverage becomes too extensive (Schneider & Faro 1975). This population was nearly extirpated early in the Russian fur trade, but slowly re-colonized its range (Kenyon 1969).

When species richness is examined for all 35 marine mammal species that occur in the high and low Arctic combined, including seasonal visitors, diversity is highest in the Bering Sea (n = 25 species present in some season of the year). Other regions with high species richness include Davis Strait (n = 23 species) and E Greenland (n = 23 species) (Fig. 3.7).

### 3.6.1.2. Trends

Many marine mammal populations were severely reduced due to extensive commercial whaling, commercial fur trade, or subsistence hunting that took place across the Arctic over the past several centuries. Heavy harvesting reduced many populations to very low numbers and contracted ranges, with most rendered close to extinct (e.g. E Greenland-Svalbard-Barents Sea bowhead whale, Wiig *et al.* 2010). Similarly, excessive harvest during the commercial whaling era extirpated the Atlantic gray whale and the Northeast Atlantic right whale *Eubalaena glacialis* (Krupnik 1993, Nowak 1999). Therefore, changes in the distributions of marine mammals in low and high Arctic areas have occurred as several populations have recovered over the past 50-100 years. In this review, we focus on recent changes (< 50 years) in distribution and abundance related to climate warming rather than changes in distribution related to recovery of populations after depletion.

> » *... once the [commercial] whalers came they killed off lots of bowhead whales, thus the very evident decrease in population among the bowhead whales ...*
>
> (Mikitok Bruce, quoted in NWMB 2000).

Changes in the distribution of species or populations of marine mammals require investigations on long time-scales, far longer than the context of most present-day ecological studies or monitoring programs (Laidre *et al.* 2008a). Obtaining this trend information for Arctic marine mammals requires extensive and expensive surveys conducted over decades. Thus relatively few data are available from the past 50 years. Recent documented examples of changes in distribution of Arctic marine mammals are varied, ranging from expansion to distributional shifts to local extirpation, making broad generalizations difficult. Here we discuss some of the best documented changes in distribution that are thought to be climate-change related.

In W Greenland, a clear relationship between the extent of annual sea ice cover in Baffin Bay and the offshore distance of beluga whales was established based on 30 years of aerial survey data. Beluga whales have shifted their distribution westward (offshore) with the receding sea ice edge as the banks off W Greenland open up earlier in spring (Heide-Jørgensen *et al.* 2010a).

Recent data suggest that geographic barriers (such as heavy sea ice in narrow straits) that have separated bowhead whales in Alaska and Greenland may be disappearing with sea ice loss. Two satellite-tagged bowhead whales, one from W Greenland and one from N Alaska, entered the Northwest Passage from opposite directions and spent approximately 10 days in the same area in 2010 (Heide-Jørgensen *et al.* 2011a). Other than ancillary evidence from harpoon remains in blubber, this is the first time geographic overlap between the Bering-Chukchi-Beaufort and the Davis Strait-Baffin Bay bowhead whale populations has been directly observed and documented. These populations were likely connected for periods during the Pleistocene, but have been assumed to be historically separated by sea ice in the Northwest Passage. Reductions in summer ice in the Northwest Passage may be facilitating exchanges between these and possibly other populations or species.

Polar bears have demonstrated shifts in summer and fall distribution in recent decades. As sea ice recedes or breaks up earlier, more polar bears are arriving on land earlier, staying for longer periods and appearing in areas not used previously (Stirling *et al.* 1999, Fischbach *et al.* 2007, Schliebe *et al.* 2008, Gleason & Rode 2009). This has been primarily documented in the Beaufort Sea and in western Hudson Bay and is attributed to sea ice loss. Polar bear denning locations have also shifted in some regions in response to changing ice conditions, with more dens appearing on land (Fischbach *et al.* 2007). Changes in access to traditional denning areas have also occurred with the disappearance of sea ice as a platform to allow movement to islands (Derocher *et al.* 2011).

Pacific walrus have recently been hauling out on land along the Alaska and Chukotka coasts of the Chukchi Sea in the summer (Garlich-Miller *et al.* 2011). This behavior is attributed to loss of annual Arctic sea ice and the retreat of the pack ice beyond the continental shelf of the Chukchi Sea in summer. While fall (October-November) migratory aggregations of Pacific walrus have been observed on the Alaska coast in the past, the summer haul outs are a new phenomenon and occur primarily north of Point Lay (Garlich-Miller *et al.* 2011).

Rosing-Asvid (2008) reported a change in distribution of whelping harp seals around W Greenland. This species is dependent on stable ice for the whelping and lactation period lasting 12 days in spring. In recent years, unprecedented high numbers of harp seals have been found concentrated along the ice edge of central W Greenland in late January and early February, including pregnant females with fetuses close to birth weight. This suggests that harp seals may be whelping in new areas. In addition, large anomalous herds of harp seals have been seen around Svalbard during winter where they previously occurred only in summer (Kovacs *et al.* 2011).

Recent studies suggest that changes in the distribution of sub-Arctic species have also been observed, although the increase in research effort and new techniques being used over the past 10 years may be responsible in part for the new information. In the Canadian high Arctic, killer whales have been reported to be expanding their range northward during the ice-free period (Higdon & Ferguson 2009). Opportunistic and anecdotal data also suggest sub-Arctic baleen whales are occurring farther north, possibly expanding their range with longer ice-free seasons (Kovacs *et al.* 2011, Higdon & Ferguson 2011). Passive moored buoys indicate that fin whales are present in the Bering Sea and Davis Strait almost year-round, when the waters are free of sea ice (Simon *et al.* 2010, Stafford *et al.* 2010). In Fram Strait, calls from blue whales have been recorded from June to October while calls from fin whales were recorded from August to March (Moore *et al.* 2012a). Mellinger *et al.* (2011) recorded data from 2007-2008 showing evidence that North Atlantic right whales may now occupy SE Greenland, an important nineteenth century whaling area from which they were thought to have been extirpated.

## 3.6.2. Population sizes and densities

### 3.6.2.1. Status

Very few populations of marine mammals have been studied anywhere in the Arctic for long enough to allow a comprehensive assessment of the possible effects of long-term climate warming on population size and demographic parameters (Laidre *et al.* 2008a). The true population size of many species and subpopulations is unknown. For the 11 endemic Arctic marine mammal species, worldwide population sizes range widely, between ~ 20,000 to many millions (Tab. 3.5).

Beluga abundance worldwide is estimated to be at least 150,000 individuals (Harwood *et al.* 1996, Boltunov & Belikov 2002, Innes *et al.* 2002, Jefferson *et al.* 2008). This species is assessed according to 29 subpopulations defined by summering areas (IWC 2000). Large populations of beluga (20,000-40,000 individuals) occur in the eastern Bering Sea, the eastern Beaufort Sea and western Hudson Bay. However current population sizes are unavailable for some of these subpopulations because surveys have not been conducted in these areas for > 15 years (Allen & Angliss 2011). Population estimates are available for some subpopulations because they are monitored at regular intervals (e.g. Cook Inlet) (Hobbs *et al.* 2011). Lowry *et al.* (2008) documented a maximum uncorrected index count in Bristol Bay of approximately 1,000 whales. Almost nothing is known about population abundance of belugas in the Russian sector of the Arctic, in a continuum including the Kara, Laptev and East Siberian Seas. Similarly, no abundance determinations have been attempted for beluga in Norwegian waters.

> » *During winter, when the high tide comes, the beach ice will be saturated with water leaking through shoreline cracks. When the high tide and strong currents come, it is time to look for beluga whales because the winds will be strong and coming from the northwest. That is when you expect to see some beluga at the floe edge.*
>
> (Noah Isaac, quoted in McDonald *et al.* 1997).

The worldwide population of narwhals is ~ 100,000 animals (Koski & Davis 1994, Innes *et al.* 2002, Heide-Jørgensen *et al.* 2010b, Richard *et al.* 2010). Similar to belugas, narwhals are divided into several subpopulations based on summering location. The narwhals that summer in the Canadian high Arctic and eastern Baffin Island number at least 70,000 animals (Innes *et al.* 2002, NAMMCO 2005, Richard *et al.* 2010), and the primary subpopulations are located at Somerset Island, Admiralty Inlet, Eclipse Sound and E Baffin Island, and northern Hudson Bay. Some areas in Canada, such as near Ellesmere Island, contain other unsurveyed aggregations which are thought to contain small numbers of whales. In W Greenland, the primary subpopulations are centered at Inglefield Bredning and Melville Bay (Heide-Jørgensen 2004, Heide-Jørgensen *et al.* 2010b). The number of subpopulations in E Greenland is unknown, but approximately 6,000 summer between Scoresby Sound and Ammassalik (Heide-Jørgensen *et al.* 2010b).

Bowhead whales number fewer than 20,000 worldwide (George *et al.* 2004, Cosens *et al.* 2006, Heide-Jørgensen *et al.* 2007). There are five recognized subpopulations: Bering-Chukchi-Beaufort Seas, Hudson Bay-Foxe Basin, Davis Strait-Baffin Bay, Svalbard-Barents Sea and the Okhotsk Sea (Rugh *et al.* 2003). Recent data have called into question the distinction between the Hudson Bay-Foxe Basin and the Davis Strait-Baffin Bay stocks (Heide-Jørgensen *et al.* 2006, Ferguson *et al.* 2010, Givens *et al.* 2010), and herein we refer to these stocks as the combined eastern Canada-W Greenland stock. The largest fraction of the global population is located in the Bering-Chukchi-Beaufort Seas, with a population estimate from 2001 of 12,631 (95% CI: 7,900-19,000) (Koski *et al.* 2010). The eastern Canada-W Greenland stock is estimated to number about 6,500 individuals (Heide-Jørgensen *et al.* 2007, IWC 2008, Wiig *et al.* 2010). The population in Svalbard-Barents Sea has not been estimated due to low numbers, although up to 17 bowhead whales were sighted on summer surveys between 2006 and 2008 in NE Greenland and the Fram Strait, indicating that whales do persist in this area (Rugh *et al.* 2003, Boertmann *et al.* 2009, Wiig *et al.* 2010). There is a small population in the Sea of Okhotsk that likely numbers < 400 animals but no recent surveys have been conducted (Ivaschenko & Clapham 2009).

The worldwide abundance of ringed seals is likely in the low millions (Frost & Lowry 1981, Reeves 1998), estimated by Kelly *et al.* (2010) as 4-7 million. There are few data available on regional population sizes. Five subspecies of ringed seals are recognized: *P. h. hispida* (Arctic ringed seal) is thought to number about 2.5 million animals, while *P. h. ochotensis* (Sea of Okhotsk ringed seal) numbers > 800,000 animals (Miyazaki 2002). The three other sub-species *P. h. botnica* (Baltic Sea ringed seal), *P. h. ladogensis* (Lake Ladoga ringed seal), and *P. h. saimensis* (Lake Saimaa ringed seal) are not assessed here. Few regional estimates exist for *P. h. hispida*. In Hudson Bay, ringed seal abundance has been estimated at over 500,000 individuals (Stewart & Lockhart 2005, Hoover

**Table 3.5.** Subpopulations or stocks for each true Arctic marine mammal together with abundance estimate (abundance may be from dedicated survey with 95% CI, ballpark/rough estimate, or simulated from Population Viability Analysis). Year for estimate is given together with known trend in abundance (increasing, decreasing, stable or unknown). See text for rates.

| Species | Subpopulation/Stock | Abundance | Year | Trend | Citation |
|---|---|---|---|---|---|
| Beluga | E Siberian & W Chukchi Seas | Unknown | | Unknown | |
| | Eastern Chukchi Sea | 3,700 | 1992 | Unknown | Frost *et al.* 1993 |
| | Eastern Beaufort Sea | 41,800 | 1999 | Unknown | Duval 1993, Kingsley & Gauthier 2002, Allen & Angliss 2011 |
| | Eastern Bering Sea | 18,000 | 1989-1991 | Unknown | Allen & Angliss 2011 |
| | Bristol Bay | 1,600 | 2000 | Increasing | Lowry *et al.* 2008 |
| | Cook Inlet | 284 (95% CI: 207-389) | 2010 | Declining | Allen & Angliss 2011, Hobbs *et al.* 2011 |
| | Western Hudson Bay | 57,300 (95% CI: 37,700-87,100) | 1978, 1987, 2004 | Unknown | Richard *et al.* 1990, Richard 1993, Richard 2005 |
| | Southern Hudson Bay | 7,000 | 1987 | Unknown | Ognetov 1987, Richard 2005 |
| | James Bay | 9,292 (95% CI: 2,828-30,530) | 2008 | Unknown | Ognetov 1987, Gosselin *et al.* 2009 |
| | Eastern Hudson Bay | 2,646 (SE = 1,959) | 2008 | Declining | Gosselin *et al.* 2009, Bourdages *et al.* 2002 |
| | St. Lawrence Estuary | 1,100 | 1997 | Stable | Gosselin *et al.* 2007, Hammill *et al.* 2007 |
| | Ungava Bay | <50 | 2007 | Unknown | Gosselin *et al.* 2009, Hammill *et al.* 2004 |
| | Cumberland Sound | 1,500 | 2001 | Unknown | COSEWIC 2004 |
| | E high Arctic-Baffin Bay | 21,200, ± 25% CV | 1996 | Unknown | Innes *et al.* 2002 |
| | W Greenland winter | 10,595 (95% CI: 4,904-24,650) | 2006 | Unknown | Heide-Jørgensen & Aquarone 2002, Heide-Jørgensen *et al.* 2003, Heide-Jørgensen *et al.* 2010a |
| | White Sea | 8,000 | 2005 | Declining | Burdin *et al.* 2009 |
| | Svalbard | Unknown | | Unknown | Kovacs & Lydersen 2006, Gjertz & Wiig 1994 |
| | Kara & Laptev Seas | Unknown | | Unknown | |
| | Gulf of Anadyr | Unknown | | Unknown | |
| | Okhotsk Sea | 18,000-20,000 | 1987 | Unknown | Ognetov 1987 |
| Narwhal | Eclipse Sound stock | 20,225 (95% CI: 9,471-37,096) | 2004 | Unknown | Richard *et al.* 2010 |
| | Admiralty Inlet stock | 18,049 (95% CI: 11,613-28,053) | 2010 | Unknown | Richard *et al.* 2010, Asselin & Richard 2011 |
| | Somerset Island stock | 45,358 (95% CI: 23,397-87,932) | 2002 | Unknown | Innes *et al.* 2002, Richard *et al.* 2010 |
| | E Baffin fiords stocks | 10,073 (95% CI: 5,333-17,474) | 2003 | Unknown | Richard *et al.* 2010 |
| | W Greenland Inglefield Bredning stock | 8,368 (95% CI: 5,209-13,442) | 2007 | Unknown | Heide-Jørgensen *et al.* 2010b |
| | W Greenland Melville Bay stock | 6,024 (95% CI: 1,403-25,860) | 2007 | Unknown | Heide-Jørgensen *et al.* 2010b |
| | Northern Hudson Bay | 5,053 ± 40% CV | 2000 | Unknown | COSEWIC 2004, Richard 2008 |
| | W Greenland winter aggregations | 7,819 (95% 4,358-14,029) | 2006 | Unknown | Heide-Jørgensen *et al.* 2010b |
| | E Greenland | 6,444 (95% 2,505-16,575) | 2008 | Unknown | Heide-Jørgensen *et al.* 2010b |
| Bowhead | Bering-Chukchi-Beaufort Seas (BCB) | 12,631 (95% CI: 7,900-19,000) | 2001 | Increasing | George *et al.* 2004, Koski *et al.* 2010 |
| | E Canada-W Greenland (BBDS and FBHB) | 6,500 | 2002-2009 | Increasing | Heide-Jørgensen *et al.* 2007, IWC 2008, Wiig *et al.* 2011 |
| | Svalbard-Barents Sea | Unknown | – | Unknown | Rugh *et al.* 2003, Boertmann *et al.* 2009, Wiig *et al.* 2010 |
| | Okhotsk Sea | <400 | 1979 | Unknown | Rugh *et al.* 2003, Ivaschenko & Clapham 2009 |

(continues >)

(continued)

| Species | Subpopulation/Stock | Abundance | Year | Trend | Citation |
|---|---|---|---|---|---|
| Ringed seal | Arctic subspecies | ~2.5 million | 1970s | Unknown | Miyazaki 2002 |
| | Okhotsk Sea subspecies | >800,000 | 1971 | Unknown | Miyazaki 2002 |
| | Hudson Bay | 516,000 | 1995 | Unknown | Stewart & Lockhart 2005 |
| Bearded seal | Bering-Chukchi Seas | 250,000-300,000 | 1970s | Unknown | Fedoseev 2000 |
| | Canadian waters | 190,000 | 1958-1979 | Unknown | Cleator 1996 |
| | Atlantic and Russian Arctic | Unknown | – | Unknown | – |
| | Okhotsk Sea | 200,000-250,000 | 1968-1969 | Unknown | Fedoseev 2000 |
| Walrus | Bering-Chukchi Seas | ~129,000 | 2006 | Unknown | Speckman *et al.* 2011 |
| | Atlantic subspecies | ~20,000 | 1995-2009 | Mixed | Born *et al.* 1995, Witting & Born 2005, COSEWIC 2006, Lydersen *et al.* 2008, NAMMCO 2009 |
| | Laptev Sea | 3,000-5,000 | 1992 | Unknown | Belikov & Boltunov 2005, Burdin *et al.* 2009 |
| Polar bear | Arctic Basin | Unknown | – | Unknown | Obbard *et al.* 2010 |
| | Baffin Bay | 1,546 (690-2,402) | 2004 | Declining | Obbard *et al.* 2010 |
| | Barents Sea | 2,650 (1,900-3,600) | 2004 | Unknown | Obbard *et al.* 2010 |
| | Chukchi Sea | Unknown | – | Declining | Obbard *et al.* 2010 |
| | Davis Strait | 2,158 (95% CI: 1,833-2,542) | 2007 | Stable | Peacock *et al.* 2013 |
| | E Greenland | Unknown | – | Unknown | Obbard *et al.* 2010 |
| | Foxe Basin | 2,578 (2,088-3,182) | 2007 | Unknown | Obbard *et al.* 2010 |
| | Gulf of Boothia | 1,592 (870-2,314) | 2000 | Stable | Obbard *et al.* 2010 |
| | Kane Basin | 164 (94-234) | 1998 | Declining | Obbard *et al.* 2010 |
| | Kara Sea | Unknown | – | Unknown | Obbard *et al.* 2010 |
| | Lancaster Sound | 2,541 (1,759-3,323) | 1998 | Declining | Obbard *et al.* 2010 |
| | Laptev Sea | Unknown | 1993 | Unknown | Obbard *et al.* 2010 |
| | M'Clintock Channel | 284 | 2000 | Increasing | Obbard *et al.* 2010 |
| | Northern Beaufort Sea | 1,202 (686-1,718) | 2006 | Stable | Obbard *et al.* 2010 |
| | Norwegian Bay | 190 (102-278) | 1998 | Declining | Obbard *et al.* 2010 |
| | Southern Beaufort Sea | 1,526 (1,210-1,842) | 2006 | Declining | Obbard *et al.* 2010 |
| | Southern Hudson Bay | 900-1,000 (496-1,050) | 2005 | Stable | Obbard *et al.* 2010 |
| | Viscount Melville | 215 (99-331) | 1992 | Unknown | Obbard *et al.* 2010 |
| | Western Hudson Bay | 935 (794-1,076) | 2004 | Declining | Obbard *et al.* 2010 |

2010). In this area, densities are greater on landfast ice (1.3-3.4 seals/km$^2$) compared with pack ice (0.2-1.8 seals/km$^2$) (Chambellant 2010), and density estimates vary considerably from year-to-year (0.5-1.6 seals/km$^2$ (Smith & Stirling 1975, Breton-Provencher 1979, Lunn *et al.* 1997, Chambellant 2010). An abundance estimate that included Svalbard's west and north coast suggested a population of 7,585 seals (95% CI: 6,332-9,085) (Krafft *et al.* 2006). In Svalbard, densities of ringed seals in the fjords range from 0.2 to 8.0 seals/km$^2$ (Krafft *et al.* 2006, Krafft *et al.* 2007) with large year to year variability due to sea ice cover. Overall ringed seals occur at lower densities in multi-year ice of the high Arctic compared with their preferred habitat in annual ice areas (Kingsley *et al.* 1985) probably because productivity is lower in the thicker ice and it is more difficult to maintain breathing holes in or between multi-year ice floes.

The global population size of bearded seals is unknown, but it has been estimated to be conservatively 438,000 (Cameron *et al.* 2010), at least 500,000 individuals (Kovacs & Lowry 2008), or even up to 750,000 (Chapskii 1966, Potelov 1975, Burns 1981, Cleator 1996). There are two putative subspecies of bearded seal, *Erignathus barbatus barbatus* and *E. b. nauticus* (Kovacs 2009), with the Atlantic subspecies *barbatus* occurring from the central Canadian Arctic east to the central Eurasian Arctic (Laptev Sea) and the Pacific subspecies *nauticus* occurring from the Laptev Sea east to the central Canadian Arctic, including the Sea of Okhotsk (Rice 1998). Rough estimates for bearded seal population size in all regions are over 50 years out of date, but range from ~ 300,000 animals in the Bering-Chukchi Seas, to about 200,000 animals in Canadian waters, to 250,000 in the Sea of Okhotsk. Numbers in the Atlantic and Russian regions are unknown (Cleator 1996, Fedoseev 2000). Lunn *et al.* (1997) estimated approximately 12,290 (SE = 2,520) bearded seals (or 0.122 seals/km$^2$ of sea ice) in western Hudson Bay.

Nineteen subpopulations of polar bears occur throughout the circumpolar Arctic (Obbard *et al.* 2010, Vongraven *et al.* 2012). The global population size of polar bears is 20,000 to 25,000 animals (Obbard *et al.* 2010). Genetic analysis indicates that there is considerable gene flow between some subpopulations, though others are relatively discrete (Paetkau *et al.* 1999). The largest polar bear subpopulation estimates are in Davis Strait with 2,158 (95% CI: 1,833-2,542) (Peacock *et al.* 2013), the Barents Sea with 2,650 animals (95% CI: 1,900-3,600) (Aars *et al.* 2009) and Foxe Basin with 2,578 animals (95% CI: 2,088-3,182) (Obbard *et al.* 2010). There are critical knowledge gaps about subpopulation sizes in E Greenland, the Russian Kara and Laptev seas, the Arctic Basin and the Chukchi Sea (Vongraven *et al.* 2012).

The size of the Pacific walrus population, which is managed as a single panmictic population (USFWS 2010), has never been known with much precision. Based on large sustained harvests in the 18th and 19th centuries, Fay (1982) speculated that the pre-exploitation population was a minimum of 200,000 animals. A recent survey conducted in the Bering Sea in 2006, estimated a population size of 129,000 individuals (95% CI: 55,000 to 507,000) in a portion of the range, or about half the potential walrus habitat (Speckman *et al.* 2011). The total population size of Atlantic walruses is thought to be about 20,000 animals (Born *et al.* 1995, Witting & Born 2005, COSEWIC 2006, Lydersen *et al.* 2008, NAMMCO 2009), comprising at least nine separate stocks: Foxe Basin, SE Hudson Bay, N Hudson Bay-Hudson Strait-N Labrador-SE Baffin Island-Central W Greenland, N Baffin Bay, W Jones Sound, Penny Strait-Lancaster Sound, E Greenland, Svalbard-Franz Josef Land, and Kara Sea-S Barents Sea-Novaya Zemlya. Walruses in the Laptev Sea are considered a separate stock based on geographical separation (Belikov & Boltunov 2005) and are estimated to number 3,000-5,000 animals.

Spotted seal range-wide abundance is poorly known. Boveng *et al.* (2009) concluded that there are likely to be at least 100,000 spotted seals in the Bering Sea (including the seasonal inhabitants of the Chukchi Sea), 100,000 in the Sea of Okhotsk and about 3,300 in the Yellow Sea and Sea of Japan. An aerial survey of a large portion of the breeding area of the eastern and central Bering Sea resulted in an estimate of 145,700 (95% CI: 96,893-331,700) (P. Boveng, pers. com.). Mizuno *et al.* (2002) flew aerial line-transect surveys over pack ice in parts of the southern Okhotsk Sea in March 2000 and estimated 13,653 spotted seals in a 25,000 km² region. Other estimates, reviewed by Boveng *et al.* (2009), are mostly outdated or unreliable due to weak or undocumented methodology or insufficient coverage.

Ribbon seal range-wide population size is poorly known. An aerial survey in 2007 of a breeding area in the eastern and central Bering Sea resulted in an estimate of about 62,478 (95% CI: 31,000 – 218,970) (P. Boveng, pers. com.). Based on that survey and historical estimates of relative numbers of ribbon seals in the eastern and western Bering Sea and the Sea of Okhotsk, Boveng *et al.* (2008) concluded that there are likely to be at least 200,000 ribbon seals. Other estimates include that from Burns (1981) who estimated the worldwide population of ribbon seals at 240,000 in the mid-1970s, with 90,000-100,000 animals in the Bering Sea and 140,000 animals in the Sea of Okhotsk. Fedoseev (2002) also reported an estimate of 120,000 to 140,000 animals for the Bering Sea in 1987 and estimated between 200,000 (1968-1974) and 630,000 (1988-1990) for the Sea of Okhotsk. Most of these historical estimates are of doubtful reliability because the methods were weak or undocumented. There are two main breeding areas for ribbon seals, one in the Sea of Okhotsk and one in the Bering Sea, but thus far there is no evidence on which to base a separation into distinct populations.

Harp seals are the most abundant pinniped species in the Northern Hemisphere (Kovacs 2008a) and worldwide number approximately 8 million. Three subpopulations of harp seals are recognized associated with the three whelping areas: (1) Labrador and Newfoundland coasts and in the Gulf of St Lawrence, (2) E Greenland (north of Jan Mayen), and (3) the White Sea (Lavigne & Kovacs 1988). Pup production at all breeding sites combined is at least 1.4 million pups per year (Potelov *et al.* 2003, Stenson *et al.* 2003, Haug *et al.* 2006). The NW Atlantic stock of harp seal numbers approximately 5.9 million animals (DFO 2005). The breeding group in E Greenland was estimated at 750,000 animals in 2008 (ICES 2008). The White Sea breeding group was estimated to be 1.8 million animals in 2000 (Potelov *et al.* 2003).

Hooded seal population size in the NW Atlantic has been estimated to be 592,000 individuals based on pup counts in 2005 (116,900 pups born) (Waring *et al.* 2005). In the NE Atlantic, hooded seal pup production in the Greenland Sea stock (West ice, near Jan Mayen) was 15,250 pups in 2005, and the stock size was estimated to be 82,000 animals in 2007 (Øigård & Haug 2007, ICES 2008, Salberg *et al.* 2008).

Few data are available on Arctic-specific population abundance for the 24 other marine mammal species that seasonally occur in the low or high Arctic. This is because the Arctic comprises only part of these species total seasonal range (e.g. humpback whales migrate to northern areas but not all enter the Arctic in summer), and worldwide or subpopulation abundance is generally assessed outside the Arctic.

Data are available for population sizes of large baleen whales in Baffin Bay due to a local subsistence harvest for these species in Greenland. In 2007, a fully corrected estimate of 3,272 (95% CI: 1,300-8,233) humpback whales was obtained for the coast of W Greenland in summer (Heide-Jørgensen *et al.* 2012). Furthermore, that same year fully corrected estimates of 16,609 (95% CI: 7,172-38,461) common minke whales and 4,468 fin whales (95% CI: 1,343-14,871) were obtained for the same area (Heide-Jørgensen *et al.* 2010c, 2010d).

In the northeastern Bering Sea (primarily within low Arctic waters) Friday *et al.* (2012) estimated cetacean abundance in 1999 and 2002 as follows: 2,729 (95% CI: 1,348-5,527) and 257 (95% CI: 84-789) fin whales, 1,048 (95% CI: 474-2,319) and 47 (95% CI: 10-215) minke whales, 12,486 (95% CI: 5,511-28,289) and 14,597 (95% CI: 8,387-25,403) Dall's porpoise, and 540 (95% CI: 185-1,580) and 87 (95% CI: 16-482) harbor porpoise. Friday *et al.* (2012) estimated 28 (95% CI: 6-130) humpback whales in the same area in 2002. There was considerable variability in estimates across years. Gray whales are commonly seen in the northern Bering and Chukchi Sea (Moore *et al.* 2000), but the portion of the overall Eastern North Pacific population (numbering ~ 21,000; Punt & Wade 2010) using Arctic waters is unknown. Bradford (2011) estimated that 140 gray whales were associated with the Sakhalin feeding ground in the Sea of Okhotsk between 1997 and 2007.

Northern fur seals in the Bering Sea constitute at least 30% of the worldwide population. The most recent estimate for the number of fur seals in this area, based on pup counts from 2008 on Sea Lion Rock, St. Paul and St. George Islands, and from 2007 on Bogoslof Island, is 653,171 seals (Allen & Angliss 2011). The Bering Sea stock of harbor seals in the low Arctic, specifically animals hauling out on the Pribilof Islands, numbers about 232 animals (Allen & Angliss 2011), and numbers in Greenland are low. There are occasional sightings of sea otters on St. George Island but no established population exists (Riedman & Estes 1990). Population size of Steller sea lions in the sub-Arctic Sea of Okhotsk is approximately 5,000 individuals (Burkanov *et al.* 2011), while northern fur seals in the Sea of Okhotsk (rookery on Tuleny Island/Robben Island) number about 100,000 animals (Ream & Burkanov 2006).

### 3.6.2.2. Trends

Detailed estimates of trends in population size for Arctic marine mammals are rare, and in several cases data are completely absent. Some populations are assumed to be stable or increasing. However, for other populations, given known harvest rates and/or associated population viability analyses, it is suspected that populations are declining, but the rate of decline is unknown. Here we present available data on population trends documented for the 11 ice-associated Arctic marine mammal species.

Trends in abundance are unavailable for most beluga subpopulations due to a lack of data or outdated surveys. Of the beluga subpopulations that have been assessed, the Bristol Bay subpopulation increased at 4.8%/year (95% CI: 2.1%-7.5%) between 1993 and 2005 (Lowry *et al.* 2008). Three subpopulations of belugas are known to be declining: Cook Inlet at -1.1% per year (SE 1.1) (Hobbs *et al.* 2011), the eastern Hudson Bay subpopulation which has declined by almost 50% since 1985 (Bourdages *et al.* 2002, Gosselin *et al.* 2009), and the White Sea subpopulation (Burdin *et al.* 2009). Although the abundance of St. Lawrence Estuary beluga has decreased from 7,800 (SE = 600) in 1866 to approximately 1,000 animals in 1985 (recent estimate 1,100 in 2006) due to overhunting, they have remained stable during the 30 years of protection from hunting (Hammill *et al.* 2007). No belugas were sighted on the latest survey of the endangered Ungava Bay subpopulation, which numbers < 50 whales (Gosselin *et al.* 2009). In some areas, specific winter aggregations of whales are surveyed to provide management advice for subsistence harvests (Heide-Jørgensen & Aquarone 2002, Heide-Jørgensen *et al.* 2010a). In W Greenland, numbers of wintering belugas have increased during the 21st century (Heide-Jørgensen *et al.* 2010a), but these aggregations constitute an unknown fraction of subpopulations (Heide-Jørgensen *et al.* 2003).

Although good population estimates are available for most narwhal stocks (Heide-Jørgensen *et al.* 2010b, Richard *et al.* 2010), they cannot be used for trends in abundance because of a lack of long-term monitoring or changes in survey methods making estimates incomparable. Surveys in central W Greenland in late winter are considered important for estimating trends in narwhals, but those surveys cover unknown proportions of whales from different summering subpopulations from W Greenland and Canada (Heide-Jørgensen *et al.* 2010b).

The Bering-Chukchi-Beaufort population of bowhead whales has increased at a rate of 3% per year since the late 1970s (George *et al.* 2004). The bowhead whales in Disko Bay, W Greenland, have increased at a rate of approximately 5% per year since 2000 (Heide-Jørgensen *et al.* 2007, Wiig *et al.* 2011) and comprise a spring aggregation which is part of the eastern Canada-W Greenland population. Trends in the subpopulations inhabiting the Svalbard-Barents Sea and the Sea of Okhotsk are unknown.

> » *It seemed that from 1964 onward the bowhead whales seemed to be increasing annually in numbers in our waters. … when you look at the year 1964 and compare it to today there are so many bowhead whales close by. We even on occasion see bowhead whales at the floe edge during the months of May and June between Baffin Island and Igloolik. … before that time you wouldn't dream of ever seeing a bowhead whale at the floe edge.*
>
> (Simon Iyyiriaq of Igloolik quoted in NWMB 2000).

The trends in global population abundance and regional population abundance for ringed seals and bearded seals are unknown. Ringed seal density estimates in western Hudson Bay from nine aerial surveys over the past 16 years showed an approximate 10-year cycle with a maximum density of 1.22 seals/km$^2$ of ice in 1995, to 0.45 in 1999, to 0.92 in 2007, to a minimum of 0.28 in 2009, followed by an increase to 0.73 in 2010 (Ferguson & Young 2011).

Among the 19 polar bear subpopulations, seven are assessed as declining (Baffin Bay, Chukchi Sea, Kane Basin, Lancaster Sound, Norwegian Bay, S Beaufort Sea, W Hudson Bay), four are considered stable (Davis Strait, Gulf of Boothia, N Beaufort Sea, S Hudson Bay) and one is considered to be increasing (M'Clintock Channel). There are not enough data to determine trend for the other seven subpopulations (Arctic Basin, Barents Sea, E Greenland, Foxe Basin, Kara Sea, Laptev Sea, Viscount Melville Sound) (Obbard *et al.* 2010). Trends are assessed by the IUCN/SSC Polar Bear Specialist Group, however the Canadian Polar Bear Technical Committee (PBTC) also considers the status of polar bear populations in Canada separately. Only a few polar bear populations are studied frequently enough for assessing trends (Stirling *et al.* 1977, Amstrup *et al.* 1986, Aars *et al.* 2009, Regehr *et al.* 2010). The W Hudson Bay and S Beaufort Sea populations have the best time series, and both of these populations have been determined to be declining. Regehr *et al.* (2007) documented a decline in W Hudson Bay of about 22% from 1,200 bears in 1987 to about 935 in 2004. This change was linked to the decline in reproduction and survival of young and very old bears due to climate warming (Stirling *et al.* 1999, Stirling & Parkinson 2006) in combination with harvesting at unsustainable levels. In the S Beaufort Sea, an intensive mark-recapture study conducted from 2001 to 2006 indicated that the subpopulation was 1,526 (95% CI: 1,211-1,841) polar bears in 2006 (Regehr *et al.* 2006). Further analyses indicated that survival and breeding during this period were affected by sea ice conditions, and that population growth rate was strongly negative in years with long ice-free seasons (Hunter *et al.* 2010, Regehr *et al.* 2010). Thus, the S Beaufort Sea population is currently considered to be declining due to sea ice loss.

> » *I think the reason why the bears come closer and closer is that the sea does not freeze over any more during the winter time of year. Therefore, the bears come closer and closer. Since our sea has begun to freeze late, some bears have become very thin. When the ice forms early, the bears we catch are usually fat and taste good. Since the late 1990s, due to the fact that the sea freezes late, almost all of the bears that we have caught have not had any fat on them. The bears we caught this year were like that too. They have no blubber on them and they are not fat. If you disregard the pingajoqqat [mothers with two cubs; author's note] that we caught, which were a little bit plump. … The rest of the bears that we catch are thin. That is because the sea out there does not freeze over – The difference is noticeable.*

(A hunter from Savissivik quoted in Born *et al.* 2011).

The trend in global population abundance for walrus is unknown. Regionally, where walrus population size estimates exist there are no or few previous reliable estimates from which a trend can be calculated. Modeling and simulation studies indicate that populations in W Greenland and the North Water have been declining due to over-exploitation, while the population in E Greenland has perhaps been increasing (Witting & Born 2005, NAMMCO 2009). The number of walruses summering in Svalbard increased from a few hundred animals to 2,629 (CI: 2,318-2,998) between the 1980s and 2006 (Lydersen *et al.* 2008). The population size and trends in Franz Josef Land are unknown, however, the population has been protected from hunting since the 1950s (Born *et al.* 1995). Large-scale commercial harvests of Pacific walrus reduced the population to 50,000-100,000 animals in the mid-1950s (Fay *et al.* 1997). This population increased rapidly during the 1960s and 1970s in response to harvest regulations limiting the take of females (Fay *et al.* 1997). Between 1975 and 1990, aerial surveys produced population estimates ranging from 201,039 to 290,000 (Udevitz *et al.* 2001); the most recent estimate from 2006 covering a portion of the range is 129,000 (95% CI: 55,000 to 507,000) (Speckman *et al.* 2011).

There are no available data for estimating trends for spotted seal and ribbon seals. The few data available lack precision.

A population model was used to examine changes in the size of the NW Atlantic harp seal population between 1952 and 2010 and resulted in an estimated exponential population growth to a total population in 2008 of 8.0 million (95% CI: 6.8-9.3 million) animals (Hammill & Stenson 2011). Harp seal pup production estimates in the White Sea stock have experienced significant declines since 2004, dropping from over 300,000 pups to approximately 150,000 pups. The reasons for the declines are not known, but changes in sea ice cover, industrial activity and hunting have been suggested (Chernook & Boltnev 2008, Chernook *et al.* 2008, Vorontsova *et al.* 2008, Zabavnikov *et al.* 2008). Recent model runs by ICES (2008) have confirmed that the population of harp seals in E Greenland may have increased in size from its earlier depleted state since ca. 1970, and it has been predicted that the population could continue to increase under the current harvest regime, which involves very small annual removals (Øigård *et al.* 2010). There are concerns that both female fecundity and neonatal survival have been reduced in recent decades in the Canadian harp seal subpopulations both in the Gulf and on the Front due to declines in sea ice stability and thickness (Bajzak *et al.* 2011, Johnston *et al.* 2012).

There was a moderate increase in hooded seal pup production and population size in the NW Atlantic between the mid-1980s and 2005 (Stenson *et al.* 1997, Hammill & Stenson 2007). In contrast, the NE Atlantic population of hooded seals has declined by 85-90 % over the last 40-60 years (Kovacs 2008b, Øigård *et al.* 2010). The cause of the decline is unknown, but it is likely related to changing ice conditions and perhaps also overharvesting. Hunting has recently been prohibited (Kovacs 2008b). Øigård *et al.* (2010) suggest that the population may now be reaching a stable lower level.

Few population trends are available for marine mammals that visit low Arctic regions seasonally. Those that are available, however, are mostly positive. Humpback whales off the coast of W Greenland have been increasing 9.4% per year (SE = 0.01) since 1984 (Larsen & Hammond 2004, Heide-Jørgensen *et al.* 2012). The population of fin whales that occurs off the west coast of Greenland has also likely been increasing, but the rate is unknown due to differences in survey methodology and correction factors (Heide-Jørgensen *et al.* 2010d). The aggregation of gray whales using the summer feeding ground in the Sea of Okhotsk has been growing at about 3% per year since 1997 (Bradford *et al.* 2008), and the population of gray whales summering in the Bering and Chukchi Seas was growing in the 1990s but may have reached carrying capacity (Rugh *et al.* 2005).

During 1998-2006, Northern fur seal pup production on St. Paul Island declined by 6.1% per year (SE = 0.45%) and by 3.4% per year (SE = 0.60%) on St. George Island (Pribilofs) (Allen & Angliss 2011). Steller sea lions in Sea of Okhotsk have been slowly increasing since the 1970s (Burkanov & Loughlin 2005, Burkanov *et al.* 2011), and northern fur seals in Sea of Okhotsk have also been increasing (Ream & Burkanov 2006).

### 3.6.2.3. Causes and prospects

#### Loss of sea ice

The loss of Arctic sea ice is the greatest threat to Arctic marine mammals, particularly to ice-associated pinnipeds and polar bears. Springtime is an especially important period for several species because it coincides with critical reproduction periods or important feeding opportunities. Sea ice declines over the past several decades have been clearly documented (IPCC 2007, Perovich & Richter-Menge 2009, Stroeve *et al.* 2012), and the latest projections indicate an ice-free high Arctic in summer within three decades (AMAP 2011, Wang & Overland 2012). Thus, further habitat loss and habitat degradation for all ice-associated species can be expected.

For pinnipeds, reduced sea ice cover and snow cover will have negative impacts on pupping, molting and resting platform availability in many areas (IPCC 2007, Hezel *et al.* 2012). Declines in reproduction and survival of ringed seals have been linked to variations in their sea ice habitat including responses to early or late ice break-up in spring, and relatively heavy or light ice conditions (Smith 1987, Kingsley & Byers 1998, Harwood *et al.* 2000). Years with low snow cover (Ferguson *et al.* 2005) and unusually warm weather or rain events in the spring (Stirling & Smith 2004) have also resulted in reduced survival. In late winter and early spring, ringed seals give birth and nurse their pups in subnivean (under snow) lairs that they excavate above the breathing holes (Smith & Stirling 1975). While some pups are born on pack ice (Wiig *et al.* 1999), landfast ice with sufficient snow cover is required to build lairs, which provide relative safety from polar bear predation (McLaren 1958, Burns 1970, Hammill & Smith 1991). Warmer conditions or rain events can destroy lairs or make them impossible to build (Kelly *et al.* 2010).

The primary threat to walruses is also considered to be the reduction of summer sea ice, especially for the Pacific population. In spring, ice is important for breeding (Fay *et al.* 1984), giving birth and nursing and care of young (Fay 1982). In the Bering and Chukchi Seas, floating pack ice serves as a substrate for resting between shallow feeding bouts (Fay 1982, Ray *et al.* 2006). In the Chukchi Sea, reduction of summer sea ice as a resting and feeding platform poses the greatest risk to females and calves. Sea ice provides access to offshore feeding areas, isolation from terrestrial predators and hunting pressure (Fay 1982, Kochnev 2004, Ovsyanikov *et al.* 2007), and protection from stormy seas (Fay 1982). On the east coast of Greenland, reduced sea ice cover may actually increase feeding opportunities for walruses (Born 2005), but this is not the situation for Atlantic walruses in other areas such as the Barents Sea-Svalbard subpopulation (Kovacs *et al.* 2011). More open water tends to support more pelagic and less benthic biomass, which could affect walrus prey (Moline *et al.* 2008).

> » *Most bears are thin. They are getting thin. … Yes…well, some of the ones that I have caught, they have been like that. They have started to be like that in recent years. … They weren't like that in the past. They used to be very fat in the past. Of course it is not each and every one that is like that. But for most of them, their layer of blubber has got thinner. Some of them have almost no blubber. This winter I caught yet another one without very much blubber.*
>
> (Hunter from Nuussuaq, Greenland, quoted in Born *et al.* 2011).

Like the true Arctic seals, the primary threat to Pacific and Atlantic low-Arctic ice seals is also seasonal sea ice loss in the late winter and spring. In the Pacific, ribbon and spotted seals rely on pack ice at the southern limit of the ice extent in the Bering Sea and Sea of Okhotsk for whelping and rearing pups (Boveng *et al.* 2008). Decreased availability of stable platforms for adults to complete their molt out of the water may also lower survival. In the Atlantic, where sea ice is declining rapidly, harp seals and hooded seals require seasonal sea ice cover for whelping, lactation, resting and molting, for short but specific periods in spring (Johnston *et al.* 2005, Kovacs & Lydersen 2008, Laidre *et al.* 2008a). Johnston *et al.* (2012) revealed negative correlations between both ice cover and the NAO index and harp seal mortality in the Gulf of St. Lawrence, indicating that lighter ice cover and lower NAO values result in higher mortality. They also assessed the long-term negative trends in sea ice cover in the breeding regions of harp seals across the entire North Atlantic during 1979 through 2011 and found that sea ice cover in all harp seal breeding regions has been declining by as much as 6% per decade. For all ice-associated pinnipeds, the quality of the ice habitat (i.e. thickness) and the age and the duration of sea ice cover also play an important role during the pupping season (Friedlaender *et al.* 2010, Bajzak *et al.* 2011). Location of traditional sites might also be an important factor, though Rosing-Asvid's (2008) finding suggests that some shifting of whelping locales might be possible for these seasonally dispersed populations.

Declining sea ice habitat has been broadly recognized as the most significant threat to polar bears (Derocher *et al.* 2004, Aars *et al.* 2006, Amstrup *et al.* 2006, Wiig *et al.* 2008, Durner *et al.* 2009, Obbard *et al.* 2010, Stirling & Derocher 2012) and has been associated with declines in population abundance (Regehr *et al.* 2007), declines in survival (Regehr *et al.* 2010, Peacock *et al.* 2012), declines in body condition (Stirling *et al.* 1999, Rode *et al.* 2010, Rode *et al.* 2012), declines in recruitment (Rode *et al.* 2010) and increased swimming (Pagano *et al.* 2012).

It is less clear what the impacts of sea ice loss will be on Arctic cetacean populations. Sea ice loss opens up new habitat (Heide-Jørgensen *et al.* 2011a) and may increase the duration of the production season allowing for increased foraging opportunities for baleen whales (Moore & Laidre 2006, Laidre *et al.* 2010). Annual sea ice cover exerts broad-scale control on energy flux, levels of biological production (Laidre *et al.* 2008a) and ultimately survival and reproduction of predators at the top of the food chain. The primary production bloom is the main food source for zooplankton (secondary production), which play a critical role in the transfer of energy between primary producers and secondary consumers like forage fish. Indirect changes in the ecosystem that occur with the loss of sea ice may have negative impacts at the population level (Laidre *et al.* 2008a, Kovacs *et al.* 2011), including increased predation (Higdon *et al.* 2012, Ferguson *et al.* 2012a, 2012b), disease (Burek *et al.* 2008) and competition from temperate species extending their range into high latitudes (Higdon & Ferguson 2011). Additionally, irregular freeze-up patterns may have negative effects for ice-associated Arctic cetaceans like belugas and narwhals, which are susceptible to sea ice entrapments if ice conditions change rapidly (Kleinenberg *et al.* 1964, Laidre & Heide-Jørgensen 2005, Laidre *et al.* 2011). Increasing frequency and intensity of storm events might also have greater impacts on Arctic cetaceans if they no longer have ice available to them; this is likely particularly important for juvenile animals.

The impacts of sea ice loss on marine mammals that seasonally use the Arctic have generally not been documented but are likely positive given that sea ice loss will allow southern species to extend their northern range limits and/or occupy previously ice-covered areas (e.g. Moore & Huntington 2008, Heide-Jorgensen *et al.* 2011b). Expected shifts in species distribution could also bring new predators such as killer whales (Higdon & Ferguson 2009) or competition with sub-Arctic species (Higdon & Ferguson 2011).

#### Harvest

Arctic marine mammals are harvested by indigenous peoples for nutritional, cultural and economic reasons. While some subsistence harvests are closely monitored by local, national, governmental and international organizations (e.g. Alaska Beluga Whale Committee, Nunavut Wildlife Management Board, U.S. Fish and Wildlife Service, North Atlantic Marine Mammal Commission, International Whaling Commission) and many hunts are sustainable, overharvest is a problem for some populations, especially where population abundance and harvest rates are unknown or harvests are not well regulated. This is still the case for some subpopulations of polar bears even when both harvest rates and population sizes are known (Obbard *et al.* 2010). Overharvest has been demonstrated to cause declines for several local or small isolated populations of Arctic marine mammals (e.g. West Greenland walrus) (Taylor *et al.* 2002, Witting & Born 2005, Taylor *et al.* 2008, Hobbs *et al.* 2011, Peacock *et al.* 2011). Sport hunting for polar bears only occurs in Canada; numbers of sport-hunted bears are set by the communities from the overall quota assigned to each community (Vongraven & Peacock 2011).

#### Anthropogenic activities

Besides hunting, known or potential anthropogenic threats include industrial activities such as oil and gas exploration and development (seismic exploration, drilling), commercial shipping and increased tourism, northward expansion of fisheries (with possible implications for bycatch, competition and resource depletion; e.g. narwhal and Greenland halibut), incidental mortality and serious injury caused by entanglement in fishing gear and ship strikes (e.g. bowhead whales), hydroelectric development (e.g. beluga whales in Hudson Bay), concomitant increases in underwater noise (Moore *et al.* 2012b), and industrial and urban pollution (Laidre *et al.* 2008a). The ringed seal subspecies that live in freshwater lakes are also vulnerable to manipulation of water levels, recreational snow machine operation, net-fishing and poaching, bycatch, boating, tourism and development, predation by terrestrial mammals, and in a few cases industrial pollution (Kovacs *et al.* 2012).

#### Pollution and disease

Pollution, emerging parasites and disease are also issues for Arctic marine mammals. Top-level carnivores accumulate heavy metals, such as mercury, and organochlorine contaminants at relatively high concentrations due to bio-accumulation. After two decades of monitoring, E Greenland polar bears have been determined to be among the most polluted animals on the planet (Sonne *et al.* 2012). In general, organochlorine contaminant concentrations are highest in marine organisms (Noyes *et al.* 2009). However, population level effects are difficult to quantify given uncertainty in population trends and multiple sources of variability. Due to the geographic distances many of these species travel, and the influx of southern species, diseases and parasites may be an important issue in the future, but specific risks are uncertain at present.

**Prospects**

Ideally, insight on the effects of climate change on Arctic marine mammal species and populations is collected through long-term monitoring of basic population metrics, life history or behavior in combination with environmental time series and quantitative modeling (e.g. Regehr *et al.* 2010, Rode *et al.* 2010, Jay *et al.* 2011). Unfortunately there are very few long-term studies. The few studies that have been conducted over a span of several decades (e.g. W Hudson Bay and S Beaufort Sea polar bears) have been critical for determining the impacts of climate change. To date, no studies have been designed or implemented that attempt to distinguish between the effects of climate change and the effects of increasing anthropogenic activity in the Arctic for marine mammals.

Unusual or rare phenological or behavioral observations that can be documented in concert with altered environmental conditions are insightful. Examples include extremely long polar bear swims (Durner *et al.* 2009, Pagano *et al.* 2012), drowning polar bears (Monnett & Gleason 2006), polar bear cannibalism (Amstrup *et al.* 2006, Stirling & Ross 2011), abandoned walrus calves (Cooper *et al.* 2006) and ice entrapments of narwhals in unusual areas (Laidre *et al.* 2011). However, because these are rarely observed events, it is difficult to quantitatively link them to the population level.

Several studies have made predictions about the possible impacts on population abundance, survival and reproduction of Arctic marine mammals from sea ice loss. Predictive modeling of the future global distribution and abundance of polar bears forecasts declines in abundance, survival and reproduction (Durner *et al.* 2009, Amstrup *et al.* 2010, Hunter *et al.* 2010, Molnár *et al.* 2010). In general, large future reductions in most subpopulations of polar bears are expected. Predictive Bayesian network models for Pacific walrus, integrating potential effects of changing environmental conditions and anthropogenic stressors, demonstrate a clear future trend of worsening conditions for the subspecies (Jay *et al.* 2011). Few predictive models exist for Arctic cetaceans, but in general it is believed impacts will be species-specific depending on how well species adapt to changing food webs and sea ice regimes (Laidre *et al.* 2008a, 2011). Increased efforts combining population and habitat modeling are needed to predict population persistence in the face of climate change (Peacock *et al.* 2011).

Conflicts between conclusions reached by scientific methods compared to those by traditional ecological knowledge have been increasing in polar bear management in Canada (Peacock *et al.* 2011). In recent years, some permits for management-oriented research on polar bears were denied by the Government of Nunavut, local hunting and trapping organizations in the Northwest Territories, and by Makivik Corporation in Quebec. Furthermore, in a 2009 resolution, Inuit Tapiriit Kanatami opposed the capture of polar bears throughout Canada. This prevented scientists from applying physical markings to polar bears in order to estimate population sizes (Stirling *et al.* 1999, Peacock *et al.* 2011). Less-invasive and non-invasive protocols for biological sampling and monitoring are increasing, such as remote biopsy darting to collect fat and tissue samples and aerial surveys to estimate abundance.

Overall, increased monitoring is needed to fill large gaps in knowledge about population sizes and trends for Arctic marine mammals. Several circumpolar Arctic marine mammal monitoring plans have been drafted by groups of experts, but these plans have not yet been implemented largely due to lack of dedicated funding (Kovacs 2008c, Laidre *et al.* 2008b, Simpkins *et al.* 2009, Vongraven *et al.* 2012). Dedicated monitoring efforts across several spatial and temporal scales, although costly and difficult, are critical for quantifying future impacts.

## 3.7. CONCLUSIONS AND RECOMMENDATIONS

### 3.7.1. Valuable areas and productivity hotspots

Three types of habitat are particularly valuable due to their unique biological richness and large-scale influence on Arctic ecosystems: caribou calving grounds, coastal zones and margins of the sea ice-pack.

Migratory tundra caribou calving grounds require special attention. Caribou choose these fairly restricted areas because of high food quality and relatively low predation risk, and thereby maximize the survival and vigor of calves. Human activities and infrastructure (e.g. aircraft flight paths, roads, off-road vehicle use, pipelines) should be prohibited or strongly regulated in these landscapes during the calving seasons when the activities can readily disrupt the optimum bonding and behavior of cows and calves with negative consequences for calf recruitment. Calving grounds are site-specific by herd, though they do shift somewhat over time. Many are currently undergoing some mineral and hydrocarbon exploration and road development (e.g. Beverly) or are under such threat (e.g. Bathurst, Porcupine).

Coastal zones, especially over the relatively shallow continental shelf and banks, are particularly productive marine areas. Along coastlines, the mixing of marine water with nutrient-rich fresh water, from land-based drainages and melting sea ice, enhances productivity and attracts large concentrations of marine mammals. Migratory marine mammals rely on this spatially-concentrated ocean productivity for foraging opportunities. Deltas and offshore plumes from the major rivers (notably the Mackenzie and Lena) are heavily used feeding areas. Coastlines and nearshore ice and barrier islands are particularly important for polar bears, combining high-value habitats for reproduction and resting with relatively high marine productivity especially in spring and summer. Coastal zones are particularly at risk because expanding human activities (e.g. shipping, fishing, oil and gas developments, transportation infrastructure and settlements) are and will be concentrated in and beside these zones of high ecological productivity and easier access to resources.

Sea ice margins are also particularly productive marine areas that attract numerous marine and some terrestrial mammals. They include the geographically widespread ice margins of the Bering/Chukchi Seas, Baffin Bay, Davis Strait, E Greenland and the Barents Sea. These zones change position somewhat between years as patterns of ice melt change, and are likely to shift systematically in response to changing climate. Nevertheless, they require particular attention because of their importance to many marine mammals.

In winter, a particular set of sea ice margins is found at polynyas or flaw leads, where substantial areas of water remain open or only occasionally frozen due to particular combinations of wind and currents. These are important habitats for winter-resident Arctic marine and terrestrial mammals as well as seabirds. They are seasonally delimited habitats, requiring particular conservation attention in winter. Key examples of polynyas include North Water (N Baffin Bay), St. Lawrence Island (Bering Sea) and North East Water (NE coast Greenland); and of flaw leads include NE Chukchi Sea, Cape Bathurst (Beaufort Sea) and Laptev Sea (see Box 14.2 in Michel, Chapter 14).

While managers need to pay attention to habitats of high ecological value, conservation attention also needs to be focused on biological ‘hotspots’ that overlap areas of particular interest to oil, gas and mining industries, because of the increased disturbance that is likely to occur in those areas. These tend to be geographically large areas in the exploration phase, leading to site-specific developments.

Four regions appear to be of particular interest to the oil and gas industry at present: Barents Sea, Beaufort-Chukchi Seas, Baffin Bay and E Greenland. These regions deserve particular attention because the exploration, development and production phases of this industry may cause displacement of species from important feeding or breeding habitats, changes in the underwater acoustic environment, impacts to calving and migratory habitats, and potentially direct mortality or changes in vital rates due to collisions, oil spills or contamination. The risks of population declines for both marine and terrestrial mammals can only be addressed, and perhaps mitigated, through environmental assessments (including collection of new data not already available to resource managers); controls on the intensity, timing and structure of exploration and development activities; and dedicated work with local communities to ensure the implementation of cautious management and harvest plans for mammals that might be affected. Given the paucity of data on many Arctic mammal populations, it is difficult to detect population changes and attribute their cause to either human-induced or natural factors. Therefore, strengthened research and monitoring programs must precede and accompany proposed development activities in Arctic regions.

The global rush for minerals is resulting in many new mine developments in the Arctic. Each potential new mine site requires focused attention to determine its potential direct and indirect impact on terrestrial mammals. Marine mammals may also be impacted by increased shipping and activity in coastal zones, and various other factors resulting from industrial development and its infrastructure. Concerted efforts must be made to forecast the impact of any one development project, as well as the cumulative impacts in a particular region. Environmental impact assessments are a necessary component of our management, but the ability of these assessments to consider multiple scales of potential impacts over both time and space is limited and must be improved. Special attention should be given to the use of new technologies that reduce the extent of infrastructure required (e.g. air ships), and to operational measures that reduce the potential for changing mammal behavior (e.g. proper garbage management, controls on human harvesting of wildlife). Monitoring of Arctic mammals and potential impacts on them must be an integral and funded portion of any developments.

### 3.7.2. Key knowledge gaps

One major conclusion of this review is that detailed, long-term data on population trends for Arctic mammals are rare. There are no abundance or trend estimates for many key populations and species of marine (e.g. all of the ice-dependent pinniped populations and several polar bear populations) and terrestrial (e.g. Arctic wolf, many lemming populations) mammals. Demographic data are also absent for many species, and if available they are rarely of high quality. This is largely explained by high costs and logistical hurdles of monitoring populations in large and remote areas. Information on population trends is important for natural resource managers to take management actions when populations face single or cumulative impacts, and to measure recovery from any perturbation. Good population monitoring is the first requirement for biodiversity assessment, and our knowledge of the status and trends of Arctic species will remain relatively poor unless we invest more resources into monitoring their numbers and understanding their ecology.

Weather patterns and extreme weather events are prominent limiting factors for Arctic herbivores. Global climate patterns, such as the North Atlantic and Arctic Oscillations, affect seasonal weather patterns and therefore timing and productivity of plant growth over multi-annual and decadal periods. These relationships deserve increased attention including investigations of patterns in a greater diversity of weather-related phenomena that impact mammals (e.g. freezing rain and icing events, thaw-freeze cycles in winter, timing of snowmelt, timing of snow onset, taiga and tundra wildfire frequency). Such investigations need to be coupled with long-term studies of how such weather phenomena are affecting demographic parameters in mammals (e.g. over-winter survival and reproductive output in rodents and lagomorphs, conception and calf survival in caribou and muskoxen). Northern community members who are frequently on the land can be employed in recording patterns of weather, especially unusual events, and animal responses (see Huntington, Chapter 19, for discussion of community-based monitoring).

Caribou herd viability, and the ability to monitor herds, depend on a good understanding of locations and temporal use of calving grounds by reproductive and barren cows. For some herds, this information is still unclear, but is crucial when population monitoring depends on calving ground counts. Improved mapping and tracking of calving grounds and the landscapes used by barren cows in the same season will allow more robust population estimation, and improved application of land management guidelines.

Cumulative impacts assessments of multiple direct and indirect anthropogenic activities over space and time need improvement. Given a general lack of predictive models for cumulative impacts assessment, we need new approaches to both detecting negative effects as quickly as possible, and combining effects in decision-making. For caribou, one approach lies in monitoring herd status by sampling individual health status (pregnancy rates, body condition, parasite load and survival) integrated in energy allocation models (Russell *et al.* 2005), coupled with research on relationships between herd status and environmental factors such as weather, snow and fire.

### 3.7.3. Recommended conservation actions

The most urgent conservation need is a stabilization and reduction of greenhouse gases at the global scale, so that climate change can be slowed and limited in intensity world-wide. Continued increases in greenhouse gas production, mostly outside the Arctic, will exacerbate the ongoing disruption of Arctic ecosystem processes. Climate warming in the Arctic has had the most dramatic effects on snow, ice and water (the cryosphere) (AMAP 2011). These are prominent components of Arctic habitats, and consequently some Arctic mammal populations that are economically and culturally important will be significantly reduced in distribution and abundance. Ice-associated mammals, especially polar bear and pinnipeds, are highly threatened by reductions in duration of the sea ice season and in spatial extent of summer ice. Some populations are at high risk of extirpation within decades. The probability of global extinction of an Arctic mammal species has not been estimated, but appears to be growing with the increasing pace of habitat and ecosystem change.

The variety of legislation, regulations and policies across the circumpolar Arctic needs to be harmonized, ideally with the assistance of the Arctic Council. Environmental legislation and regulations vary in strength and intensity across jurisdictions. These include: (1) environmental impact assessment for major industrial projects, (2) endangered species protection, (3) harvest management, (4) marine transportation safety, pollution and routing regulations, (5) offshore oil and gas drilling and extraction standards, and (6) identification of responsibility for providing resources for necessary studies before new anthropogenic activities occur. Without such harmonization, the level of environmental risk and consequent negative impact on a population will vary from jurisdiction to jurisdiction and negative impacts in one region will affect other regions. For example, some jurisdictions require substantial environmental impact assessments where the risks to impacted mammal populations are minimized with mitigation measures imposed; other jurisdictions lack a robust assessment process. Transboundary populations may experience relatively heavy negative impacts in a jurisdiction with weaker legislation and regulations, despite strong conservation efforts in a jurisdiction with higher environmental standards. The chances of one jurisdiction suffering the consequences of poorer environmental standards in another jurisdiction will continue to increase as development proceeds.

A coordinated mammal population abundance monitoring plan needs to be developed and implemented in the field, with the support of jurisdictions. Strategic attention should be focused on specific combinations of species and region from which most inferences can be drawn. Such a plan needs to build on long-term data sets and requires integration with existing local or national monitoring through the circumpolar Arctic. Particular attention to monitoring in Eurasia is warranted. Such monitoring plans have already been discussed for marine mammals such as belugas, ringed seals and polar bears, but none has actually been fully developed or implemented. Migratory tundra caribou are the subject of an international monitoring effort (CircumArctic Rangifer Monitoring and Assessment Network (CARMA)), but many other species are currently overlooked.

The Circumpolar Biodiversity Monitoring Program (CBMP) is a valuable start to the large task of archiving, reporting and making accessible data on population distribution and abundance for Arctic species. This program needs to be maintained and supported in its goal of better integration with field-based monitoring programs. However, merely tracking population size and demographic parameters is not enough. Monitoring must be designed to test alternative hypotheses about the role of limiting factors (e.g. weather, primary production, disturbance, harvest) on distribution and abundance. Hypotheses explaining past, present and future changes must be set and tested as integral parts of monitoring activities. Maximizing the number of counted populations is not as important as investigating limiting factors in conjunction with following a suite of strategically chosen populations.

In conjunction with abundance monitoring, all user groups need to collaborate in improved monitoring and record keeping of animal harvest levels across jurisdictions, so the sustainability of the total harvest can be assessed for biological populations. Harvest of wildlife is a critical component of human subsistence in the Arctic. Harvest can be a factor in population declines, and science-based harvest management can reduce the risk of population collapse and ensure that subsistence resources are available for future generations. Some components of these harvests are monitored by scientific or co-management committees. However, some are not monitored at all, and many of them involve transboundary populations. Harmonization of harvest reporting and documentation across jurisdictions would improve conservation and management regimes.

Previously depleted populations of harvested Arctic mammal species, and of species currently well below historical levels, need to be recovered wherever possible, especially where there is high likelihood that excessive human harvesting was (e.g. SW Greenland beluga), or still is (e.g. W Greenland walrus), a major factor in reducing abundance. The international moratorium on commercial whaling appears to have facilitated the recovery of some bowhead whale sub-populations (George *et al.* 2004, Heide-Jørgensen *et al.* 2007). Harvest restrictions also can assist caribou population recovery at low density, but the inherently cyclic nature of caribou population abundance confounds the definition of a targeted abundance for recovery and complicates the suite of management actions to facilitate recovery.

There is an urgent need for the establishment of a comprehensive set of protected areas, based on eco-regional representation, biodiversity hotspot analyses, the subsistence economy of northern peoples, and climate change risk assessment. Protected areas with minimal human activity are valuable as ecological benchmarks for understanding ecological processes and as refuge areas during key seasonal periods in the life cycle. If chosen well they can also be relative refuges from the effects of climate change. Northern peoples often harvest mammals in traditional areas related to animal concentrations and accessibility, and precluding other developments to maintain harvests in these areas is a strong rationale for protection. There are a considerable number of land-based protected areas, but relatively few marine protected areas in the Arctic. As climate change is known to be causing environmental changes throughout Arctic ecosystems, some administrative flexibility is needed to ensure that protected areas can be modified or adaptively managed to continue to cover the necessary areas, both now and in the future. Protected areas have spatial but also potentially temporal dimensions. For example, calving grounds of migratory tundra caribou need strong protection during the calving season, but could conceivably sustain some human activities and functioning infrastructure in other seasons.

### 3.7.4. Other key messages

Many Arctic mammal populations are co-managed between national or sub-national government agencies and indigenous government or community agencies. Knowledge derived from both community experience and scientific studies are expected to contribute to decision making. Smooth decision making has been thwarted in some cases by breakdowns in communication and trust. Solutions are not always clear, but do depend on open-mindedness, honest communication and joint realization that the sustainability of the population is a shared goal of all involved.

Scientific understanding of the direct and indirect effects of climate change and other stressors on Arctic ecosystems is still in its infancy. Society's ability to manage change and implement a valid conservation agenda depends on increased funding for both hypothesis-driven monitoring and basic research into factors driving the distribution and abundance of Arctic mammals.

The Arctic encompasses many of the last wilderness regions on the planet, with species that are marvels of adaptation to difficult conditions, and ingenious human cultures that are intimately linked to harvesting mammals. Conserving the biological and cultural diversity of the Arctic deserves society's utmost efforts and attention in these changing times.

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Appendix 3: www.abds.is/aba-2013-appendix-3

Incubating red knot *Calidris canutus* after a snowfall at Cape Sterlegova, Taimyr, Siberia, 27 June 1991. This shorebird represents the most numerically dominating and species rich group of birds on the tundra and the harsh conditions that these hardy birds experience in the high Arctic. Photo: Jan van de Kam.

*Chapter 4*

# Birds

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## Contents

> » **I have started to notice birds which I used to only see on TV, little birds which have multi-coloured bills, that fly home with multiple cod in their beaks and that burrow into the soil. I think these are the puffins, which are located some distance south migrating north due to the disappearance of the ice cover during the summer months.**
>
> Pijamin: Elders Conference on Climate Change 2001.

## SUMMARY

The Arctic is seasonally populated by roughly 200 species of birds, corresponding to about 2% of global avian species diversity. In contrast to more southerly latitudes, the dominant ecological and taxonomic groups among Arctic birds are waterfowl, shorebirds and seabirds, while songbirds are less prominent and much less diverse than at lower latitudes. The vast majority of species only spends a small portion of each year in the Arctic – but it is here that reproduction takes place.

Of the 162 species for which more than half of their breeding range falls in the terrestrial or marine Arctic, about half have a circumpolar distribution while the others are confined to either the Nearctic or Palearctic or to the Atlantic or Pacific ocean basins. A particularly high species richness is found on both sides of the Bering Strait. Overall, species diversity is more than twice as high in the low Arctic than in the high Arctic.

Because of the migratory nature of most Arctic birds, these animals connect the Arctic to all other parts of the globe. Arctic birds winter as far south as the southern tips of the continents, and some even reach Antarctica. The extent of migratory behavior also means that the population sizes and trends of Arctic birds are sometimes affected, either positively or negatively, by events and activities occurring outside the Arctic. There are many examples of such extra-Arctic effects. As a consequence, conservation of Arctic birds will almost always necessitate international cooperation throughout the range of the migratory species. This is especially critical for the endangered species among Arctic birds, such as the Siberian crane *Leucogeranus leucogeranus* or the spoon-billed sandpiper *Eurynorhynchus pygmeus*, the latter currently facing extinction.

Global climate change has the potential to influence Arctic bird populations in many ways, through effects acting in the Arctic itself as well as on migration routes or in wintering areas. However, although there are some indications that climate-induced changes are already taking place, the anthropogenic factors that are independent of climate – disturbance, habitat loss, fishing, hunting, agricultural intensification – have a much larger impact on populations at present.

## 4.1. INTRODUCTION

Despite its harsh environment, the Arctic is populated by a variety of different bird species. Arctic breeding birds benefit from a short but strong seasonal outburst of food availability, be it growing plants for herbivores, invertebrate biomass for insectivores or zooplankton for seabirds and their fish prey. This plentiful seasonal food supply is coupled with relative safety from predation created by continuous daylight, a low diversity of predators and the sheer numbers of prey swamping predator pressure (McKinnon *et al.* 2010). Diseases and parasites are also less prevalent than in warmer climates (Kutz *et al.* 2005). After the breeding season, however, most birds leave the Arctic to spend the winter in warmer climate zones; in fact, the majority of 'Arctic birds' spend only a small fraction of each year on their Arctic breeding grounds (Meltofte 1996, Newton 2007). Their migrations connect the Arctic to all other parts of the globe.

Being highly visible and audible as well as diurnally active, birds are one of the groups of organisms that are best known to humans worldwide. Hence, Arctic birds also have a strong cultural significance to the indigenous peoples of the Arctic. The arrival and departure of migratory birds marks the changing of the seasons, and in addition to their significance as a food source birds also play a role for festivals and the planning of family and community events.

Roughly 200 bird species breed in the Arctic, amounting to 2% of the global avian biodiversity. However, the relative weight of higher taxonomic groups is different from the global total. The Anseriformes (waterfowl) and Charadriiformes (shorebirds, gulls, auks) make up the majority of avian diversity in the Arctic and are therefore treated in detail in separate sections of this chapter. By contrast, the songbirds, being the most diverse group elsewhere, are underrepresented in the Arctic and are treated together with the other 'landbirds' below.

Whereas some species occur mostly in temperate latitudes and only reach the Arctic at the fringes of their distribution, others are more or less confined to the Arctic during the breeding season. These 'true Arctic' species will be the main focus of the analyses below. Among them there are species with a circumpolar distribution while others are confined to one of the hemispheres or have even more restricted distributions. The diversity of distributions create variation in species richness within the Arctic. In this chapter we address these species richness patterns as well as the current status, trends and future prospects of individual species.

## 4.2. STATUS OF KNOWLEDGE

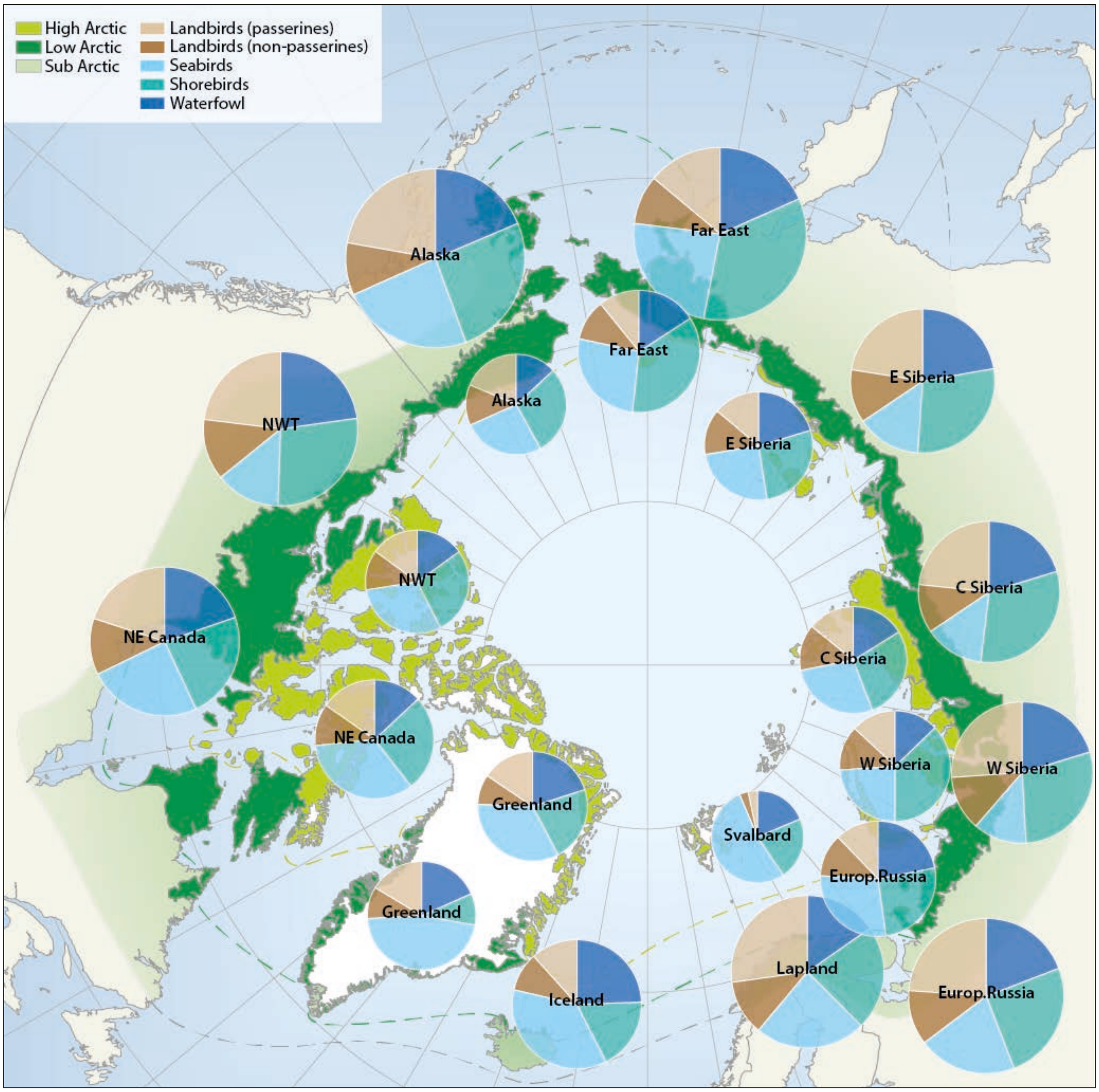
### 4.2.1. Sources and regions

Species distributions were considered on the basis of known breeding ranges. Separate brief consideration is also given to wintering birds. Data on bird breeding distributions were obtained from standard sources (Del Hoyo *et al.* 1992-2009, Poole 1992-2011, Beaman & Madge 1998, Sibley 2000, Olsen & Larsson 2003) and vetted by local corresponding authors. Species names and classification follow the list compiled by the International Ornithological Congress (Gill & Donsker 2012). Data on IUCN red listed species was obtained from (IUCN 2012).

Our analysis concentrates on species using habitats north of the tree-line, within the geographical areas defined as low and high Arctic in the Circumpolar Arctic Vegetation Map (CAVM Team 2003). We include the whole of Iceland (apart from the south coast) and areas of oceanic tundra (e.g. Aleutian Islands). Many species occur to the limit of trees, and a large number of predominantly boreal species touch the low Arctic zone around the mouth of the MacKenzie Valley. We have omitted from our Arctic list those species which only reach the low Arctic there (e.g. spruce grouse *Falcipennis canadensis*, northern hawk-owl *Surnia ulula*, yellow-rumped warbler *Dendroica coronata*), but include species which cross the low Arctic boundary across a broader geographical area (e.g. wandering tattler *Tringa incana*, lesser yellowlegs *Tringa flavipes*, golden eagle *Aquila chrysaetos,* great grey shrike *Lanius excubitor*).

In the Nearctic, the western mountain ranges contact the Arctic in Alaska, allowing several Arctic species to extend southwards into boreal latitudes (e.g. ptarmigans *Lagopus* spp., white-crowned sparrow *Zonotrichia leucophrys*, grey-crowned rosy finch *Leucosticte tephrocotis*), but in Asia there is only slight contact between the mountains of central Asia and the Arctic and no typically Arctic birds extend south in this way. In Europe, a few otherwise Arctic species extend southwards through the mountains of Scandinavia and into the uplands and islands of northern Britain (e.g. red-throated loon *Gavia stellata*, dunlin *Calidris alpina*, Eurasian dotterel *Charadrius morinellus*, snow bunting *Plectrophenax nivalis*). Likewise, in the Baltic Sea several marine birds occur in

**Figure 4.1.** Avian biodiversity in different regions of the Arctic. Charts on the inner cirle show species numbers of different bird groups in the high Arctic, on the outer circle in the low Arctic. The size of the charts is scaled to the number of species in each region, which ranges from 32 (Svalbard) to 117 (low Arctic Alaska).



essentially a boreal climate (e.g. common eider *Somateria mollissima*, Arctic tern *Sterna paradisaea*, ruddy turnstone *Arenaria interpres*; Snow & Perrins 1998).

For discussion of distributions we have divided the terrestrial Arctic into Nearctic (four regions, including Greenland; Fig. 4.1) and Palearctic (eight regions, including Iceland), partly based on convenient political boundaries (North America) and partly on geographical boundaries (Siberia). Seabirds were divided by ocean basins into those breeding predominantly on Atlantic, Pacific or Arctic Ocean coasts. In addition, each region was divided into high and low Arctic, where appropriate. Species were classified as high Arctic specialists where most of their breeding distribution (> 50% by area) fell in the high Arctic, low Arctic specialists where most fell in the low Arctic, sub-Arctic where most of the range fell within the taiga/boreal forest zone and cosmopolitan where the range encompassed both Nearctic and Palearctic and included areas outside the Arctic and boreal zones.

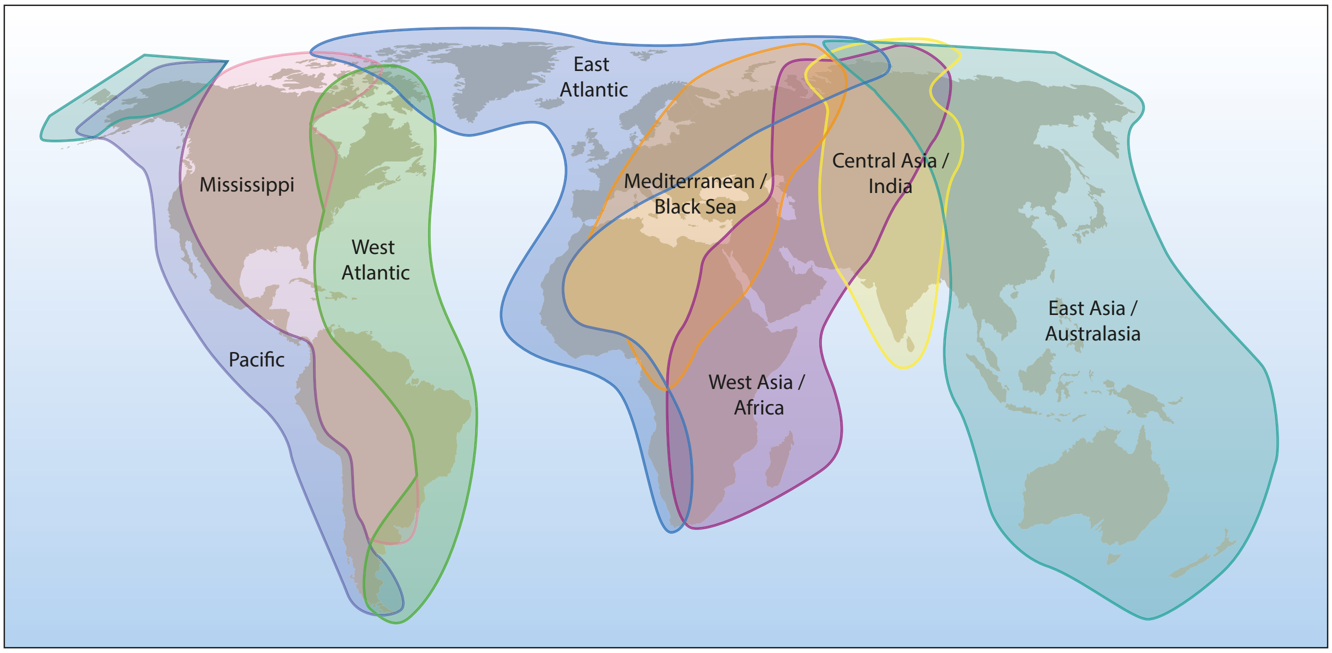
Diversity is analyzed mainly in terms of species richness, as reliable population estimates to allow the calculation of more sensitive diversity indices are not available for many Arctic species. We also discuss diversity at higher taxonomic levels and the prevalence of endemicity within the Arctic. Taxa were considered endemic to the Arctic if > 90% of the population or breeding range fell within the low and high Arctic.

Information on population trends was sparse and varied among taxonomic groups, with substantial information available for waterfowl, colonial seabirds and a few raptors, especially those populations wintering in western Europe or North America. Much less is known about trends in non-colonial seabirds, shorebirds and landbirds and especially for populations wintering in Asia, Africa and Latin America. Even where populations trends are known, the assignment of causes may be speculative.

Among landbirds, only the raven *Corvus corax*, the ptarmigans, the gyrfalcon *Falco rusticolus*, the snowy owl *Bubo scandiaca* and the Arctic redpoll *Acanthis hornemanni* remain over substantial areas of the Arctic throughout the winter, along with some marine birds (black guillemot *Cepphus grylle*, thick-billed murre *Uria lomvia*, ivory gull *Pagophila eburnea* and Ross's gull *Rhodostethia rosea*) and the eider ducks. Practically all shorebirds and most members of other groups migrate away from the Arctic in winter (93% of species), some moving to peripheral areas in the boreal and temperate regions (most waterfowl, passerines, owls, birds of prey, auks and gulls), some to the tropics (some shorebirds, phalaropes, Sabine's gull *Xema sabini*) and a few to austral temperate, Antarctic or sub-Antarctic regions (some shorebirds, Arctic tern, some jaegers/skuas *Stercorarius* spp.) (Fig. 4.2).

Because of the widespread dispersal of Arctic birds to lower latitudes in winter, population trends in migrant species are not necessarily determined by changes in Arctic environments. For example, Arctic-breeding snow goose *Chen caerulescens* populations have expanded enormously in North America over the past 30 years, predominantly as a result of the geographical expansion and increased productivity of agricultural crops in their wintering areas (Jefferies *et al.* 2004). Likewise, the decline in Arctic-breeding red knot *Calidris canutus* ssp. *rufa* has been attributed to changes in feeding conditions in their staging area, on Delaware Bay, USA (Morrison *et al.* 2004), rather than to changes on their Arctic breeding grounds. The only Arctic bird to become extinct in historical times, the eskimo curlew *Numenius borealis* ('Possibly extinct'; Butchart *et al.* 2006) was the victim

**Figure 4.2.** Major flyways of Arctic birds. Bird migration links Arctic breeding areas to all other parts of the globe. (Adapted from ACIA 2005).



of hunting on its migration areas in E North America (Bodsworth 1963).

## 4.2.2. Biogeography

The avifauna of the Arctic is dominated by birds of the orders Charadriiformes (76 spp.), and the Anseriformes (32 spp.). Species richness is generally low in Arctic avian communities, compared with those at lower latitudes (see Fig. 2.1 in Payer *et al.*, Chapter 2). Among the Charadriiformes, the families Scolopacidae (sandpipers and allies), Laridae (gulls) and Alcidae (auks; the latter two sometimes treated as sub-families) and among the Anseriformes the subfamilies Mergini (sea ducks) and Anserini (geese) contribute most species to the Arctic avifauna. These two orders comprise 108 of 162 species (67%) for which more than half their breeding range falls within either the terrestrial or marine Arctic. Conversely, the highly diverse order of Passeriformes (songbirds), which comprises more than 50% of bird species worldwide, is represented in the Arctic by only 34 species (21%). The difference is even more striking when we consider only the high Arctic, where Anseriformes and Charadriiformes make up 70% of 68 species and Passeriformes only 13%.

Two families are mainly confined to the Arctic and sub-Arctic: the loons/divers (Gaviidae) and the auks (Alcidae), while the geese (11 species in the Arctic) and sandpipers and allies (39 species) reach their highest diversity there. At the level of genus, the ducks *Somateria* and *Polysticta* (eiders) and *Melanitta* (scoters), the turnstones *Arenaria*, the *Pluvialis* plovers, the little auk *Alle alle,* the monotypic gull genera *Xema*, *Rhodostethia* and *Pagophila* and the passerine buntings *Plectrophenax* are all confined to the Arctic and sub-Arctic. Two species of ptarmigan *Lagopus* are mainly confined to the Arctic and sub-Arctic, but are also found in alpine areas at lower latitudes. The diversity of Arctic gulls is especially noteworthy because five out of the 10 currently recognized genera (the above plus *Rissa* and *Chroicocephalus*) of this cosmopolitan family are confined to the Arctic, sub-Arctic and adjacent north temperate zones. In the highly diverse genus *Larus*, nine out of 24 species worldwide occur in the Arctic. The passerine genus *Eremophila* (horned larks) has an Arctic/alpine distribution, although one species also occurs in Palearctic deserts. Several other genera are found primarily in both Arctic/alpine and desert or prairie regions (cranes *Grus*, pipits *Anthus,* wheatears *Oenanthe*, longspurs *Calcarius*).

Species richness is generally low in Arctic avian communities, compared with those at lower latitudes. However, this generalization does not apply to seabirds, where species richness peaks in subpolar waters (Gaston 2004) or shorebirds where breeding diversity is highest on lowland Arctic tundra (Taylor 2006). Within ecoregions, altitude and distance from the coast are both important predictors of avian biodiversity in the Arctic, with species richness falling off quickly with altitude, especially in the high Arctic and, in some regions, being inversely related to distance from the coast, as coastal species form an important fraction of the species richness.

## 4.2.3. Climate and ecosystem change

"Birds breeding in alpine and arctic habitats suffer a seasonal reproductive disadvantage compared to birds at lower latitudes or elevations because the breeding window is short and in late years, nest failure may be high with little opportunity for renesting. Coping mechanisms may only be effective below a threshold of climactic extremes. Despite strong resilience in fecundity parameters, when snowmelt is extremely delayed breeding success is greatly reduced... [they] will be further challenged as they attempt to cope with anticipated increases in the frequency and severity of weather events (climate variability), as well as general climate warming" (Martin & Wiebe 2004).

Ongoing changes in global climate are well known and disproportionately affect high latitudes (IPCC 2007). Changes in the timing of events in the physical environment over the past several decades, especially an advance in the date of Arctic spring sea ice break-up (Parkinson & Cavalieri 2008, Perovich & Richter-Menge 2009), and substantial increases in air temperatures, both in summer and winter, at many Arctic stations (Tedesco *et al.* 2009) have been well documented. A wide range of phenological changes in components of biological systems have also been documented, with many species of plants and animals showing advances in the timing of seasonal events (e.g. Visser & Both 2005, Høye *et al*. 2007, Jia *et al.* 2009, Gauthier *et al*. 2011a). For birds, such advances have been seen in timing of migration (Sparks 1999) and reproduction (Winkler *et al.* 2002, Both *et al.* 2004, Thackeray *et al.* 2010). Although timing effects may be mediated by advances in the timing of food resources, there is evidence that birds may respond to temperature *per se* (Both *et al.* 2006, Visser *et al.* 2009).

As the timing of seasonal events changes under the influence of changing climate, corresponding adjustment in the timing of crucial life-history events for birds (e.g. breeding, migration, molt) becomes an important issue. For example, in species where the timing of reproduction is determined by invariant mechanisms, such as day length, or on regional rather than local conditions (Frederiksen *et al.* 2004a), the ability to adjust to changes in the physical environment may be limited, resulting in a mis-match between physical and biological events (Coppack *et al.* 2001, Stenseth & Mysterud 2002, Nussey *et al.* 2005, but see also Durant *et al.* 2005). Where adjustment of life history events fails to keep pace with changes in the timing of prey availability (generally referred to as 'life history mis-match'; Visser & Both 2005) reproduction and other seasonal events may be compromised (e.g. Dickey *et al*. 2008). Conversely, in situations where late snow-melt or sea-ice breakup sometimes reduces reproduction, general warming may make breeding more predictable for some populations (e.g. Gaston *et al.* 2005a, 2005b, Love *et al.* 2010).

Arctic birds are highly susceptible to variation in weather conditions during breeding (Ganter & Boyd 2000, Meltofte *et al.* 2007a, Dickey *et al.* 2008). In particular, the timing of snow melt determines the availability of suitable nesting and feeding areas for many species, and in general, because species may be breeding close to the limits of their physiological tolerance, adverse weather conditions are more likely to cause breeding failure than at lower latitudes (Martin & Wiebe 2004). Given the likely amelioration in climate over coming decades, we might assume that conditions for breeding of many Arctic species will improve (e.g. Jensen *et al.* 2008) – at least until expanding vegetation types from the south overtake their habitats (Meltofte *et al.* 2007a). However, climate change will also bring new competitors, predators and diseases, as well as rearranging the structure of biological communities (Kutz *et al.* 2004, 2005, Bretagnolle & Gillis 2010, Brommer & Møller 2010). Depending on the rate of change of different factors, any number of different scenarios is possible. The empirical evidence reviewed here is based on a small number of studies in very localized areas, many peripheral to the Arctic, and involving, for the most part, only tiny fractions of total populations. We should be extremely cautious about any future scenarios based on such a tiny sampling of the regional avifauna.

## 4.3. WATERFOWL: DUCKS, GEESE AND SWANS

> » *When the geese first arrived, they didn't stay only in one place. They went to the areas where the snow had melted first, like on the riverbanks. They look for available food. When it is time to lay their eggs, they probably nest where food is available. After the eggs hatch, the parents bring their goslings all over the tundra and they are no longer seen. They stay mostly around the evget* [Carex subspathacea]. *They say that when they molt, even though there are lots, they become quiet. It is said that they are scared. You could see a lot of their tracks on the mud between the small grasses.*
>
> (Michael John of Newtok, Alaska, in Fienup-Riordan 1999).

The waterfowl (family Anatidae) are one of the most diverse and visible groups in the Arctic bird fauna with numerous large-bodied and abundant species, many of which breed exclusively in the Arctic. Most species leave the Arctic after the breeding season to winter in temperate regions of the Northern Hemisphere; the seaducks, however, largely remain in Arctic waters in the winter. Some species undergo molt migration within the Arctic prior to leaving for southern wintering areas, as observed e.g. by indigenous peoples of Nunavut:

> » *Canada geese are numerous now, but they do not nest here. Rather, they come here to fledge their feathers and there are so many that they do not flee.*
>
> (Novalinga: Elders Conference on Climate Change 2001).

Because waterfowl are large, numerous, migratory and palatable there has long been a close relationship between waterfowl and humans through hunting. Most species are hunted during migration and in winter, resulting in major impacts on population sizes and dynamics that occur away from the Arctic breeding grounds. Hunting and egg collecting also occur in the Arctic, but at present are generally less relevant to populations compared with hunting during migration (Kostin 1996, Arctic Goose Joint Venture Technical Committee 2008, Merkel & Barry 2008). Until the mid-20th century, however, the impact of persecution on the breeding grounds was probably significant for some populations (Storå, 1968, Nowak 1995; see also Fig 4.3 and Box 4.1).

Hunting of waterfowl has considerable economic importance, and thus much attention is paid to management of populations along the flyways. Arctic-breeding waterfowl populations are subject to various international protection agreements (e.g. African-Eurasian Waterbird Agreement (AEWA), Ramsar, North American Waterfowl Management Plan (NAWMP)). However, there is a large discrepancy between the intensity of population monitoring and management in the Western Hemisphere and W Palearctic as opposed to the E Palearctic, where flyway populations are less well monitored and hunting is less regulated.

Another important factor acting on population sizes, especially of the herbivorous geese, is change in agricultural practice on staging areas along migration routes and in wintering areas. During recent decades, Arctic-breeding geese have increasingly benefitted from foraging opportunities in agricultural fields on the wintering grounds and along the flyways of North America and Europe (Jefferies *et al.* 2004, Fox *et al.* 2005, Gauthier *et al.* 2005, van Eerden *et al.* 2005).

### 4.3.1. Species richness and distribution

#### 4.3.1.1. Status

Of a total of 39 species of waterfowl breeding in the Arctic, 21 occur in the high Arctic, but none are confined to the high Arctic. There are two species of swans (*Cygnus*), the tundra swan *Cygnus columbianus* being an Arctic specialist. The geese (*Anser*, *Chen* and *Branta*) have the center of their distribution in the Arctic; 13 species occur here and 11 of them are more or less confined to tundra habitats during the breeding season, while two have ranges extending further south into northern temperate regions. These three genera include only four other species which breed entirely outside the Arctic. The ducks are represented by 24 species, the dabbling ducks being mostly boreal species with part of their distribution in the low Arctic while most of the diving ducks and seaducks also occur in the high Arctic. Eight species of ducks, all of them diving ducks or seaducks, are Arctic specialists, among them the endemic genera *Somateria* (eiders, 3 species), *Polysticta* and *Clangula* (Steller's eider and long-tailed duck, both monotypic).

Overall diversity is highest along and near both sides of the Bering Strait, i.e. in the low Arctic of W North America and E Siberia, with 22 species breeding in Arctic Alaska, 20 in the W Canadian Arctic and 20 in the Russian Far East Arctic. The other low Arctic zones have between 15 and 17 breeding species of waterfowl, with the exception of Greenland where only eight species breed in the low Arctic. In the high Arctic zones, between five and 11 species occur, with the European Russian zone (i.e. the islands of Novaya Zemlya and Vaigach) having the highest diversity.

Several taxa have been elevated to species status only recently and were previously considered sub-species. These splits mainly involve distinguishing Eurasian and North American populations (Eurasian/green-winged teal *Anas crecca/carolinensis*, common/black scoter *Melanitta nigra/americana*, velvet/white-winged scoter *Melanitta fusca/deglandi*), but also the larger-bodied (*Branta canadensis*) and smaller-bodied (*Branta hutchinsii*, now cackling goose) forms of Canada geese. Moreover, the tundra bean goose *Anser serrirostris* has been split from the boreal taiga bean goose *Anser fabalis*. On the other hand, the previously separated Bewick's (Eurasia) and whistling (North America) swans are now considered a single species, the tundra swan *Cygnus columbianus*.

Many Arctic-breeding waterfowl species have very large ranges, and for some of them several morphologically distinct subspecies are recognized. Examples are dark- *Branta bernicla bernicla*, black- *B.b. nigricans* and light-bellied brant geese *B.b. hrota*; lesser *Chen c. caerulescens* and greater snow geese *C.c. atlantica*. The subspecific taxonomy of Canada and cackling geese is unclear. Some subspecies are confined to small breeding ranges, such as the Greenland race of mallard *Anas platyrhynchos conboschas* and the Greenland white-fronted goose *Anser albifrons flavirostris*.

### 4.3.1.2. Trends

> » *In the Kivalliq region, we are the northernmost people, and we are not yet subjected to the changes to the degree the other delegates have noted, but things are changing nonetheless. However, geese were quite rare in our area, both snow and Canada geese. We now have geese in more areas, not just in Qaggitalik, which was the main area for hunting geese.*
>
> (Qaunaq: Elders Conference on Climate Change 2001).

Trends in ranges of Arctic-breeding waterfowl appear to be always connected to trends in numbers (see Section 4.3.2). In recent decades, range expansions have been recorded for a number of goose species. In the Nearctic, breeding snow geese have expanded southwards along the coast of Hudson Bay (Mowbray *et al.* 2000), and Canada geese have expanded into W Greenland where they continue to increase (Malecki *et al.* 2000). Similarly, Ross's geese *Chen rossii* showed a major eastward expansion as the species now breed in large numbers in areas such as west Hudson Bay or south Baffin Island where only snow geese used to breed (Kelley *et al.* 2001, Kerbes *et al.* 2006). Dark-bellied brant geese have expanded eastwards, and Pacific black-bellied brant have expanded westwards in Siberia, so that both subspecies now meet in the Lena Delta, where they interbreed; both populations have moved into the gap left by the Asian population of black-bellied brant which is close to extinction (Syroechkovskiy 2006). Russian barnacle geese *Branta leucopsis* have expanded their range towards the W and SW: while they were confined to the islands of Novaya Zemlya and Vaigach in the 1980s they are now breeding along the mainland further to areas W and with tens of thousands of pairs on the island of Kolguev (and, in addition, have expanded their range outside the Arctic, SW to the coasts of the Baltic and W Europe, where they now breed with several thousand pairs; van der Jeugd *et al.* 2009). By contrast, the breeding range of the lesser white-fronted goose *Anser erythropus* has contracted and it has now almost disappeared from northern Scandinavia and the European part of the Russian Arctic (Morozov 2005). No strictly Arctic waterfowl species has gone extinct during historic times, however, the sub-Arctic Labrador duck *Camptorhynchus labradorius* was hunted to extinction in the late 19th century (Fuller 2000).

In Greenland, there are two examples of recent northward range expansions of duck species: common eiders have expanded their range within Greenland (Boertmann & Nielsen 2010), and Eurasian teal together with northern pintail *Anas acuta* have recently been breeding or supposed to breed, respectively, in Greenland (Boertmann 1994, Glahder & Walsh 2010, Meltofte & Dinesen 2010, Jensen & Rasch 2011). Apart from these, we are not aware of any records of boreal or temperate duck species expanding their range northwards into the Arctic as is the case with some shorebirds (see Section 4.4.1.2). However, ducks are generally less well researched on the breeding grounds than are geese, especially in the Palearctic. Still, there are some reports from local people about range changes of several duck species. In sub-Arctic northernmost Finland, the late Saami reindeer herder Ilmari Vuolab had noted that ducks were increasing again after a time when all kinds of ducks were disappearing from the region.

> » *But then again, what we call sea birds, like long-tailed ducks, velvet scoters and common scoters – they are all gone. There used to be great flocks of them and now they are so few.*
>
> (Helander *et al.* 2004).

### 4.3.1.3. Causes and prospects

Range expansions are expected to continue as long as populations continue to grow (see Section 4.3.2.3). A model of the distribution of pink-footed geese *Anser brachyrhynchus* on Svalbard under even modestly warmer climate scenarios (1-2 °C increase in summer temperatures) predicted a large north- and eastward expansion of the breeding range on Svalbard (Jensen *et al.* 2008).

## 4.3.2. Population sizes and densities

### 4.3.2.1. Status

Order of magnitude population sizes for Arctic-breeding waterfowl are given in Appendix 4. Population sizes are typically monitored on the wintering grounds through the International Waterbird Census (Wetlands International 2012), and for those species that have only part of their breeding distribution in the Arctic it is often impossible to separate Arctic breeders from boreal or temperate birds at the time of counting. Therefore, we discuss status and trends of population sizes only for species that are predominantly (> 50% of the population) confined to the Arctic during the breeding season (Category 1 and 2 in Appendix 4). All but three of these species have populations numbering in the hundreds of thousands (7 species) or millions (7 species). Only the lesser white-fronted goose, the emperor goose *Chen canagicus* and the red-breasted goose *Branta ruficollis* number less than 100,000 birds; these species are classified by the IUCN as vulnerable, endangered and near threatened, respectively, and are subject to conservation efforts. Despite large population sizes the Steller's eider *Polysticta stelleri*, the long-tailed duck *Clangula hyemalis* and the velvet scoter *Melanitta fusca* are listed as vulnerable or endangered because of rapid population declines in recent decades. Some of the more numerous species, have (sometimes morphologically distinguishable) populations that use distinct breeding areas and migration corridors; some of these populations number less than 10,000 individuals. Because international agreements focus on conservation at the population level, special

## Box 4.1. Common eiders: circumpolar sea ducks

The common eider *Somateria mollissima* has a circumpolar distribution breeding mainly on small islands in Arctic and boreal marine areas in Alaska (Bering Sea region), Canada, Greenland, Iceland, N Europe and the Barents Sea region. In mainland Russia, there is a gap in distribution from the Yugorski Peninsula (Kara Sea) to Chaunskaya Bay in E Siberia (Box 4.1 Fig. 1). Important wintering areas include the Gulf of Alaska/Bering Sea/Aleutian region, SE Canada, SW Greenland, Iceland and NW Europe. Six or seven subspecies are recognized, of which four occur in North America (Bustnes & Tertitski 2000, Goudie *et al.* 2000).

The common eider is a highly valued living resource in the Arctic. The birds or their products are harvested throughout most of the circumpolar region. As the largest duck in the Northern Hemisphere, it is important for traditional food and lifestyle not only in many Arctic communities, but also in SE Canada and the Baltic region (Merkel & Barry 2008). In some countries, especially Iceland, down feather collection constitutes a significant commercial industry (Bédard *et al*. 2008).

The common eider is dependent on benthic organisms in shallow marine waters for food throughout the year, making it a potential indicator of the health of marine coastal environments. This is similar to situations in which fish-eating seabirds can indicate changes in the pelagic marine ecosystem (Wanless 2007). Year-round movements have been studied intensively over the past 10-15 years by satellite telemetry (e.g. Mosbech *et al.* 2006, Petersen 2009), and this provides a good foundation for monitoring change in the future.

The world population of common eiders probably ranges from 1.5 to 3.0 million breeding pairs (Bustnes & Tertitski 2000). Around the early 1990s, it was clear that common eiders in the Arctic, along with other eider species, had generally suffered large declines over several decades, and the need to stabilize and manage eider populations was increasingly recognized. As part of the Arctic Environmental Protection Strategy, signed in 1991, the Circumpolar Seabird Group under CAFF developed a Circumpolar Eider Conservation Strategy and Action Plan (1997).

The factors behind several eider population declines reported in the 1980s and 1990s (including populations in Alaska, Canada, Greenland and Russia) were often unknown, but in some cases involved human disturbances, excessive harvest of eggs and birds together with severe climatic events (Robertson & Gilchrist 1998, Suydam *et al.* 2000, Merkel 2004a). The current trend of common eider populations varies but at least some populations in Alaska, Canada and Greenland (see Fig. 1.4 in Meltofte *et al.*, Chapter 1) are now recovering with improved harvest management as a likely contributing factor (Goudie *et al.* 2000, Chaulk *et al.* 2005, Gilliland *et al.* 2009, Merkel 2010 , Burnham *et al.* 2012). Breeding populations in the Barents Sea region appear reasonably stable (Bustnes & Tertitski 2000).

Along with other gregarious bird species, common eiders are sometimes affected dramatically by diseases. A recent outbreak (2005-present) of avian cholera in the Hudson Strait of E Canada abruptly reversed a population increase and reduced the population of a large colony there by 30% in just three years (Buttler 2009). By-catch in fisheries gillnets is also a significant problem in some areas (Bustnes & Tertitski 2000, Merkel 2004b, Merkel 2011) and may be a more widespread concern. The search for oil and gas reserves in the Arctic is increasing and may put eider ducks at further risk in the future. The direct response of eiders to climate change is currently under investigation in several countries. In Iceland, local weather conditions appear to affect nesting dates and clutch sizes, although not consistently between colonies (Jónsson *et al*. 2009). The management of human harvest of eiders or their products, and the management of introduced predators such as foxes and mink, will remain important issues in the conservation of common eider populations.

attention is paid to such small populations, such as the E Atlantic light-bellied brant goose, the 'grey-bellied brant goose' *B.b. hrota/nigricans* of the W Canadian high Arctic or the Tule white-fronted goose *Anser albifrons gambeli*.

Geese of the genera *Chen* and *Branta* as well as eiders tend to be colonial nesters. Colonies can consist of only a few pairs on an islet, but some species, especially barnacle geese and snow and Ross's geese can form very large aggregations. These colonies sometimes number more than 100,000 pairs (Alisauskas *et al.* 2006), with densities of up to 3,000 pairs/km$^2$ (Baranyuk *et al.* 2001, Mooij *et al.* 2011). The other species are generally dispersed nesters with lower densities over large ranges. Examples for goose densities in the genus *Anser* are c. 1 pair/km$^2$ (van den Bergh 1999) or 20-80 pairs/km$^2$ (Kondratyev & Zaynagutdinova 2008).

Large and dense aggregations of birds can also be formed by non-breeding and post-breeding birds during molt, often in specific molting areas that are not used as breeding sites but are reached after a molt migration within the Arctic (e.g. Petersen *et al.* 1999, Flint *et al.* 2008). Because waterfowl are flightless for several weeks during wing molt, they are particularly sensitive to predation and disturbance at this time (Mosbech & Glahder 1991, Miller 1994, Madsen *et al.* 2009).

#### 4.3.2.2. Trends

Most Arctic-breeding goose populations have increased markedly in the last 30-50 years, many of them recovering from alarmingly low population levels in the mid-20th century. In the W Palearctic, 12 out of 14 Arctic-breeding goose populations belonging to seven species

**Box 4.1 Figure 1.** Breeding and wintering range of common eiders *Somateria mollissima* in the circumpolar region (not all southern breeding areas included). (Modified from CAFF 2010).

had positive long-term (20-50 yr) population trends with annual growth rates between 1.1% and 7.8%, with the largest increases in barnacle geese (Fox *et al.* 2010). The exception is the lesser white-fronted goose, where the N European population has declined to almost zero and the larger Russian population appears to be stable. In the Nearctic, snow and Ross's geese have experienced dramatic and ongoing population growth on all flyways during the past decades, while greater white-fronted goose numbers now appear to be stable and there is currently no clear trend for brant geese (Canadian Wildlife Service Waterfowl Committee 2011).

By contrast, populations of four goose species breeding in the E and far E Russian Arctic and wintering in E Asia (mainly China) have undergone steep declines in the late 20th century (Syroechkovskiy 2006). Red-breasted geese that breed in central N Siberia and Steller's eiders with a circumpolar but patchy breeding distribution are also declining (Wetlands International 2012). The other species of eider have stable population sizes (see Box 4.1); no consistent global trends have been reported for tundra swan, greater scaup *Aythya marila* and the circumpolar long-tailed duck, although the large wintering population of the latter in the Baltic Sea has apparently declined by two thirds in the past 20 years (Skov *et al.* 2011).

#### 4.3.2.3. Causes and prospects

Cause for declines in red-breasted geese (Fox *et al.* 2010) and Steller's eiders (Petersen *et al.* 2006) are unclear and need further examination. The lesser white-fronted goose is threatened by hunting on migration and in winter, when it mixes with the morphologically similar and much more numerous greater white-fronted goose, which makes it vulnerable to accidental shooting despite its protected status (Lorentsen *et al.* 1999).

The marked and continuing increases in many North American and W Palearctic goose populations have been attributed to a combination of two main factors: agricultural change on staging and wintering areas providing plentiful food resources for geese, and reduction of hunting pressure during migration and in winter. The latter applies especially to the W Palearctic and is a result of conservation measures initiated in the second half of the 20th century when populations of brant and barnacle geese were threatened with extinction (Madsen *et al.* 1999). In addition, intensive persecution of geese on the Russian breeding grounds until the first half of the 20th century (see e.g. Storå 1968 and Fig. 4.3) may have further decimated populations, and this is no longer the case (Nowak 1995).

Beginning in the mid-1990s, increased population size of lesser snow geese in the North American mid-continent and of greater snow geese *Chen c. atlantica* in E North America was identified as a conservation problem because rapidly growing numbers of geese increasingly degrade sub-Arctic and Arctic coastal habitats in the vicinity of breeding colonies and at staging sites (Ankney 1996, Batt 1997, 1998; see Ims & Ehrich, Chapter 12). Subsequently, unprecedented management efforts were made to increase hunting pressure and thereby reduce survival of adult geese to ultimately reverse population growth. However, these efforts failed to have the desired effect, and population size of mid-continent snow geese was estimated to be between 15 and 25 million in 2006, about twice as many as in 1995 (Alisauskas *et al.* 2011). In contrast, these management actions were much more successful in stabilising the population of the greater snow goose between 800,000 and 1,000,000 birds in recent years after the population had exceeded the 1 million mark for the fist time in 1999 (Reed & Calvert 2007). In this population, management efforts will have to be maintained at a high level to prevent further popula-

**Figure 4.3.** Mass captures of up to 3,000 flightless geese in one go and up to 26,000 flightless ducks in three days took place in northern Eurasia well up into the 20th century, probably contributing to the critically low population sizes in several goose populations in the middle of the century (from Storå 1968).

tion growth. In the W Palearctic, a management plan for preventing the Svalbard population of pink-footed geese from further increase is under development among the range states (Madsen & Williams 2012).

Jensen *et al.* (2008) predict that climate change may lead to a further growth in population size of many Arctic breeding geese. As conditions on the Arctic breeding grounds ameliorate with climatic warming, density-dependent mechanisms that regulate population size on the breeding grounds may relax through prolonged breeding seasons and improved access to more nesting and feeding areas (see also Madsen *et al.* 2007). However, other mechanisms may counteract these positive impacts of climate warming. In several areas, wetlands used by geese are formed by patterned ground, i.e. tundra polygons. The stability of these polygons depends on the integrity of the frozen ground, and they are particularly vulnerable to the rapid melting of ice-wedges in the ground (Fortier *et al.* 2007). Recent degradation of these ice-wedges due to thermal erosion has drained several wetland areas on Bylot Island (Godin & Fortier 2010), which led to a rapid shift toward drier plant communities and a loss of feeding habitat for broods (Gauthier *et al.* 2011a). Such phenomena are likely to increase with climate warming. Sea ducks may benefit from improved access to marine benthic food sources through reduced ice cover in time and space. On the other hand, Fox *et al.* (2010) report a trend for decline in reproductive output in many W Palearctic goose populations, which may be a first sign of density-dependent processes impeding further population growth at present.

Away from the breeding grounds, predicted future changes in agricultural land use in the staging and wintering areas of Arctic waterfowl may be detrimental to populations (van Eerden *et al.* 2005, Wisz *et al.* 2008). Increased human population pressure on wintering areas may lead to habitat loss for wintering waterfowl. Those species that utilize specialized food resources during winter and migration, such as brant geese feeding on seagrass *Zostera* spp. (Ganter 2000) or tundra swans feeding on pondweed *Potamogeton* spp. (Drent 1996), are especially sensitive to changes in the availability of these forage species e.g. caused by eutrophication (e.g. Meltofte & Clausen 2011). The situation, however, may not apply to some goose populations that have thoroughly adapted to the agricultural landscape during winter (e.g. Jefferies *et al.* 2004, Gauthier *et al.* 2005).

For many of those Arctic waterfowl populations that are faring less well, the main stressor appears to be hunting during migration and on wintering grounds. This is rather well managed and carefully monitored in North America and the W Palearctic, but much less controlled in Asia.

For seaducks wintering in Arctic waters, often concentrated in small areas at high density, spills from oil exploration and increased shipping in Arctic waters constitute a potentially serious threat if offshore oil exploitation increases as currently expected (AMAP 2007). Spectacled eiders *Somateria fischeri* wintering in polynyas in the Bering Sea are dependent on both benthic food sources and opportunities to rest on sea ice. Increased sea temperatures could lead to a major shift in benthic communities and at the same time will cause loss of sea ice, potentially threatening the well-being of this species (Grebmeier *et al.* 2006, Lovvorn *et al.* 2009).

## 4.3.3. Other issues

### 4.3.3.1. Changes in phenology

Herbivorous waterfowl follow the wave of new growth of forage plants northwards during spring migration and through brood rearing (van der Graaf *et al.* 2006). If phenology of spring plant growth changes with climate change in the Arctic, herbivorous waterfowl will have to adjust their migration schedules to ensure sufficient food resources during brood rearing. Some goose populations can apparently adapt their migration schedules to changed patterns of food availability and climate as shown by case studies on changing use of European stopover sites by pink-footed and barnacle geese (Bauer *et al.* 2008, Tombre *et al.* 2008, Eichhorn *et al.* 2009). Residents of European Russia have noticed a local decline in migrating geese despite the overall population increase, probably reflecting changes in migration routes and/or stopover schedules. Arkady Khodzinsky, a reindeer herder from Lovozero community on the Kola Peninsula has observed the following:

> » *There is very little goose now. It used to be that they were all over. Before, when we were at the camp and we would see geese we would know the spring is coming. Nowadays we see no geese. Occasionally one or two flocks fly over but this is a rare event.*
>
> (Cherenkov *et al.* 2004).

However, not all populations may show such flexibility, in particular those migrating to the high Arctic. In E North America, greater snow geese nesting on Bylot Island have not advanced their laying date over the past 20 years despite a significant advance of spring in the area (Dickey *et al.* 2008). In very early years, this causes a mismatch between the hatching date of goslings and the phenology of their food plants, which reduces gosling growth. As the climate warms, this mismatch will likely increase, which may reduce the recruitment into the population (Gauthier *et al.* 2011a).

### 4.3.3.2. Predator-prey interactions

Together with other breeding birds of the central N Siberian Arctic (see Section 4.4.3.1), brant geese have been showing a marked boom-and-bust pattern of reproductive performance that is closely linked to the cyclical dynamics of the populations of lemmings (*Lemmus* spp. and *Dicrostonyx* spp.) and their predators (Summers & Underhill 1987), a relationship that also applies to other species in several parts of the Arctic (Bêty *et al.* 2002, Meltofte *et al.* 2007b, Morrissette *et al.* 2010). In lemming peak years, the densities of predators such as Arctic fox *Vulpes lagopus* build up; in the following year, after the collapse of lemming populations, when numbers of foxes are still high, they switch to alternate prey such as shorebird and waterfowl eggs and chicks (Roselaar 1979, Summers & Underhill 1987, Bêty *et al.* 2002, Lecomte *et al.* 2008). Under changed climatic regimes, lemming cycles tend to be less pronounced in some areas (Ims *et al.* 2008, Kausrud *et al.* 2008, Gilg *et al.* 2009a, Reid *et al.*, Chapter 3, Ims & Ehrich, Chapter 12), which is expected to have implications for the entire Arctic food web. Ebbinge (2009) already reported a lack of regularity in lemming peaks in central N Siberia in recent years affecting the breeding success of brant geese: while breeding success had in previous decades shown regular peaks of up to 50% juveniles in the wintering population in every third year, following lemming peaks in the preceding summer, this pattern has been more irregular since the early 1990s.

Another recent example of changes in predator-prey relations is the apparently increasing predation on breeding geese by polar bears *Ursus maritimus* on the Hudson Bay coast and in other areas. As receding sea ice is causing bears to spend more time ashore during the summer months, increased predation of goose eggs and adults by polar bears has been reported from various places in the Arctic in recent years (Stempniewicz 2006, Drent & Prop 2008, Smith *et al.* 2010, Rockwell *et al.* 2011). By contrast, breeding brant geese on Svalbard suffer heavily from predation by polar bears in years when sea ice makes their breeding islands easily accessible for these predators (Madsen *et al.* 1998), and they may thus benefit from reduction in spring sea ice cover.

Lecomte *et al.* (2009) recently showed that water availability and rainfall could affect the interaction between geese and another important predator, the Arctic fox. They found that egg predation was reduced in years of high rainfall because fox predation occurs mostly when incubating females leave their nest to drink or feed and the probability of a successful attack increases with distance of the female from her nest. High rainfall increases water availability near the nest, which reduces the distance traveled by females to drink and increases her ability to defend her nest from a predator attack. Because climate change should affect precipitation regimes in the Arctic (IPCC 2007), this may impact nesting success of geese by changing water availability for incubating females.

### 4.3.4. Conclusions

Waterfowl are one of the dominant species groups in the breeding bird communities of Arctic wetlands, and the geese (*Anser* spp., *Chen* spp. and *Branta* spp.) and the seaducks (*Somateria* spp., *Melanitta* spp., *Polysticta* and *Clangula*) are largely Arctic specialists. Because of their migratory nature and their exploitation by humans on the one hand and utilization of anthropogenic food resources in temperate regions on the other hand, population sizes and trends of many Arctic waterfowl species are largely influenced by events outside the Arctic. However, climate change may have major impacts, both positive and negative, on breeding opportunities for waterfowl in the Arctic in the future. New areas of the Arctic may become suitable for breeding and wintering, while at the same time interactions with competitors and predators may change to the worse. Also, Arctic developments (both on- and offshore) are expected to have impacts, with an increase in Arctic shipping particularly affecting the seaducks.

## 4.4. SHOREBIRDS: OYSTERCATCHERS, PLOVERS, SANDPIPERS AND SNIPES

Although they typically spend only several weeks each year on the Arctic breeding grounds, shorebirds are one of the most prominent groups of the circumpolar Arctic bird species assemblage. Many of them breed exclusively in the Arctic, and several species are specialized breeders of the high Arctic. Practically all Arctic shorebirds are long-distance migrants, linking the Arctic breeding grounds to all other continents including the southern tips of Africa, South America and Australia and even islands near the Antarctic Peninsula. Not only the Arctic as a whole, but also geographically restricted areas within the Arctic can be connected to various continents through migrating shorebirds (Fig. 4.4). The combination of breeding in harsh conditions in remote high Arctic areas and record performances on migration (Gill *et al.* 2009) contributes to the charisma of this species group.

### 4.4.1. Species richness and distribution

#### 4.4.1.1. Status

A total of 59 shorebird species breed in the Arctic, 18 of which have their main distribution south of the Arctic, while 41 breed in the Arctic only. Twenty-nine have breeding ranges extending into the high Arctic. None is confined to the high Arctic only, but three (red knot, sanderling *C. alba* and curlew sandpiper *C. ferruginea*) occur mainly there.

The majority of Arctic shorebirds are representatives of the two families, Charadriidae (plovers) and Scolopacidae (sandpipers and snipes); in addition, one member of the cosmopolitan oystercatchers (Haematopodidae) reaches the Arctic in a few places. While the plovers are a large family with only a few Arctic species, the Scolopacidae, and especially the calidrine sandpipers, have their center of diversity in the Arctic. Of 93 species of Scolopacidae, 50 occur in the Arctic and 34 breed in the Arctic only, including 18 of 19 sandpiper species of the genus *Calidris* (see Fig. 1.2 in Meltofte *et al.*, Chapter 1) and two of three species of phalaropes *Phalaropus*.

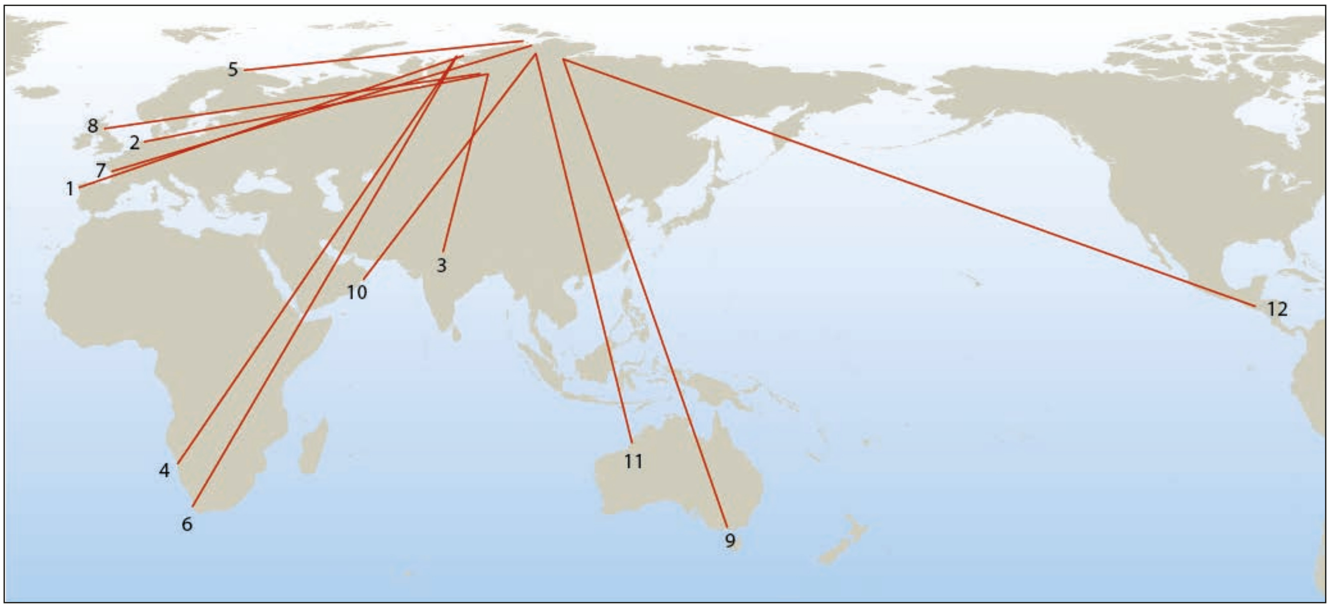


**Figure 4.4.** Migratory links of shorebirds breeding on the Taimyr Peninsula, N Central Siberia, based on recoveries of banded individuals. Only one connection per species is shown. Species: 1) grey plover *Pluvialis squatarola*, 2) European golden plover *Pluvialis apricaria*, 3) ruff *Philomachus pugnax*, 4) little stint *Calidris minuta*, 5) purple sandpiper *Calidris maritima*, 6) sanderling *Calidris alba*, 7) red knot *Calidris canutus*, 8) bar-tailed godwit *Limosa lapponica*, 9) red-necked stint *Calidris ruficollis*, 10) dunlin *Calidris alpina*, 11) curlew sandpiper *Calidris ferruginea*, 12) pectoral sandpiper *Calidris melanotos* (data from Tomkovich *et al*. 2000 and Soloviev *et al*. 2012; map prepared by M.Y. Soloviev).

Shorebird genera that are endemic to the Arctic and sub-Arctic (at least during the breeding season) are *Arenaria* (turnstones, two species) and the monotypic genera *Aphriza* (surfbird), *Eurynorhynchus* (spoon-billed sandpiper) and *Tryngites* (buff-breasted sandpiper). The monotypic genera *Limicola* (broad-billed sandpiper) and *Philomachus* (ruff) have a mainly sub-Arctic and boreal breeding distribution and penetrate into the Arctic in various places.

As in waterfowl, overall diversity is highest in the low Arctic zones on either side of the Bering Strait, with 38 species of shorebirds breeding in the low Arctic of the Russian Far East and 30 species in low Arctic Alaska. The remaining low Arctic zones have between four (Greenland) and 24 different breeding shorebird species. In the high Arctic zones, between seven (Svalbard) and 20 (Russian Far East) species breed. Hence, the Russian Far East has by far the highest diversity of shorebirds in the Arctic.

Some species have small or very small breeding ranges: bristle-thighed curlew *Numenius tahitiensis*, black turnstone *Arenaria melanocephala* and surfbird *Aphriza virgata* are confined to Alaska, great knot *Calidris tenuirostris* and the endangered spoon-billed sandpiper to the Russian Far East, western *Calidris mauri* and rock sandpipers *C. ptilocnemis* (the latter highly substructured with at least four recognised subspecies; Gill *et al*. 2002) to both sides of the Bering Strait. Sharp-tailed sandpipers *Calidris acuminata* and red-necked stint *C. ruficollis* breed in central and E Siberia only. By contrast, grey plover *Pluvialis squatarola*, common ringed plover *Charadrius hiaticula*, ruddy turnstone and dunlin *Calidris alpina* together with red-necked *Phalaropus lobatus* and red phalarope *P. fulicarius* occur throughout the Arctic in nearly all of the zones. Pacific *Pluvialis fulva* and American golden plover *P. dominica* were only recognized as separate species in the 1980s, and the Nearctic Wilson's snipe *Gallinago delicata* has recently been split from the Palearctic common snipe *G. gallinago*.

Molecular studies of subspecific diversity in a number of species with circumpolar distributions have yielded contrasting results: the genetic structure of the sub- and low Arctic dunlin shows very old splits between populations probably resulting from isolated refugia during late Pleistocene glaciations (Wenink *et al.* 1993), while population structuring in the high Arctic red knot appears to be much more recent, suggesting recolonisation of the entire Arctic after a severe population bottleneck during the last glaciation, possibly followed by survival of small populations in tundra refugia during the most recent thermal optimum when high Arctic tundra was reduced to a minimum (Buehler & Baker 2005). The widely distributed ruddy turnstone shows no genetic substructuring, again indicative of a relatively recent severe population bottleneck (Wenink *et al.* 1994). A recent molecular study of Temminck's stint *Calidris temminckii* showed low genetic diversity as well as signs of recent population expansion, and the existence of two lineages in the mitochondrial DNA suggested recolonisation of the present range from two glacial refugia (Rönkä *et al*. 2011).

### 4.4.1.2. Trends

Recent range expansions have been reported for several Arctic species in Russia. The semipalmated plover *Charadrius semipalmatus* has recently expanded across the Bering Strait into the Russian Far East; semi-palmated

*Calidris pusilla*, western and buff-breasted sandpipers *Tryngites subruficollis* have spread westwards from there. Westward expansion has also been recorded for long-billed dowitcher *Limnodromus scolopaceus* and sharp-tailed sandpiper, while whimbrels *Numenius phaeopus* have expanded eastwards in the Far East. Several sub-Arctic or boreal species (jack *Lymnocryptes minimus*, pin-tailed *Gallinago stenura* and common snipe, wood *Tringa glareola*, common *Actitis hypoleucos* and terek sandpipers *Xenus cinereus* and long-toed stint *Calidris subminuta*) have expanded northwards in the Russian Arctic, and jack snipe has also expanded eastwards; pin-tailed snipe has expanded its range both E and W. The ruff *Philomachus pugnax* has shifted its breeding distribution eastwards with populations decreasing in N Europe and the European Russian Arctic and increasing in W Siberia, possibly as a consequence of deteriorating conditions on spring staging sites in W Europe (Verkuil 2010, Rakhimberdiev *et al.* 2011). By contrast, the range of the endangered spoon-billed sandpiper has contracted in recent decades, and many formerly known breeding sites are now deserted (Syroechkovskiy 2005, Zöckler *et al.* 2010a).

#### 4.4.1.3. Causes and prospects

Northward expansion of sub-Arctic or boreal species is likely to be connected to climate amelioration and is expected to continue with ongoing global warming. Other range trends are closely connected to trends in population sizes (see below).

### 4.4.2. Population sizes and densities

#### 4.4.2.1. Status

Order of magnitude population sizes for Arctic-breeding shorebirds are given in Appendix 4. Of the 41 shorebird species that are confined to the Arctic during the breeding season, most have populations numbering in the hundreds of thousands (20 species) or millions (12 species). Six species have population sizes of tens of thousands of birds, among them the buff-breasted sandpiper, which is listed as near threatened by the IUCN because it has failed to recover from a hunting-induced population low in the 1920s. The bristle-thighed curlew numbers less than 10,000 birds; this species is listed as vulnerable because its population is now small and believed to be declining, largely as a result of predation on the wintering grounds, when perhaps more than 50% of adults are flightless during autumn molt (IUCN 2012). The spoon-billed sandpiper is critically endangered with the remaining population now probably under 1,000 individuals and continuing to decline (Syroechkovskiy 2005, Zöckler *et al.* 2010a). The eskimo curlew, although still listed as critically endangered by the IUCN, is most probably extinct (Gill *et al.* 1998). Recently, the great knot and the semipalmated sandpiper were uplisted to the categories vulnerable and near threatened, respectively, because of marked population declines (see 4.4.2.2).

Although population sizes and range sizes often correspond, there are also species with small ranges despite large population sizes. For instance, western sandpipers number about 3.5 million birds (Wetlands International 2012) despite a rather restricted breeding distribution around the Bering Strait within which they can reach very high nesting densities (Wilson 1994).

Breeding densities in suitable habitat vary according to species and site. Larger species such as whimbrel or bar-tailed godwit *Limosa lapponica* defend large territories so that breeding densities mostly are below 1 pair/km$^2$ (Lappo *et al.* 2012), whereas some of the smaller *Calidris* sandpipers or red-necked phalaropes often reach densities of 15-20 pairs/km$^2$ or more (Sandercock *et al.* 1999, Meltofte 2006, Lappo *et al.* 2012, Kruckenberg *et al.* 2012). Among the smaller-bodied species there are large variations in density according to geographic region and latitude. The highest densities of several hundred pairs of shorebirds per km$^2$ are reached in the low Arctic of Beringia, whereas in high Arctic desert only a few pairs per km$^2$ can be found (Meltofte *et al.* 2007a).

#### 4.4.2.2. Trends

Population estimates of shorebirds are usually derived from counts on migration sites or wintering grounds at great distances from the Arctic breeding areas (Wetlands International 2012). Because shorebirds are mostly small-bodied and often have widespread wintering areas, precise counts of entire populations are hard to achieve and trends are accordingly difficult to determine with certainty. Additionally, climate change has been shown to cause distribution shifts of wintering shorebirds (MacLean *et al.* 2008), so that long-term population counts in the same wintering areas may suggest numerical trends that are in fact geographical shifts to different areas. Thus, most trend estimates have to be treated with some caution.

Of 28 Nearctic-breeding shorebird populations for which Morrison *et al.* (2006) compiled population estimates, 16 were thought to be stable or had unknown trends, 10 were thought to be possibly decreasing, and for two (semipalmated sandpipers and the red knot subspecies *Calidris canutus rufa*, see Box 4.2) there was good evidence for a decline. For shorebirds breeding in the W Palearctic there are recent trend estimates from the Russian breeding grounds (Lappo *et al.* 2012) and from the W European Wadden Sea, a major migratory stopover site (Laursen *et al.* 2010). Nearly all populations in this part of the Arctic appear to be stable or increasing. In the Wadden Sea, a clear decrease was noted only for the ruff, a mainly boreal and sub-Arctic breeder, and this may be the result of a range shift (see 4.4.1.2).

Trend estimates for E Palearctic shorebirds are available from winter counts in Australia where large proportions of many populations winter and rather precise counts are possible. According to Garnett *et al.* (2011), eight Arctic-breeding shorebird species wintering in

## Box 4.2. Red knots: connecting continents

The red knot *Calidris canutus*, a typical representative of high Arctic shorebirds, is an exemplar of a long-distance migrant shorebird; it has been the subject of extensive research worldwide including the breeding cycle, winter ecology and stopover sites. It is one of nature's most prodigious travelers, and excites the interest of wildlife enthusiasts, scientists and conservationists around the world. For this reason, its migration system is among the best known of all shorebirds; even so many mysteries remain.

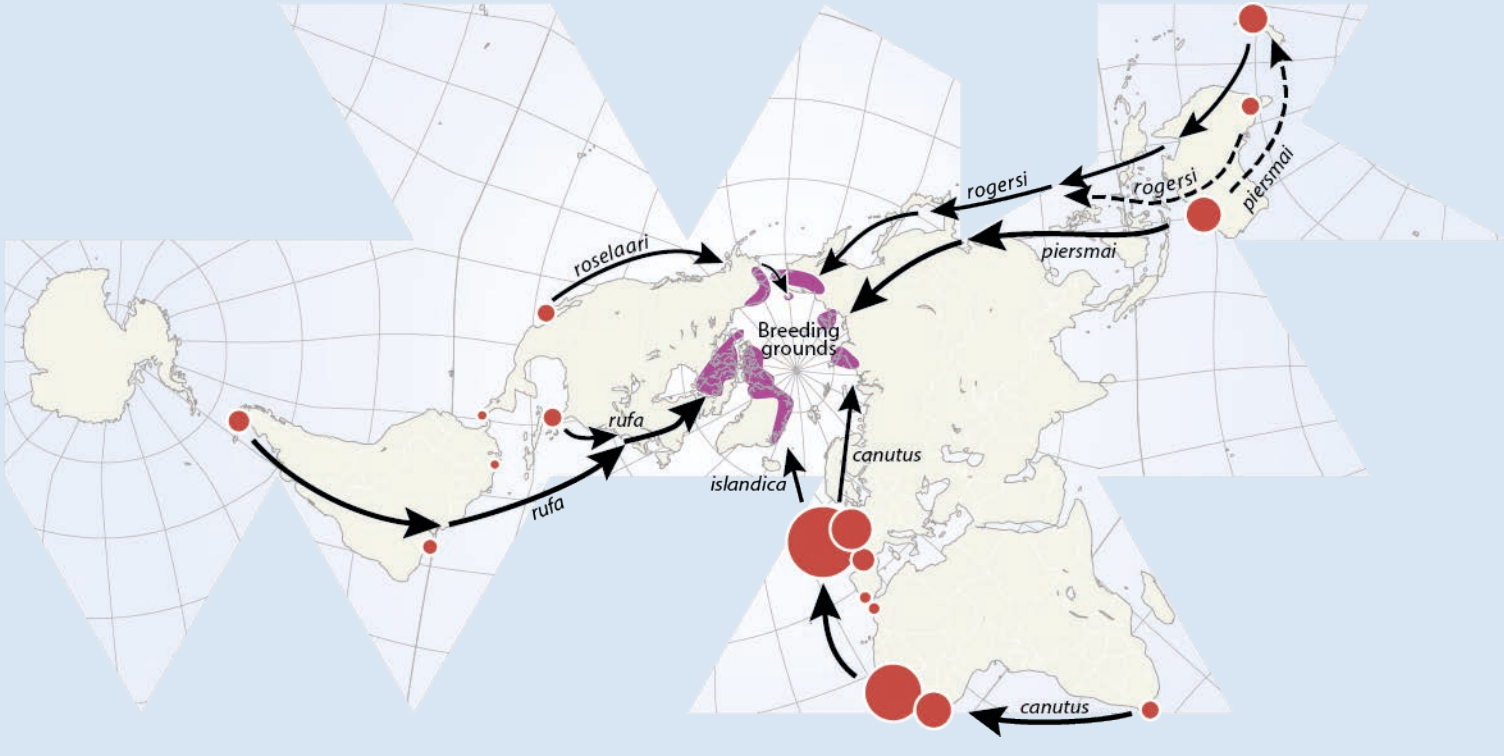
Red knots have a disjointed Arctic breeding distribution ranging from just south of the Arctic Circle at 63° N (*C.c. rufa* and *C.c. rogersi*) to 83° N, nearly the most northerly land in the world (*C.c. islandica*). They nest in areas of sparse vegetation, often close to a damp area where the chicks can feed. They arrive on the breeding grounds in late May to early June, and the eggs hatch from around 1 July whereupon the females depart from the nesting area leaving the chicks in the care of the males. The males leave in late July or early August and the young during the following month.

Breeding success can be very variable depending mostly on weather conditions and the abundance of predators. If there is a late snowmelt, or if the weather is cold leading to a reduction in invertebrate food for the young, and/or if there is an abundance of egg or chick predators such as Arctic foxes and jaegers, breeding success can be almost negligible. But in years when such factors have least impact, as many as half the birds seen on the non-breeding grounds may be juveniles. Year-to-year variation in breeding success arises from random changes in Arctic weather and the often cyclic abundance of predators.

Together, the six red knot subspecies have a circumpolar Arctic breeding distribution though each breeds in a discrete area and mainly winters separately. Non-breeding sites range as far south as New Zealand, South Africa and Tierra del Fuego (Box 4.2 Fig. 1). Of the six subspecies, by far the largest populations are those of *C.c. canutus* and *C.c. islandica*. *C.c. canutus* winters mainly in W Africa and has its breeding grounds entirely on the Taimyr Peninsula of N Siberia. *C.c. islandica* winters in NW Europe and breeds in high Arctic Greenland and NE Canada. Large numbers of both populations, however, are highly dependent on one very large site, the Wadden Sea. In the part of the Wadden Sea belonging to the Netherlands, mechanical shellfish harvesting has so severely depleted the food supply that regional numbers of red knots have declined and negative effects on the two populations as a whole were thought possible (van Gils *et al*. 2006). However, recent analyses of long-term count data from the entire Wadden Sea show stable numbers of red knots over the past 20 years (Laursen *et al*. 2010). Mechanical shellfish harvesting was stopped in 2006, but it is too early to know whether it has had a beneficial effect on the regional population (van Gils *et al*. 2006).

(continues >)

**Box 4.2 Figure 1.** Worldwide distribution of the six recognized subspecies of the red knot *Calidris canutus*. All breeding areas (dark purple shading) are on high Arctic tundra where the adults spend June-July. After their long-distance migrations they spend the non-breeding season (August-May) mainly in intertidal, soft-sediment habitats (red dots, which are scaled according to mid-winter population size). (Modified from CAFF 2010).



**Box 4.2. continued**

The two red knot subspecies of the E Asian-Australasian Flyway, *C.c. rogersi* and *C.c. piersmai*, are both thought to be declining with several sites recording lower non-breeding numbers in recent years (Garnett *et al*. 2011). Their relative status is not clear because although most *C.c. piersmai* are found in NW Australia and most *C.c. rogersi* are found in E Australia and New Zealand, there appears to be considerable overlap. The migration route of both subspecies takes them through the coastal regions of E Asia, especially along the shores of the Yellow Sea. These regions are currently undergoing extensive development with whole estuaries being reclaimed for human use. Quite likely it is loss of habitat in this region that is having a detrimental impact on both populations, but this has yet to be proved (Rogers *et al*. 2010).

The populations of both Western Hemisphere subspecies, *C.c. rufa* and *C.c. roselaari*, appear to be vulnerable. The status of *C.c. roselaari*, which breeds in Alaska and on Wrangel Island and winters along the American Pacific coast, is unclear. The population of *C.c. rufa* was thought to be as high as 170,000 as recently as 2001 (Brown *et al.* 2001), but is now down to 30,000 (Niles *et al.* 2008). Undoubtedly, the most significant factor has been the depletion of the food supply at the final northbound stopover in Delaware Bay on the eastern seaboard of USA. There, knots and other shorebirds time their migration to coincide with the mass spawning of horseshoe crabs *Limulus polyphemus*, and in the past they made rapid mass gains to fuel their onward migration by feeding on crab eggs. Since the mid-1990s, the horseshoe crab population has been overharvested for use as bait, and the supply of eggs has been greatly reduced (Niles *et al.* 2008). Studies have shown that red knots which fail to gain sufficient mass in Delaware Bay have lower survival (Baker *et al.* 2004).

With a total world population of a little over one million, the red knot is not at present threatened as a species, but there are good reasons to be concerned for its future. Like most long-distance migratory shorebirds, red knots are highly dependent on a limited number of key stopover and wintering sites, making them particularly vulnerable to habitat change. Among the most vital sites are the last major stopovers before the final flight to their Arctic breeding grounds. These are of key importance because in those places the birds require sufficient food resources not only to sustain their long flight but also to ensure their survival during the the first time on the breeding grounds when Arctic food resources can be scarce (Meltofte *et al.* 2007a). Other sites may be of equal importance when they form part of a chain of 'stepping stones' in which each link is indispensible.

Australia have suffered severe declines over the last c. 25 years, and their conservation status has accordingly been changed to a less favorable category since 2000. Declines have been especially severe for grey plover, bar-tailed godwit, great knot and red knot. From the Russian breeding grounds, trend information is reported as unclear (13 spp.), presumably stable (9 spp.) or slightly increasing (9 spp., mostly as a result of range expansions, see 4.4.1.2), whereas eurasian dotterel and red knot are thought to be declining (Lappo *et al*. 2012). The most severe decline, however, has been experienced by the far eastern spoon-billed sandpiper, and this species is now facing imminent extinction (Zöckler *et al*. 2010a, Lappo *et al*. 2012).

### 4.4.2.3. Causes and prospects

For the highly migratory shorebirds, the known causes of changes in population size are found mainly outside the breeding grounds. The vast majority of Arctic-breeding shorebirds winter in littoral areas, many of them in the Southern Hemisphere, and during migration depend on coastal sites for stop-over and refueling, making use of the rich invertebrate food resources of intertidal mudflats. Many coastal areas within both staging and wintering ranges are subject to high human population pressure, and large-scale habitat alterations have taken place in recent decades such as in the Yellow Sea, which supports an estimated two million shorebirds on migration, whereas about 600 million people live in the area (Barter 2006, Kelin & Qiang 2006, MacKinnon *et al*. 2012). Vast intertidal areas have been reclaimed and lost to shorebirds, and in the remaining areas shorebirds are competing with fisheries and other forms of development (see Box 4.2). There is good evidence that the loss of staging habitat and/or food resources and thereby loss of refueling opportunities for migrating birds has led to severe population declines at least in one subspecies of red knot in the Nearctic (see Box 4.2) and in the E Palearctic great knot (Moores *et al*. 2008, Garnett *et al*. 2011, MacKinnon *et al*. 2012, Wetlands International 2012).

In addition, intertidal shorebird staging and wintering habitats are threatened by sea level rise resulting from climate change (Rehfisch & Crick 2003, Galbraith *et al*. 2005). Intertidal areas may become subtidal with rising sea levels, or be overgrown with mangroves, as has been reported from estuaries in SE Asia and Australia (Straw & Saintilan 2006).

Compared with staging and wintering grounds, the Arctic breeding grounds are still relatively undisturbed. Here, climate warming is expected to have a major effect on the distribution of habitats. With the northward movement of vegetation zones it is expected that high Arctic species such as red knot, sanderling or curlew sandpiper will eventually run out of suitable breeding habitat, while the already observed trend of sub-Arctic/boreal species expanding their ranges northwards is likely to continue. Shorebirds breeding in the high Arctic benefit from a reduced predation pressure on their nests compared with those breeding at lower latitudes (McKinnon *et al.* 2010). However, as climate warms and some predators expand their range northward, this may negatively impact the productivity of high Arctic-nesting shorebirds.

Some species benefit from human development. For example, common ringed plovers start breeding near man-made structures in previously undisturbed tundra almost immediately upon arrival (Paskhalny 2004, Lappo *et al.* 2012) and appear to have increased in many places in the Russian Arctic. Development may favor populations of some predators of ground-nesting birds, however, resulting in potential negative impacts on breeding shorebirds (Liebezeit *et al.* 2009).

The Eskimo curlew was brought to (near or complete) extinction by market hunting in the late 19th and early 20th centuries in combination with habitat loss outside the breeding area, and hunting continues to be an issue especially for the larger shorebird species. Subsistence harvest of large-bodied shorebirds in Alaska may be substantial (Alaska Shorebird Group 2008), and Arctic shorebirds are hunted for food and sport in staging and wintering areas in the Carribean, South America, Africa and Asia. For the semipalmated sandpiper, there are indications that hunting in South America negatively affects population size (Hicklin & Gratto-Trevor 2010). In the Russian Arctic, hunting during migration may be at least partially responsible for the decline in numbers of the great snipe *Gallinago media* on their European and W Siberian breeding grounds. For the spoon-billed sandpiper, hunting on the wintering grounds in Myanmar, although mainly directed at larger-bodied shorebird species, is probably the main cause for the recent precipitous population decline (Zöckler *et al.* 2010b). However, reliable data on the overall impact of hunting on Arctic shorebird populations are currently not available, and much more information is needed to properly evaluate the situation.

## 4.4.3. Other issues

### 4.4.3.1. Predator-prey interactions

Predation risk appears to play a central role in the reproductive ecology of Arctic-nesting shorebirds at several spatial scales (McKinnon 2011). The breeding success of many Arctic shorebirds is closely linked with the cyclical dynamics of lemming populations because predators like foxes will switch to other prey when lemmings crash (see Section 4.3.3.2). However, because shorebird eggs and chicks may be more an incidental prey than a genuine alternative prey, predation risk for shorebirds may result from a complex interaction betwwen lemming abundance and more profitable alternative prey such as goose eggs (McKinnon 2011). With climate change, lemming cycles have been reported to have been reduced and more irregular in Arctic and alpine ecosystems in Greenland and Europe (Ims *et al.* 2008, Kausrud *et al.* 2008, Gilg *et al.* 2009a, Reid *et al.*, Chapter 3, Ims & Ehrich, Chapter 12) and the same may occur elsewhere, with the potential of markedly altering the dynamics between predators, shorebirds and other prey species.

Interspecific interactions between shorebirds and terns have been reported from Greenland, where the disappearance of Arctic tern colonies from a number of islands was followed by a steep decline in the number of breeding red phalaropes *Phalaropus fulicarius*, suggesting that red phalaropes benefit from tern colonies as a defense against predators (Egevang *et al.* 2006). Similarly, semipalmated plovers in the Canadian Arctic had higher nest survival when breeding in the vicinity of Arctic terns (Nguyen *et al.* 2006).

### 4.4.3.2. Changes in phenology of shorebirds and their prey

Arctic-breeding shorebirds feed mostly on terrestrial invertebrates during the breeding season, and they depend on the short seasonal outburst of insect abundance from the time of their arrival and egg-laying through the period of rapid chick growth (Meltofte *et al.* 2007a, 2007c). However, late arrival of birds in spring or early emergence of insects may result in a mis-match between hatching and insect abundance. During years of mis-match, growth of chicks is reduced (McKinnon *et al.* 2011). Tulp & Schekkerman (2008) showed that in Taimyr in central N Siberia the peak of insect abundance now occurs earlier than 30 years ago. If this trend continues, birds will have to adjust their breeding and migration schedules to avoid a mis-match between timing of breeding and seasonal food availability or face higher rates of reproductive failure.

## 4.4.4. Conclusions

The Arctic supports a large portion of shorebird diversity, especially in the family Scolopacidae. Shorebirds spend only a short period of the year on their Arctic breeding grounds, and anthropogenic stressors such as habitat loss or hunting currently are far greater during southward migration and wintering than on the breeding grounds.

Global climate change is expected to affect shorebirds at various stages of their annual cycle (Boyd & Madsen 1997, Lindström & Agrell 1999). On the breeding grounds, a northward shift of vegetation zones may negatively affect high Arctic breeders and favor boreal species; northward range shifts of boreal shorebirds have already been reported. In addition, northward expansion of the range of some predators may negatively affect shorebird productivity. During migration and in winter, sea level rise may reduce the amount of intertidal feeding habitat, which is already being restricted even further through human activities.

Because of the strongly migratory nature of shorebirds, all conservation efforts will have to take place in an international framework covering entire flyways from Arctic breeding grounds to – often Southern Hemisphere – wintering areas.

## 4.5. SEABIRDS: LOONS, PETRELS, CORMORANTS, JAEGERS/SKUAS, GULLS, TERNS AND AUKS

Unlike most animals, seabirds are more abundant and as diverse in cold seas as they are in warm ones (Gaston 2004). This is principally because diving birds (auks, penguins, diving petrels and marine cormorants) are practically absent from the tropics. In both hemispheres, diving seabirds reach their maximum diversity in sub-polar latitudes (Fig. 4.5), and the species richness of non-diving seabirds is little affected by latitude. In the Northern Hemisphere the highest breeding densities of seabirds occur in Arctic waters (Cairns *et al.* 2008). The Arctic supports several endemic seabird genera as well as a number of endemic, or near-endemic species. Because of this concentration of numbers and endemic taxa, seabirds have a disproportionate influence on Arctic marine ecosystems and on Arctic biodiversity compared with lower latitudes (see also Michel, Chapter 14).

Substantial research has been devoted to studying seabirds as indicators of marine environmental change or of fisheries (Mallory *et al.* 2006, Einoder 2009). Their sensitivity to changes in the availability of major prey species has been demonstrated frequently (Cairns 1992, Monaghan 1992, Montevecchi & Myers 1995, 1997, Davoren & Montevecchi 2003, Wanless *et al.* 2005). Because of the large literature relating seabird biology to changes in marine environments, we have focused specifically on links between changes in Arctic populations and diversity and changes in Arctic marine environments.

Examination of many seabird populations worldwide has demonstrated that populations are seldom stable, so that monotonic trends on a scale of decades can be considered normal and may not signal any recent change in environmental conditions. Instead, such trends may relate to residual effects from changes on a scale of centuries, such as ecosystem adjustments following overfishing of whales and other marine resources (Conroy 1975, Croxall & Prince 1979, Fraser *et al.* 1992) or reduction (Montevecchi & Tuck 1987) or intensification (Kampp *et al.* 1994) of harvest. These background trends have not been clearly identified for Arctic seabirds, but are likely to have occurred following the destruction of large whale populations in the Arctic during the 18th-19th centuries (Bockstoce 1986), as well as overfishing of certain commercial fish stocks, such as that of the Barents Sea capelin *Mallotus villosus* (Barrett & Krasnov 1996, Barrett 2007; see also Fig 1.3 in Meltofte *et al.*, Chapter 1, Christiansen & Reist, Chapter 6 and Michel, Chapter 14).

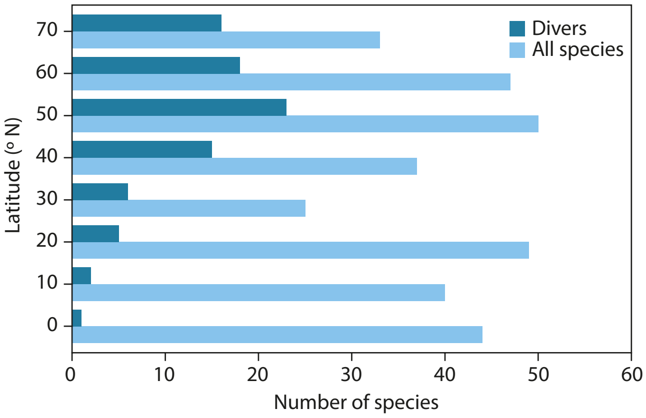


**Figure 4.5.** Numbers of seabird species in the Northern Hemisphere in relation to latitude, by 10° N zones, beginning at the Equator. Only Atlantic and Pacific species are included (compiled from maps in Harrison 1996).

In the Bering Sea, declines in seal and sea lion populations over the past 40 years have been attributed to redirected predation by orcas *Orcinus orca* following the near-elimination of large whale stocks in the 19th century (Springer *et al.* 2003). Reverberations from these adjustments may also have extended to marine birds through the redirection of predation by bald eagles *Haliaeetus leucocephalus* from sea otters *Enhydra lutris* to seabirds (Anthony *et al.* 2008). Such wide-ranging ecosystem adjustments complicate the identification of causal mechanisms relating to population trends (Croxall *et al.* 2002).

### 4.5.1. Species richness and distribution

#### 4.5.1.1. Status

Forty-four species of marine birds breed within the Arctic, including 23 in the high Arctic and 41 in the low Arctic. The majority are members of the order Charadriiformes (34 species, including four endemic genera, all monotypic (little auk, ivory gull, Sabine's gull, Ross's gull). Fifteen species are circumpolar in their distribution, occurring in Canada, Alaska and over most of the Russian Arctic. Among non-circumpolar species, nine occur only in the Atlantic Basin (E Canada-Svalbard) and 12 in the Pacific Basin (E Siberia-Canada). The diversity of high Arctic specialists is similar in Atlantic and Pacific basins (5 species in each). There are two 'bi-polar' genera, found at high latitudes in both hemispheres – the fulmars *Fulmarus* and the skuas and jaegers *Stercorarius,* the former likely originating in the Southern Hemisphere (Voous 1949), the latter in the Northern Hemisphere (Furness 1987). All four species of *Stercorarius* found in the Northern Hemisphere are endemic to the Arctic and sub-Arctic, as is the single petrel, northern fulmar *Fulmarus glacialis*.

Overall diversity is highest in the low Arctic of the Pacific Basin (Chukchi and Bering Seas and adjacent coasts) where 28 species occur in the Alaskan low Arctic (including islands south to 60° N) and 26 species on the Asian side. Other biodiversity hotspots occur in W Greenland (24 species), the E Canadian Arctic (Nunavut, N Quebec and Labrador, 22 species), and Iceland (22 species excluding the sub-Arctic/boreal species found only on the south coast).

Diversity at the sub-species level is relatively low, and most often comprises divergence between Pacific and Atlantic populations (common *Uria aalge* and thick-billed *U. lomvia* murres, black-legged kittiwakes *Rissa tridactyla*, northern fulmars) with only a few species having more than one Arctic race within an ocean basin. However, many species have different races in temperate latitudes, with morphological characteristics often intergrading clinally with the Arctic race (lesser black-backed gull *Larus fuscus*, common murre [Atlantic and Pacific], black guillemot *Cepphus grylle*, Atlantic puffin *Fratercula arctica*).

Several taxa have been elevated to species status only recently and were previously considered sub-species. These splits mainly involve distinguishing North American and Eurasian populations (black-throated/Pacific loons *Gavia arctica/pacifica*; American/European herring gull *Larus smithsonianus/argentatus*). The large white headed gulls of the genus *Larus* are divided into several poorly differentiated and mostly allopatric species in N Asia and on the W coast of North America. Much of their diversity was regarded as intra-specific until recently (cf. Vaurie 1965, Liebers *et al.* 2004, de Knijff *et al.* 2005).

#### 4.5.1.2. Endemicity

There are two near-endemic families: Alcidae (auks; 23 species, of which eight are endemic to Arctic and sub-Arctic waters and the remainder are found exclusively in temperate and sub-Arctic waters of the Northern Hemisphere; Gaston & Jones 1998) and Gaviidae (loons; five species, three of which are endemic to the sub-Arctic and Arctic and the other two occur in both Boreal and Arctic regions). Within the Laridae (gulls and terns), in addition to the three endemic genera mentioned above (*Pagophila*, *Rhodostethia*, *Xema*), two species of tern are endemic or near endemic to the Arctic and sub-Arctic (Arctic tern, Aleutian tern *Onychoprion aleuticus*) and within the cosmopolitan genus *Larus* there are four Arctic endemic species: Vega *Larus vegae*, Thayer's *L. thayeri*, Iceland *L. glaucoides* and glaucous gulls *L. hyperboreus* (*thayeri* and *glaucoides* are sometimes regarded as conspecific; Snell 2002).

Iceland supports an endemic race of the black guillemot *Cepphus grylle islandica*, and this species, along with the razorbill *Alca torda* and common murre, also has separate races on either side of the Atlantic (Gaston & Jones 1998). Franz Joseph Land and Severnaya Zemlya support a distinct race of little auk *Alle alle polaris* which, at least in Franz Joseph Land, differs in some details of its breeding biology from the nominate race found elsewhere (Stempniewicz *et al.* 1996).

#### 4.5.1.3. Trends

The distributions of many species of Arctic marine birds were poorly known until the latter half of the 20th century. In addition, many species are long-lived and conservative in their breeding site adherence, making them slow to alter their breeding range. Consequently, we have few data with which to assess trends in biodiversity among Arctic seabirds. No strictly Arctic species has become extinct during historic times, although two sub-Arctic species, spectacled cormorant *Phalacrocorax perspicillatus* (Commander Islands) and great auk *Pinguinus impennis* (Newfoundland, Greenland and Iceland) were hunted to extinction in the 19th century (Fuller 2000). Two species are listed by IUCN/Birdlife International as near-threatened, threatened or endangered at a world scale, yellow-billed loon *Gavia adamsii* and ivory gull (IUCN 2012). The sub-Arctic red-legged kittiwake *Rissa brevirostris* is considered vulnerable.

There is some evidence for the recent northward spread of predominantly temperate or low Arctic species: ancient murrelet *Synthliboramphus antiquus* (Gaston & Shoji 2010) and glaucous-winged gull *Larus glaucescens* (Winker *et al.* 2002) in the Bering Sea, horned puffin *Fratercula corniculata* in the Beaufort Sea (Moline *et al.* 2008), common gull *Larus canus* in Iceland (Petersen & Thorstensen 2004), great skua *Stercorarius skua* in Svalbard (Anker-Nilssen *et al.* 2000, Krasnov & Lorentsen 2000), black-headed gull in southernmost Greenland (Salomonsen 1979, Boertmann 1994, 2008) and Labrador (Chaulk *et al.* 2004), great black-backed gull *Larus marinus* in Greenland (Boertmann 1994), razorbill in Hudson Bay (Gaston & Woo 2008) and lesser black-backed gull in Greenland, the latter now breeding as far as 74° N (Boertmann 2008, Jensen & Rasch 2009). At the same time, there is evidence of a retreat for at least one high Arctic species, with the range of the ivory gull contracting in N Nunavut, and most colonies on N Baffin Island and E Devon Island deserted, while numbers have remained stable farther north on central Ellesmere Island (Environment Canada 2010). Southern colonies are also decreasing in Greenland (Gilg *et al.* 2009b). The population trend in Russia is unclear (Gilchrist *et al.* 2008), but some colonies at their western extremity in the Barents Sea region have been deserted (Gavrilo 2010). The population of Kittlitz's murrelet *Brachyramphus brevirostris*, a species associated with tidewater glaciers in Alaska, as well being distributed in low and sub-Arctic of the North Pacific, may be declining in its core breeding range in central S Alaska and perhaps elsewhere (Kuletz *et al.* 2003, Stenhouse *et al.* 2008).

#### 4.5.1.4. Causes and prospects

With little evidence for range changes, it is difficult to ascribe causes. The spread of razorbill in Hudson Bay has been linked to an increase in sandlance *Ammodytes* spp., perhaps related to diminishing ice cover (Gaston & Woo 2008). A change in diet has been observed for little auks in Svalbard where the large copepod *Calanus hyperboreus* is replaced in warmer conditions by the smaller *C. finmarchicus* with potentially negative consequences for chick-rearing (Karnovsky *et al.* 2010). Reduced ice cover is likely to be involved in the arrival of horned puffin in the Beaufort Sea. The association of Kittlitz's murrelet with tidewater glaciers makes it likely that recent declines are caused by the retreat of many Alaskan coastal glaciers (Stenhouse *et al.* 2008). In the longer run, changes in ice cover must affect the distribution of ice-associated species such as Ross's and ivory gulls and thick-billed murre.

## 4.5.2. Population sizes and densities

### 4.5.2.1. Status and trends

The population sizes of Arctic-breeding seabirds are given in Appendix 4. Most species have populations numbering in the hundreds of thousands, and only seven are believed to number less than 100,000 breeding individuals: yellow-billed loon, great skua, Thayer's gull, ivory gull, Ross's gull, Aleutian tern and Kittlitz's murrelet (Birdlife International 2009, Wetlands International 2012). Among high Arctic specialists, the ivory gull appears to have decreased precipitously in Canada (by 80% since the 1980s), has decreased in southern Greenland and shows range contraction in the N Barents Sea, although individual colonies in Russia fluctuate widely, making trends there hard to discern. In all cases, the southern parts of the range seem to be more affected than northern parts (Gilchrist & Mallory 2005a, 2005b, Gilg *et al*. 2009b, Environment Canada 2010).

Of the other two exclusively high Arctic species, population size is poorly known for Thayer's gull, which breeds only in E and central parts of the Canadian high Arctic, although the population appears to be stable (Gaston *et al.* 2012). The little auk, although well-distributed in small pockets around the Arctic Ocean, is numerically concentrated into three major colony assemblages around Thule in NW Greenland with about 70 million individuals (Egevang *et al.* 2003), Scoresby Sund in E Greenland with 3.5 million individuals (Kampp *et al.* 1987) and Svalbard with > 1 million (Isaksen & Gavrilo 2000). Censusing such aggregations is almost impossible, and no information is available on trends. Some small colonies of this species farther S in Greenland and in Iceland have disappeared since the 1930s (Nettleship & Evans 1985).

Black-legged kittiwake, an abundant species throughout circumpolar Arctic and Boreal waters, has shown significant population declines almost throughout the Atlantic sector of the Arctic, especially around the Barents Sea (Barrett *et al.* 2006), in Iceland (Garðarsson 2006) and in W Greenland (Labansen *et al.* 2010), as well as farther south, in Britain (Frederiksen *et al*. 2004b).

Thick-billed murre and, to a lesser extent, common murre populations have shown downward trends over much of their range in the past thirty years (see Box 4.3). The population of thick-billed murres in central W Greenland is much depressed compared with numbers in the early 20th century, as a result of heavy harvesting of adults at colonies (Evans & Kampp 1991, Kampp *et al.* 1994) and perhaps, drownings in gill-net fisheries (Tull *et al.* 1972; but see also Falk & Durinck 1991, Kampp 1991 and Kampp *et al.* 1994). Furthermore, it shows no sign of recovery, with the population south of Thule District remaining at < 20% of historical levels, and at least 18 out of 31 small and large colonies having been exterminated (Kampp *et al.* 1994 and unpubl., F. Merkel unpubl.; see also Box 18.5 in Huntington, Chapter 18). Numbers in E Greenland, although small, have also declined.

Similarly, numbers in Novaya Zemlya are considerably lower than in the early 20th century when the population numbered two million birds. Currently, there are thought to be about one million breeders (Bakken & Pokrovskaya 2000). In Svalbard, numbers of thick-billed murres were thought to be stable up to the 1990s, but have since decreased, especially in the southern part of the archipelago (CAFF Circumpolar Seabird Working Group unpubl.).

In Iceland, numbers of thick-billed murres decreased at 7% per year between 1983-1985 and 2005-2008, while numbers of common murres decreased abruptly between 1999-2005 after modest increases earlier (Garðarsson 2006). Northern fulmar, black-legged kittiwake and razorbill also decreased, although some small colonies increased (Garðarsson *et al.* 2009).

### 4.5.2.2. Causes and prospects

With the exception of overharvest dealt with in Section 4.5.2.1, the causes of population and range changes can rarely be confidently attributed to a single source. The decline of ivory gulls in the Canadian Arctic illustrates a case where several potential contributory causes can be identified: mortality from hunting of adults in Upernavik District, Greenland (Stenhouse *et al.* 2004), high levels of mercury in eggs (Braune *et al.* 2006) and changes in ice conditions associated with global warming (Gilchrist *et al.* 2008, Environment Canada 2010). All may have contributed to the recent population decline, although shooting of ivory gulls in Greenland is thought to have declined since the 1980s when most band recoveries occurred (Gaston *et al.* 2008, Gilchrist *et al.* 2008). Only where population declines are abrupt and associated with strong environmental signals can causes be confidently assigned. This was the case for common murre populations in the S Barents Sea in 1985-87 when numbers of birds attending colonies fell by 80% in response to starvation following the collapse of the Barents Sea capelin stock (Anker-Nilssen *et al.* 1997). The population subsequently recovered to near its former level (Krasnov *et al*. 2007; see Fig. 1.3 in Meltofte *et al.*, Chapter 1). Similarly, an 80% decrease in lesser black-backed gulls in N Norway coincided with a collapse in the stock of spring spawning herring *Clupea harengus* (Bustnes et al. 2010).

Most changes in demography and population status of Arctic seabirds that have been linked with climate changes have, to date, been ascribed to causes operating through the food chain (Durant *et al.* 2004, 2006, Harris *et al.* 2005, Sandvik *et al.* 2005, Irons *et al.* 2008). However, there are a few cases where direct effects have been documented. White *et al.* (2011) have shown that expansion of the great cormorant population in central W Greenland may be related to increased sea surface

## Box 4.3. Murres as indicators of a changing Arctic

The two species of murres, thick-billed *Uria lomvia* and common *U. aalge*, both have circumpolar distributions, breeding in Arctic, sub-Arctic and temperate seas from California and N Spain to N Greenland, high Arctic Canada, Svalbard, Franz Josef Land and Novaya Zemlya (Box 4.3 Fig. 1). The more northern thick-billed murre occurs mostly in Arctic waters, where it constitutes a higher proportion of biomass than any other species of seabird. It occurs commonly in the vicinity of sea ice throughout the year, making its distribution strongly dependent on sea ice occurrence. Common murres, although overlapping extensively with thick-billed murres in the Pacific, are more characteristic of sub-Arctic and temperate waters. Murres are among the most abundant seabirds in the Northern Hemisphere with both species exceeding 10 million adults (Gaston & Jones 1998).

Murres feed from coastal to pelagic waters, with common murres concentrating over the continental shelf and slope, while in winter thick-billed murres are spread more or less throughout Arctic and sub-Arctic waters (Gaston & Hipfner 2000). While breeding, both species are tied to feeding within ~150 km of their breeding colonies. They take a wide range of small fish (< 50 g) and invertebrates, especially crustaceans and squid. Adults of both species dive regularly to depths greater than 100 m, reaching a maximum depth of approximately 150 m. Their diving capacity, allied to their typical foraging radius of up to 150 km, means that murres sample a relatively large volume of the marine environment around their colonies (Falk *et al.* 2000, Elliott *et al.* 2008).

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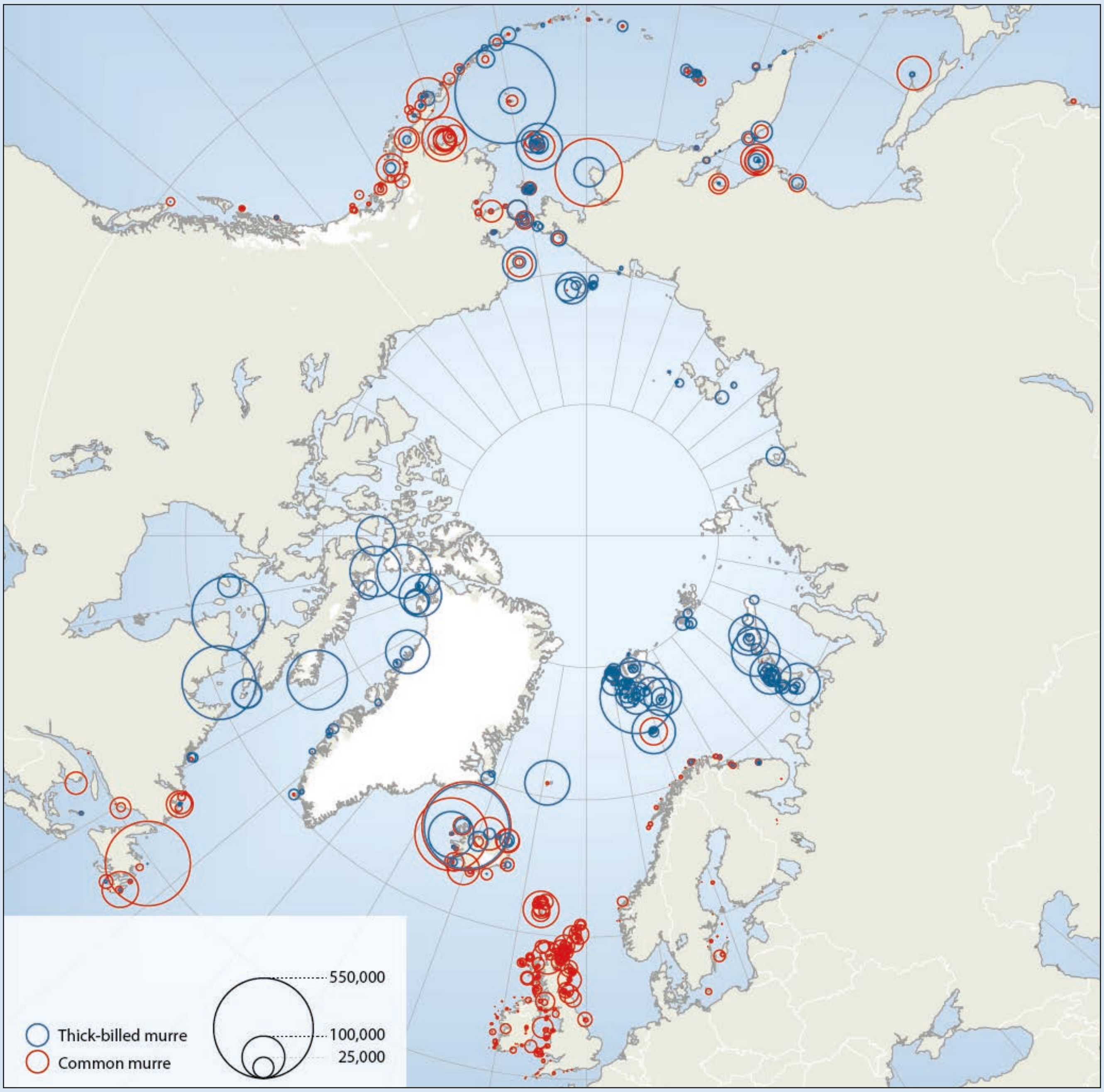


**Box 4.3. continued**

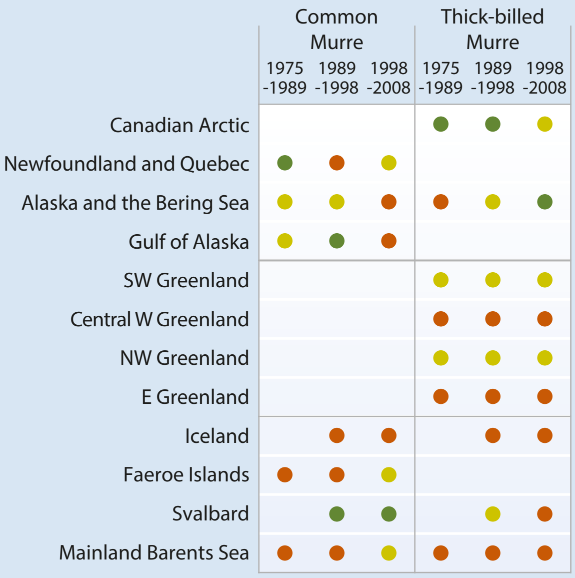
Murres breed in very large colonies of up to one million birds on mainland cliffs or offshore islands. In most places, they breed in the open. Consequently, their population trends are relatively easy to assess and this, allied to their abundance, widespread distribution and sensitivity to oceanic changes, makes them ideal indicators of changes in marine ecosystems.

Apart from hunting induced decreases in Greenland and Novaya Zemlya, both species have shown regional population changes over the past three decades, with trends in the North Pacific and NW Atlantic generally positive or stable when trends in the European Arctic were negative and vice versa (Box 4.3 Fig. 2). The sensitivity of murre populations to changes in environmental conditions has been demonstrated on a hemispheric scale in recent studies by the Seabird Working Group of CAFF (Irons *et al.* 2008). Trends in different regions switched direction with regime shifts. Generally, thick-billed murre populations have declined in all regions except the E Canadian Arctic since the 1970s, whereas no unidirectional global trends can be identified for common murres.

By combining population trend data from around the Arctic with information on sea surface temperature changes (SST) and decadal-scale climate-ocean oscillations, Irons *et al.* (2008) showed that both species tended to show negative population trends where there was a large change in SST. Colony growth was most often positive where conditions remained relatively stable (Box 4.3 Fig. 3) and negative when change, either colder or warmer, was large. This result suggests that not only the direction but the magnitude of change may be important in determining biological outcomes of climate (Irons *et al.* 2008).

Climate change is already affecting the foraging of thick-billed murres in places: e.g. Arctic fishes have been replaced by more southerly species in the diet of nestlings in N Hudson Bay (Gaston *et al.* 2003). Drowning in fishing nets and crashes in the forage-fish prey stocks have caused population declines in several countries (e.g. Norway; Barrett & Krasnov 1996), but populations have generally recovered.

Although both species of murre are currently abundant, many populations have been declining for several decades (Box 4.3 Fig. 2). Problems facing murres include fisheries interactions, contaminants and oil spills and, in some parts of their range, hunting (especially of thick-billed murres; see Section 4.5.2.1). For thick-billed murres, changes in the extent and timing of sea-ice cover over the past several decades are leading to changes in phenology and reproduction with adverse consequences for nestling growth (Gaston *et al*. 2005a). These changes seem likely to intensify. Levels of some contaminants, especially mercury, have increased in murre eggs in the North American Arctic since the 1970s, although they remain at sublethal levels (Braune *et al*. 2001). If climate change leads to increased shipping and oil and gas exploitation in Arctic waters, the increased risk of spills would also pose a potential hazard for murres, which are extremely susceptible to mortality from oil pollution (Wiese & Robertson 2004). In the long term, range contraction of thick-billed murres in response to the retreat of Arctic sea ice appears likely. Eventually they may be replaced by common murres and other more southern auks.



| | Common Murre | | | Thick-billed Murre | | |
|---|---|---|---|---|---|---|
| | 1975 -1989 | 1989 -1998 | 1998 -2008 | 1975 -1989 | 1989 -1998 | 1998 -2008 |
| Canadian Arctic | | | | 🟢 | 🟢 | 🟡 |
| Newfoundland and Quebec | 🟢 | 🔴 | 🟡 | | | |
| Alaska and the Bering Sea | 🟡 | 🟡 | 🔴 | 🔴 | 🟡 | 🟢 |
| Gulf of Alaska | 🟡 | 🟢 | 🔴 | | | |
| SW Greenland | | | | 🟡 | 🟡 | 🟡 |
| Central W Greenland | | | | 🔴 | 🔴 | 🔴 |
| NW Greenland | | | | 🟡 | 🟡 | 🟡 |
| E Greenland | | | | 🔴 | 🔴 | 🔴 |
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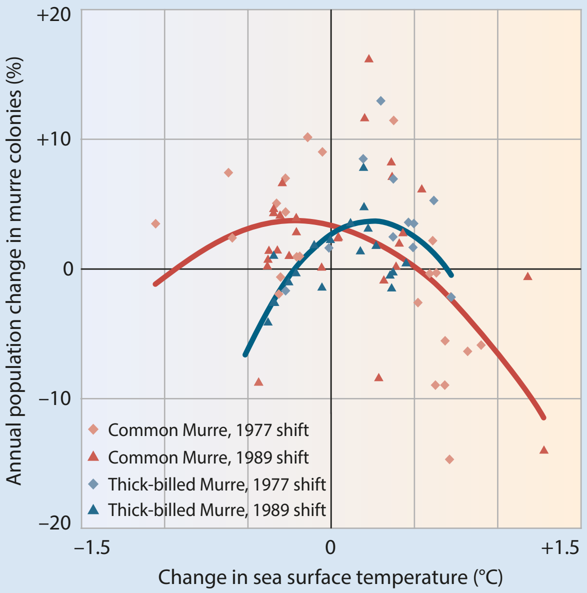
| Faeroe Islands | 🔴 | 🔴 | 🟡 | | | |
| Svalbard | | 🟢 | 🟢 | | 🟡 | 🔴 |
| Mainland Barents Sea | 🔴 | 🔴 | 🟡 | 🔴 | 🔴 | 🔴 |

**Box 4.3 Figure 2.** Changes in murre (thick-billed *Uria lomvia* and common *Uria aalge*) populations since 1975 by region and 'decade' (as defined by regime shifts in the Pacific Decadal Oscillation; see Irons *et al*. 2008). Green indicates positive population trends, yellow indicates stable populations, and red indicates negative population trends. (From CAFF 2010.)



**Box 4.3 Figure 3.** Annual rates of population change of individual murre colonies during 12 years after the 1977 climatic regime shift in the North Pacific and during nine years after the 1989 regime shift, in relation to changes in sea surface temperatures around the colonies from one decadal regime to the next. Population data are from 32 common murre *U. aalge* and 21 thick-billed murre *U. lomvia* colonies, encompassing the entire circumpolar region and expected not to be significantly influenced by hunting. Ten sites supported both species, so 43 different study areas were represented. (From Irons *et al*. 2008.)

temperature. Mallory *et al.* (2009) reported a wide range of weather-related mortalities at Arctic seabird colonies and suggested that some types of mortality, especially those associated with increased frequency of extreme weather events, could create increased mortality in the future. Changes in the timing of snow and ice melt affect the availability of breeding sites for crevice, scree and burrow-nesting species, such as puffins and little auks (Birkhead & Harris 1985). Such changes in accessibility can result in altered interactions with predators, as observed for Antarctic petrels *Thalassoica antarctica* where access to nest sites is critical in evading predation by skuas (van Franeker *et al.* 2001).

Substantial research has been carried out in the Barents Sea region and in the Canadian Arctic on concentrations and trends in contaminants, especially organohaline compounds and heavy metals (Braune *et al.* 2001, Helgason *et al.* 2008, Letcher *et al.* 2010). Very high levels of mercury have been found in the eggs of ivory gulls from Canada (Braune *et al.* 2006) and high levels of organohaline compounds in those from Svalbard (Miljeteig *et al.* 2009). High organohaline concentrations occur also in glaucous gulls from Svalbard (Bustnes *et al.* 2003, 2004), perhaps causing mortality in some cases (Gabrielsen *et al.* 1995, Sagerup *et al.* 2009). These species scavenge marine mammal carcasses, putting them high up the food chain and hence subject to biomagnification effects. They may also frequent garbage dumps around human population centers. Levels of contaminants in other species generally do not approach those likely to impact populations (Gabrielsen 2007, Letcher *et al.* 2010), except in the case of point-source pollution resulting from industrial sites (e.g. Kuzyk *et al.* 2003).

## 4.5.3. Other issues

### 4.5.3.1. Changes in seasonal events

Changes in the timing of seasonal events for high-latitude marine birds have been identified for many Southern Hemisphere species (Croxall *et al.* 2002, Rolland *et al.* 2010), as well as some Arctic seabird populations (Gaston *et al.* 2005a, 2005b, Byrd *et al.* 2008a, 2008b, Moe *et al.* 2009, Wojczulanis-Jakubas & Bech 2009). For some Arctic species, reproductive success declines as the season progresses so that late laying birds fare worse than early layers (e.g. little auks; Moe *et al.* 2009), but this relationship may vary among geographical areas; it is true for thick-billed murres breeding at Prince Leopold Island, Nunavut, but not for the same species breeding in N Hudson Bay (Gaston *et al.* 2005a). The importance of timing of breeding in determining the dynamics of Arctic seabird populations is supported by a correlation found between colony size and the timing of sea ice withdrawal in adjacent waters for thick-billed murres in Greenland (Lairdre *et al.* 2008).

Mismatching of breeding initiation with the seasonal peak of food availability may be a common phenomenon among seabirds confronted with rapidly changing seasonal timing (Bertram *et al.* 2001, Wilhelm *et al.* 2008, Watanuki *et al.* 2009). It has been identified as a likely cause of reduced nestling growth for thick-billed murres in N Hudson Bay (Gaston *et al.* 2009), as well as accounting for some of the variation in reproductive success of black-legged kittiwakes and common murres in sub-Arctic Alaska (Suryan *et al.* 2006, Shultz *et al.* 2009) and Newfoundland (Wilhelm *et al.* 2008).

In N Hudson Bay in the late 1990s, a combination of warm summer weather and earlier emergence by mosquitoes, leading to heavy blood-sucking, caused the death of some incubating thick-billed murres through a combination of dehydration and hyperthermia. In addition, some birds left their eggs unattended for periods of several hours, resulting in many losses to predatory gulls (Gaston *et al.* 2002). These effects had not been recorded previously in 20 years of observations.

### 4.5.3.2. Changes in diet

Changes in seabird diets both from year to year and over decades have been reported from many sites. Diet switching is likely a fairly routine aspect of seabird biology (e.g. Montevecchi & Myers 1995, 1997, Barrett 2002). At Coats Island, N Hudson Bay, thick-billed murres switched from feeding their chicks predominantly the ice-associated polar cod *Boreogadus saida* to the more sub-Arctic capelin in the mid-1990s (Gaston *et al.* 2003; Fig. 4.6). The change was associated with an advance in the date of sea-ice clearance in the region.

Not all prey are equally suitable, especially for rearing nestling birds, and some prey switches can result in reduced productivity (Litzow *et al.* 2002, Wanless *et al.* 2005, Gremillet *et al.* 2008). In the SW Barents Sea in recent decades herring has come to dominate over capelin as a forage fish. This change has coincided with a decline in numbers of breeding black-legged kittiwakes (-8% per year after 1995). Apparently herring is not as satisfactory as capelin as food for kittiwakes (Barrett 2007). At the Pribilof Islands, Sinclair *et al.* (2008) also observed a reduction in the proportion of capelin in black-legged kittiwake and thick-billed murre diets between the 1980s and 2000s, while changes in the zooplankton diet of least auklets *Aethia pusilla* were also observed over the same period (Springer *et al.* 2007, Guy *et al.* 2009). These changes were associated with a warming of the adjacent surface waters and a retreat of winter sea ice. Similarly, in Iceland, the diet of most seabirds switched from sandlance to other fishes in the 2000s (Garðarsson 2006), a change also observed in boreal waters of the North Sea (Wanless *et al.* 2005). This diet change was contemporary with declines in most seabird populations.

### 4.5.3.3. Range extensions of predators and parasites

Many seabirds are very conservative in their breeding sites, returning faithfully to large colonies that, in some

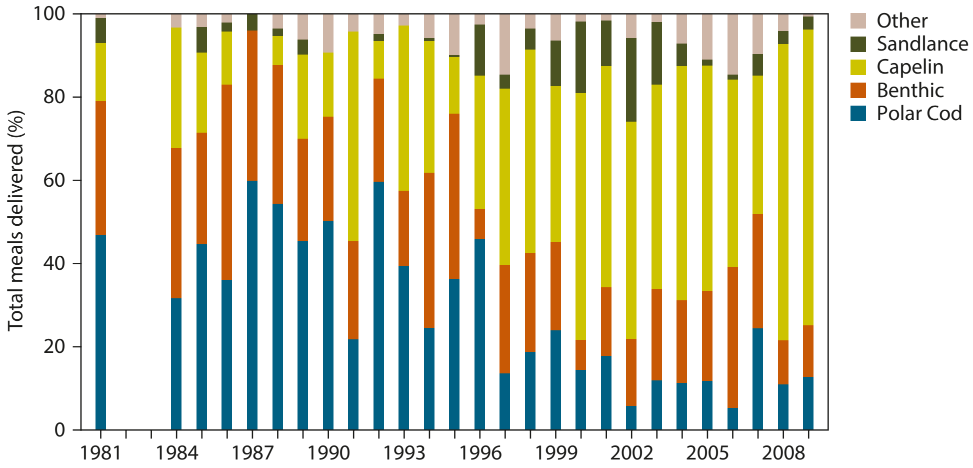


**Figure 4.6.** Change in the diet of nestling thick-billed murres *U. lomvia* at Coats Island, 1981-2009. The 'Benthic' category includes sculpins (Cottidae, Agonidae) and blennies (Sticheidae, Pholidae, Bleniidae, Zoarcidae). 'Other' consists principally of invertebrates.

cases, have been in existence for millennia (Gaston & Donaldson 1995). If climate change alters environmental conditions around such colonies, it is unlikely that a mass exodus will take place in search of new colony locations. There are examples of large colonies suffering repeated reproductive failure over many years without any substantial emigration (e.g. Atlantic puffins at Røst, Norway, reared few chicks between 1969 and 1982; Anker-Nilssen & Rostad 1993). However, parasites and predators may be more mobile in response to climate change and may initiate or expand their activities at new sites. Some examples of such expansions have already been observed, with an increase in the incidence of tapeworms in alcids in Labrador and Greenland since the 1960s (Muzaffar 2009), and the appearance of the parasitic tick *Ixodes uriae* on murres in Svalbard after 2000 (Coulson *et al.* 2009). The implications of these parasite range expansions are not yet clear, but adverse consequences for the seabird populations involved are possible (see also Hoberg & Kutz, Chapter 15). Range expansion or population increase of other seabirds can also lead to novel interspecific transmission (Brooks & Hoberg 2007): this may explain the recent discovery of a gull cestode in Atlantic puffins in Newfoundland (Muzaffar *et al.* 2007).

Currently, golden eagle and the northern sea-eagles (*Haliaeetus leucocephalus, H. albicilla, H. pelagicus*), all of which cause disruption to nesting seabirds by killing breeding adults and disturbing many others, occur principally in the sub-Arctic. Their northward spread could create problems for gulls, murres and other open-nesting seabirds (Hipfner *et al.* 2011), a phenomenon that is being seen especially in N Norway, where the increase in white-tailed eagles *Haliaeetus albicilla* has caused declines in murres and black-legged kittiwakes (Barrett *et al.* 2006). In Finland, waterbirds make up more than half of white-tailed eagle diet (Sulkava *et al.* 1997). Increasing predation of birds and their nests by polar bears has also been observed, probably as a result of the bears coming ashore earlier in the season (Rockwell & Gormezano 2009, Smith *et al.* 2010). This could affect especially accessible species such as local little auks (Stempniewicz 2007) and ivory gulls. Because of the availability of alternative prey, it is extremely difficult to predict how predators will affect seabird populations, or how those populations will respond to changes in predation pressure (Gaston & Elliott 2013).

### 4.5.4. Conclusions

The Arctic is an important area for marine bird diversity and endemism. Most Arctic seabird populations for which information is available over several decades have shown negative trends in recent years. These trends are superimposed on a situation where several important populations were substantially depressed by anthropogenic mortality, compared with numbers in the first half of the 20th century (especially thick-billed murres in Greenland and Novaya Zemlya).

Only a few instances are available where recent trends can be traced to particular causes, but stressors include fisheries activities, pollution and climate change. The last, especially as manifested in changes in the timing of the open water season, is affecting the timing of seasonal events in marine ecosystems, and this is affecting the optimal timing of breeding, especially in low Arctic areas. These changes are also encouraging the northward expansion of sub-Arctic species, although such changes in range are relatively small, as yet. Changes in the distributions of predators and parasites have also been noted, and these may have important consequences for Arctic seabirds. Because of the number of Arctic endemic seabird taxa, the decline of Arctic marine birds presages a significant loss of global biodiversity.

## 4.6. LANDBIRDS: RAPTORS, CRANES, PTARMIGANS AND SONGBIRDS

Although most Arctic land areas support one or more landbird species, this group is not well-represented in the Arctic, compared with more temperate latitudes. In addition, most Arctic landbirds are small passerines which are not hunted either in their breeding areas by northern residents or on their wintering grounds by southerners, and hence have little economic value. Such birds do not attract much research. Only the grouse and relatives (Phasianidae) and the cranes (Gruidae) attract any significant attention from hunters. Several species of raptors are also present in the Arctic and play an important role as top predators of the tundra food web (Legagneux *et al.* 2012, Therrien 2012).

Landbird ranges in North America are taken from species accounts in Birds of North America (Poole 1992-2011), and in Eurasia from Snow & Perrins (1998) and Beaman & Madge (1998). Population trends are not monitored directly within most Arctic regions, but may be assessed from surveys of migrating and wintering birds at lower latitudes. In North America, Christmas Bird Counts (National Audubon Society n.d.; see also Niven *et al.* 2004), Project FeederWatch (Cornell Laboratory of Ornithology and Bird Studies Canada n.d.) and the Canadian Migration Monitoring Network (Butcher & Niven 2007, Bird Studies Canada n.d.) all provide information for some Arctic species of interest. The Northwest Territories-Nunavut Bird Checklist Survey (NNBCS) provides information on range changes for the period since 1987 (Canadian Wildlife Service – Prairie & Northern Region 2009). Recently, Gauthier *et al.* (2011c) and Watson *et al.* (2011) reviewed the status of several species of Arctic raptors. Except for those referred to below, similar overall data are not available for Arctic landbirds in Eurasia.

## 4.6.1. Species richness and distribution

Most landbird species belong to genera widespread at lower latitudes. There is a strong negative gradient of species richness from sub-Arctic to high Arctic, with the northern limit of trees and shrubs bounding many distributions. Consequently, defining the species to be included in this section has been somewhat arbitrary.

### 4.6.1.1. Status

There are no landbird families endemic to the Arctic and only a few endemic genera, although the longspurs (Passeres: Calcariidae) are mainly found in the Arctic (4/6 species). All other species belong to families widespread in the Northern Hemisphere. Only two genera are endemic to the Arctic, sub-Arctic and contiguous mountains: the ptarmigans *Lagopus* spp. and the snow buntings *Plectrophenax* spp. The snowy owl *Bubo scandiacus,* gyrfalcon, rough-legged buzzard and Arctic redpoll breed only in the low and high Arctic. The Siberian crane *Grus leucogeranus*, a low Arctic/sub-Arctic species, is considered by some authorities to constitute a monotypic genus (*Leucogeranus*) that separated from other cranes as far back as the Miocene (Krajewski *et al.* 2010). All other species have substantial parts of their ranges within the sub-Arctic, many extend into boreal regions and a few are cosmopolitan (raven, peregrine falcon *Falco peregrinus*). The pipits and wagtails (Passeres: Moticillidae) form the most diverse family in the low Arctic, with nine species occurring there (20% of Arctic-breeding passerines).

Many Arctic landbirds are circumpolar in distribution, including all non-passerine genera (except for *Leucogeranus*, the Siberian crane), and all genera extend their breeding ranges into the high Arctic. Among non-circumpolar genera, seven are Nearctic in distribution and five Palearctic. However, small adjustments to the sub-Arctic/low Arctic boundary would qualify or disqualify many species, so these numbers have little significance. Within the Arctic, few species are differentiated into subspecies, either between Arctic and sub-Arctic, or among different Arctic regions. Some, such as the gyrfalcon, appear to have colonized their current range entirely during the past 10,000 years from a single glacial refugium (Johnson *et al.* 2007). The wagtails are exceptions with both white wagtail *Motacilla alba* and yellow wagtail *M. flava* comprising several regional races (Vaurie 1963). The eastern race of yellow wagtail, which extends into Alaska, is now considered a separate species, eastern yellow wagtail *Motacilla tschutschensis*. The horned lark *Eremophila alpestris* has two races in Arctic North America and several more farther south (Beason 1995).

Only six species remain in the Arctic during the winter: the two ptarmigans, raven, snowy owl, gyrfalcon and Arctic redpoll, although parts of the populations of the last three species frequently move at least as far as boreal regions. White-tailed eagles remain year-round in Greenland. Most fruit- and seed-eating species (thrushes Turdidae [most], accentors Prunellidae, longspurs Calcariidae, buntings/sparrows Emberizidae and finches Fringillidae) and raptors are relatively short-range migrants, wintering in temperate and boreal regions (Newton 2007), although some Arctic-breeding peregrine falcons travel to tropical and subtropical regions (Fuller *et al.* 1998). Conversely, most insectivores migrate to the Mediterranean or tropical regions (wagtails/pipits [most], Eurasian flycatchers Muscicapidae, Old World warblers Sylviidae, New World warblers Parulidae).

### 4.6.1.2. Trends

The most obvious change in species richness over the past several decades has been the appearance of sub-Arctic species in the low Arctic. Northward movement of range boundaries for sub-Arctic species has been documented in Finland (Brommer 2004) and seems likely elsewhere. There are numerous anecdotes and comments from northern peoples to this effect, but the evidence is slight from scientific surveys, possibly because the numbers involved are still small. In Iceland, several sub-Arctic or boreal species have colonized in the past century, including blackbird *Turdus merula* and goldcrest *Regulus regulus* (Hilmarsson 2000). These range expansions may relate to land use changes rather than to climate amelioration. However, the rock ptarmigan, a near-endemic in the Arctic, is declining in Iceland despite little habitat change (Storch 2007). Increases in southern species and decreases in more typically sub-Arctic species have been noted in forest habitats in Finland (Brommer 2008, Virkkala & Rajasärkkä 2011), while the redwing *Turdus iliacus* has begun to breed in

Greenland in recent years (D. Boertmann unpubl.). Northward range expansion has also been reported for some raptors (Gauthier *et al.* 2011c). In North America, the peregrine falcon expanded its range in several areas in the 1980s (e.g. Mossop 1988, White 1994). Range expansion of the short-eared owl *Asio flammeus* in the eastern Canadian Arctic has been recently documented on Bylot Island, 1,000 km north of the previously documented northern limit of their range in eastern North America (Therrien 2010). In western Siberia, the snowy owl moved northward in Yamal, with possibly a contraction of its range in the south. For instance Osmolovskaya (1948) found several nests as far to the south as 67.5° N, but in recent decades all those reported were north of 69.5° N. Likewise, Potapov (2011) suggested that the southern range boundary of gyrfalcon in Siberia has retreated northwards.

#### 4.6.1.3. Causes and prospects

Range extension of boreal and sub-Arctic species into Arctic regions is most likely related to increasing spring and summer temperatures, allowing migrant species to settle farther north than previously. Westward range extensions of Nearctic species are ongoing, with grey-cheeked thrush *Catharus minimus* and sandhill crane *Grus canadensis* expanding their range in E Siberia in the past 30 years (E. Lappo unpubl.). The extent to which these expansions may relate to climate change is unknown. Conversely, neither bluethroat *Luscinia svecica*, Arctic warbler *Phylloscopus borealis*, nor eastern yellow wagtail, predominantly Asiatic species that extend into Alaska, have expanded eastward over the past century (Badyaev *et al.* 1998, Guzy & McCaffery 2002, Lowther & Sharbaugh 2008; see also Box 17.6 in Cook, Chapter 17). Nor is there clear evidence of range expansions on the basis of the NWT-Nunavut Bird Checklist Survey (B.L. Collins unpubl. data).

For raptors, range expansion may be partly or mostly explained by change in their prey base. For instance, northward expansion of some raptor species in Yamal, W Siberia may be due to a local shift in small rodents community as the Siberian brown lemming *Lemmus sibiricus* has been replaced by voles *Microtus* spp. in some areas (Sokolov *et al.* 2010). For some species like the peregrine falcon, expansion in the 1980s may actually be largely a recolonization of its former range following population decline during the mid 20th century (Carrière *et al.* 2003).

### 4.6.2. Population sizes and densities

#### 4.6.2.1. Status

Population numbers can be estimated for very few landbirds, mainly those with very small populations. Estimates for North American populations have been attempted, based on extrapolations from densities and range extents, but these estimates do not consider habitat quality and probably represent orders of magnitude only (Niven *et al.* 2004, Rich *et al.* 2004). Only one species is considered endangered by IUCN/BirdLife, the Siberian crane, which has decreased from tens of thousands to only a few thousand since the mid-20th century. The cause of its decline is thought to be hunting and habitat degradation on migration routes and in wintering areas in E and S Asia, rather than any causes specific to the Arctic (Meine & Archibald 1996). McKay's bunting *Plectrophenax hyperboreus* is considered near threatened on the basis of its small range and a population size estimated at 6,000 birds (Rich *et al.* 2004). The two ptarmigan species, although both abundant and widespread, are listed as 'Lower Risk' (Storch 2007).

#### 4.6.2.2. Trends

In North America, Christmas Bird Count (CBC) indices suggest significant declines in wintering numbers of snowy owl, Arctic redpoll, American tree sparrow *Spizella arborea* and buff-bellied pipit *Anthus rubescens*, while snow bunting has decreased by 40% since the 1970s, although the decrease does not reach statistical significance (Downes *et al.* 2011). Arctic redpoll, snow bunting and snowy owl may be wintering farther north than in earlier decades, with a greater proportion of the population remaining outside of the area commonly covered by the CBC in recent years. Consequently, these declines need to be interpreted with caution. However, snowy owls are thought to be declining in Siberia (E. Lappo unpubl.) and Nunavut (see below). The wintering ranges of American tree sparrow and buff-bellied pipit are well covered by CBCs, and buff-bellied pipit is also showing significant reductions at some migration monitoring sites in Canada (National Audubon Society 2012). According to CBC records, the American tree sparrow has declined by > 2% per year since the 1970s (Downes *et al.* 2011). Its breeding range is almost entirely in the low Arctic, while that of the buff-bellied pipit includes all the low Arctic, as well as the southern parts of the high Arctic (Naugler 1993). The horned lark and Lapland longspur *Calcarius lapponicus* have also shown a decline since the 1960s.

> *» The Lapland longspurs are disappearing in our area and I have noted that a late frost in the spring killed hundreds of small birds, which were caught unprepared for a lasting cold snap.*
>
> (Qaunaq: Elders conference on Climate Change 2001).

In fact, according to the CBC, none of the Arctic songbirds covered has increased since the 1960s (Fig. 4.7). Conversely, several species characteristic of the sub-Arctic show increasing numbers at migration monitoring stations; e.g. white-crowned sparrow and yellow-rumped warbler (Bird Studies Canada 2012), suggesting population increases.

Preliminary results from the NWT-Nunavut Bird Checklist Survey for 1987-2007 also suggest that the Arctic redpoll and snowy owl may be contracting their range in N Canada (B.L. Collins unpubl.). Those species showing the greatest decreases on these surveys are all raptors or owls: rough-legged buzzard, gyrfalcon and short-eared owl. The only landbird species showing a significant increase is the sub-Arctic savannah sparrow *Passerculus sandwichensis*.

On the Yukon north slope (British Mountains and coastal plain), historical data indicate a cyclic pattern of population change of nesting gyrfalcons attributed to cyclic changes in the abundance of their primary prey, willow ptarmigan *Lagopus lagopus* (Mossop 2011). Surveys of gyrfalcon nests in this area since 2002 showed decreasing numbers of nesting birds and low productivity of nests. This may be a low phase of another population cycle, or may represent an overall decline in the abundance of this species. Similarly, in the Yamal Peninsula, Russia, gyrfalcon numbers decreased after the 1990s (Mechnikova *et al.* 2011). However, gyrfalcons in the Colville River valley, Alaska, showed no change in numbers between 1981 and 2005 (Swem & Matz 2011). Nor is there any evidence for changes in the number of gyrfalcons in northern Fennoscandia over the past 150 years (Koskimies 2011).

In the European Arctic, numbers of breeding horned larks underwent a marked decline during the second half of the 20th century. This decline may have been caused by habitat loss on their wintering quarters through embankment of salt-marshes in W Europe (Dierschke 1997).

Some Arctic populations of peregrine falcons were affected by the accumulation of organochlorine pesticides during the 1950s and 1960s, but most have since recovered (Rowell *et al.* 2003, Vorkamp *et al.* 2009). However, Franke *et al.* (2010) showed that a population near Rankin Inlet, Nunavut, has decreased since 1982, simultaneous with a halving of chick production and a 40% decline in the number of chicks reared per pair. This observation may not be explained by pesticide pollution and could be related to climatic changes in the region.

#### 4.6.2.3. Causes and prospects

For the most part, there is no clear indication of what is driving trends in Arctic landbirds. Gyrfalcons in Russia are strongly affected by the taking of young birds for falconry (Mechnikova *et al.* 2011, Potapov 2011). Such poaching has also occurred in North America (Watson *et al.* 2011), but is unlikely to affect other species. In North America, where most Arctic landbirds seem to be in decline, such widespread trends suggest some general cause. The possibility that the common cause is some derivative of climate change cannot be excluded, but at present the way in which such an effect might be operating is unclear. The gradual northward advance of the tree-line and retreat of permafrost will undoubtedly create conditions for sub-Arctic species to spread northwards: in some places this is already happening. For instance, at the southern border of low Arctic Alaska, elder Betty Anagick, an Iniupiaq woman, made an observation of a new bird in the community:

> » *I have seen hummingbird here, which is strange.*
>
> (Mustonen *et al.* 2009).

How these changes will affect the current avifauna of the Arctic remains to be seen, but the eventual loss of some specialist species seems inevitable.

### 4.6.3. Other issues

#### 4.6.3.1. Predator-prey interactions

Several species of tundra raptors such as the snowy owl and rough-legged buzzard feed primarily or entirely on lemmings (Gauthier *et al.* 2011b, Therrien 2012). Popu-

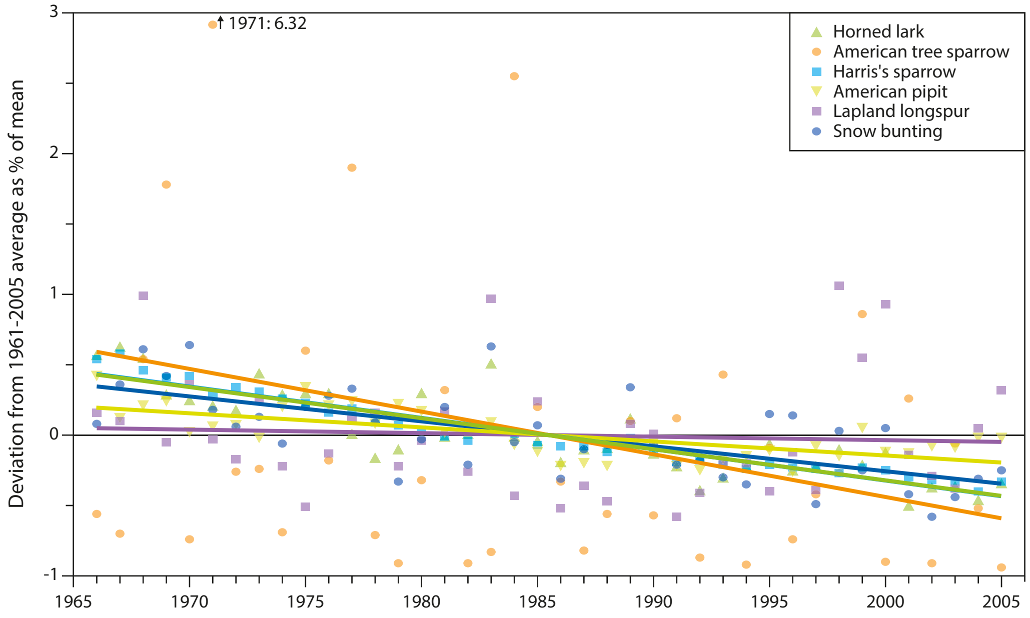


**Figure 4.7.** Trends in Arctic landbirds from Christmas Bird Count records between 1966 and 2005 (data courtesy of National Audubon Society and P. Blancher).

lation cycles of lemmings and voles thus have a strong impact on the local abundance and reproduction of most avian predators (Gilg *et al.* 2003, Gauthier *et al.* 2004, Therrien 2012). In turn, these predators may contribute to regulate the abundance of lemmings in some areas, thereby playing a key role in the tundra food web (Reid *et al.* 1997, Legagneux *et al.* 2012).

#### 4.6.3.2. Movements of raptors

Recent satellite tracking of some tundra predators such as snowy owls and gyrfalcons revealed a previously unsuspected wintering strategy (Burnham & Newton 2011, Therrien *et al.* 2011). These studies confirmed that both species winter predominantly in the Arctic in E Canada and Greenland. However, they also revealed that both species may winter on sea ice: adult female snowy owls marked on Bylot Island spent up to 101 days on the sea ice between December and April every winter (Therrien *et al.* 2011), concentrating their activity in the Hudson and Davis Straits and in Hudson Bay at a median distance of 40 km from the coast but sometimes as far as 210 km. These owls were primarily gathering around polynyas, presumably feeding on seabirds (Robertson & Gilchrist 2003). The satellite tracking of snowy owls also showed that individuals can breed from one year to the next in areas far apart, showing a remarkable average annual breeding dispersal distance of 725 km (Therrien *et al.* 2012). The large-scale movements allowed owls to settle in an area where lemmings are at peak densities.

#### 4.6.3.3. Anticipated threats related to climate change

In many areas of the circumpolar world such as N Fennoscandia or NE Greenland, a recent collapse of lemming population cycles has been reported (see 4.3.3.2, 4.4.3.1, Reid *et al.*, Chapter 3 and Ims & Ehrich, Chapter 12). This may represent a significant threat for the populations of many species of predatory birds as their breeding success is so closely tied to the abundance of small mammals. The decline of snowy owls reported in Fennoscandia is mainly due to the recent absence of lemming peaks in these areas (Jakobsen 2005), though during the lemming peak of 2007 several pairs were breeding successfully in Finnmark. In central E Greenland (Traill Island), no snowy owls and very few long-tailed jaegers *Stercorarius longicaudus* have successfully nested since the collapse of the lemming cycles in the early 2000s (B. Sittler and O. Gilg pers. com.).

The use of the sea ice by snowy owls and gyrfalcons suggests that they may not only be vulnerable to changes affecting their prey base in the tundra but also to those in the marine environment. Change in the sea ice regimes due to climate warming will likely alter the abundance and distribution of wintering seabirds, their primary prey in this environment (Gauthier et *al.* 2011b).

Another threat facing some species of raptors may be the collapse of nesting structures during the nesting season. In northern Yukon, rough-legged buzzards, peregrine falcons and snowy owls often build their nests on mud or sandy cliffs. In a recent study in northern Yukon, up to half of the nests monitored failed when the soil cliffs collapsed due to permafrost thaw under these slopes (Gauthier *et al.* 2011c). Such nest loss was not reported in the 1980s and thus may be a recent phenomenon due to climate warming.

## 4.7. CONCLUSIONS AND RECOMMENDATIONS

With about 2% of the global species total, the Arctic supports only a small fraction of the world's avian biodiversity, but adaptation to the harsh Arctic environment has created a variety of highly specialized species and a number of Arctic endemics. Because almost all Arctic birds are migratory, population trends for many species are driven by events outside the Arctic. For year-round resident Arctic birds, little trend information is available. Where trends are known for migratory populations, the main pattern of trends can be summarized as follows: increases in many Nearctic and W Palearctic waterfowl populations, especially geese; and decreases in many shorebird populations and waterfowl of the E Palearctic. For some species wintering in E Asia, habitat loss and hunting in the wintering grounds have been identified as the main causes of population decline. Problems with food supply on critical staging areas have also been diagnosed for a few shorebirds migrating through the Americas. Because of the international nature of migratory birds, conservation action for endangered Arctic breeders must include international cooperation on a flyway level both in and outside the Arctic, to ensure safeguarding of critical habitats and proper management of hunting. This is especially critical for highly endangered migratory species such as the spoon-billed sandpiper and the Siberian crane.

On the Arctic breeding grounds, known causes of population changes have been excessive harvest and climate variability, while potential threats include oil, gas and mineral exploitation. Oil exploitation at sea and increased transport of oil through Arctic waters, with its associated risks of oil spills, is especially hazardous for the great number of marine and coastal birds of the Arctic. The aggregation of very large numbers of birds in breeding colonies or molting sites, often associated with areas of high productivity and a high diversity of other taxa (e.g. fish, marine mammals), makes the protection of such colony and molting sites and adjacent waters from the risk of oil spills a priority. Breeding and molting birds can also be negatively affected by disturbance resulting from industrial development and tourism, which can increase predation and/or keep birds from using suitable habitats. Again, this is especially severe where large concentrations of birds are affected. The overharvesting of Arctic birds is a problem mainly of inhabited regions, principally in the sub-Arctic or the fringes of the Arctic. In some cases these problems are either solved or on the way to solution: eider populations affected by over-harvesting in the late 20th century are recovering, and the greatly diminished population of thick-billed murres in Novaya Zemlya has stabilized.

In the true Arctic, some heavily harvested species, particularly geese, are increasing rapidly. Because 'overabundant' geese are causing degradation of sensitive habitat in some Arctic areas, management efforts have been initiated to reduce population sizes through increased hunting outside the Arctic. The problem with use of hunting as a management tool is that the massive shooting needed to significantly reduce numbers may cause high crippling rates, greatly increased shyness and create widespread disturbance of other waterfowl species on the staging and wintering grounds (Madsen & Fox 1995, Noer & Madsen 1996).

Climate change may act on Arctic bird populations in various indirect ways (Boyd & Madsen 1997). These include changes in food supply; predators, prey, parasites and diseases; mis-match between the peak of availability of food and the timing of arrival on breeding grounds, hatch, brood rearing or migration. The northward shift of vegetation zones will affect both food and habitat, in addition to habitat loss due to permafrost thawing in some areas. However, even though single effects have been shown at a local scale for some bird populations, the complexity of these interacting factors makes it very hard to predict future impacts of a warming climate on Arctic bird populations. Some effects, like the impact of egg-eating by polar bears, may attenuate, as bear populations at lower latitudes decline (see Reid *et al.*, Chapter 3).

Some species found mostly or entirely in the Arctic are showing signs of population decline which may be related to climate change (ivory gull, thick-billed murre, gyrfalcon, perhaps snowy owl). The exact causes are unknown, but may relate directly or indirectly (e.g. through changes in their food supply) to increasing temperatures. We need much more extensive monitoring, especially in Canada and Siberia, to better assess the causes of population change. Greater integration of national monitoring programmes under the Arctic Monitoring and Assessment Programme, the Arctic Breeding Bird Condition Survey (ABBCS) and the Circumpolar Seabird Data Portal (Seabird Information Network 2012) would be useful and the CAFF seabird group could provide the necessary incentive. We particularly need better information on the non-game Arctic endemics: gyrfalcon, snowy owl, shorebirds, ivory, Sabine's and Ross's gulls, jaegers/skuas and little auks. With their breeding distributions restricted to Arctic biomes, these birds are likely to be the first to exhibit symptoms of climate change effects. Likewise, we need regular monitoring of important wintering areas for Arctic seabirds and waterfowl, such as SW Greenland (Boertmann *et al.* 2004), waters off Newfoundland and Labrador (Frederiksen *et al.* 2011) and polynyas supporting eiders in the N Bering Sea (Petersen & Douglas 2004).

If climate change proceeds as predicted, many of the bird species characteristic of the northern taiga and sub-Arctic are likely to expand northwards as temperatures increase. However, this cannot be viewed as an improvement in the richness of the Arctic avifauna, but rather constitutes a contraction in the area of the Arctic, as we have hitherto defined it in biological terms. Ultimately, much of the region now characterised by a high Arctic fauna may become low Arctic in character, and the eventual disappearance of typically high Arctic birds such as gyrfalcon, ivory gull and little auk seems probable.

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Appendix 4: www.abds.is/aba-2013-appendix-4

A few amphibians and reptiles extend their distribution into the Arctic, such as this moor frog *Rana arvalis* of Eurasia.
Photo: Konstantin Mikhailov.

*Chapter 5*

# Amphibians and Reptiles

**Authors**
Sergius L. Kuzmin and David F. Tessler

## Contents

> » **We have lizards. We have seen them this year even at the upper reaches of 'Afanas'ki'.**
>
> Leader of the Saami indigenous obschina 'Piras' in the Kola Peninsula, Andrey Yulin on northwards expansion of lizards; Zavalko & Mustonen (2004).

## SUMMARY

The herpetofauna of the Arctic is depauperate relative to temperate and tropical regions. Only five amphibians and a single reptile range into the Arctic, and none are circumpolar. All Arctic amphibian and reptile taxa are currently categorized as 'Least Concern' according to IUCN criteria. However, basic survey and inventory data for these species are lacking across most of the Arctic, and there are few quantitative data on abundance, status or trends for Arctic herpetofauna. At the same time, isolated populations of amphibians and reptiles in the Arctic exist at or near their current physiological limits and likely face a number of escalating challenges stemming primarily from habitat alteration.

## 5.1. INTRODUCTION

Although amphibians and reptiles account for nearly 15,000 species worldwide, only five amphibians and a single reptile are found in the Arctic. The majority of Arctic herpetofauna are found in the eastern hemisphere; there are no circumpolar taxa (Tab. 5.1). Amphibian species richness (number of species) in the Arctic is as low as in desert regions. Amphibians and reptiles are phylogenetically the oldest of terrestrial vertebrates, and their limited representation in the Arctic is due in large measure to their poikilothermic physiology (body temperature determined by ambient conditions).

A number of recent publications have suggested major changes to herpetological systematics (Frost *et al.* 2006, Roelants *et al.* 2007), but because these proposed changes are not yet universally accepted and many names remain in a state of flux, we follow stable herpetological taxonomy as described in Collins & Taggart (2002) and Kuzmin & Semenov (2006).

Eastern hemisphere taxa:
- Siberian newt *Salamandrella keyserlingii*
- Common frog *Rana temporaria*
- Moor frog *Rana arvalis*
- Siberian wood frog *Rana amurensis*
- Common lizard *Lacerta vivipara*

Western hemisphere taxa:
- Wood frog *Rana sylvatica*

## 5.2. STATUS OF KNOWLEDGE

The first scientific records of Arctic amphibians are from expeditions in the 19th and early 20th centuries. Since then, despite intensive study of Arctic regions, little attention has been paid to understanding the distribution and ecology of Arctic amphibians and reptiles. Few works on the distribution, morphology, genetics, phenology, development, hibernation and diet of Arctic amphibians have been published.

Amphibians and reptiles reach Arctic regions only on the periphery of their ranges, where their overall abundance is low. Due to their limited dispersal capabilities and because their distributions are defined by fine-scale microhabitat associations, their actual distributions may be quite patchy (Olson 2009). Because focused research on amphibian and reptile biology in the Arctic is scarce, much of the data available were obtained as a by-product of other efforts.

### 5.2.1. Historical overview

Historical information on the Arctic distributions of amphibians and reptiles is very limited. To date, there have been only two published studies on the historical phylogeography of Arctic herpetofauna using molecular techniques.

Poyarkov & Kuzmin (2008) investigated molecular genetics in the Siberian newt throughout its range and found that patterns of genetic differentiation of Siberian populations are likely the result of repeated processes of colonization of new territories during inter-glacial epochs and subsequent retreats into more temperate belts during glacial peaks. Following the peak of the most recent glacial maximum, the Siberian newt likely first colonized territories in E Siberia, followed by colonization events west towards the Urals and east towards Beringia and Kamchatka. Dispersal to the north and west appears to have taken place very quickly.

In North America, an investigation of the historic phylogeography of the wood frog using mitochondrial genes suggests a post glacial range expansion that differs from most other herpetofaunal taxa on the continent (Lee-Yaw *et al.* 2008). The wood frog appears to have radiated

**Table 5.1.** Amphibian and reptile taxa of the Arctic. 'Redlisted' denotes taxa on the IUCN Red List of Threatened Species.
* denotes known trends over the past 10-20 years.

| Region | Orders | Families | Genera | Species | Subspecies | Stable* | Increasing* | Decreasing* | No Info.* | Redlisted |
|---|---|---|---|---|---|---|---|---|---|---|
| Arctic | 2 | 3 | 3 | 5 | – | ? | – | – | 5 | 0 |
| WH Arctic | 1 | 1 | 1 | 1 | – | ? | – | – | 1 | 0 |
| WH high Arctic | – | – | – | – | – | ? | – | – | – | 0 |
| WH low Arctic | 1 | 1 | 1 | 1 | – | ? | – | – | 1 | 0 |
| EH Arctic | 2 | 3 | 3 | 4 | – | ? | – | – | 4 | 0 |
| EH high Arctic | – | – | – | – | – | ? | – | – | – | 0 |
| EH low Arctic | 2 | 3 | 3 | 4 | – | ? | – | – | 4 | 0 |

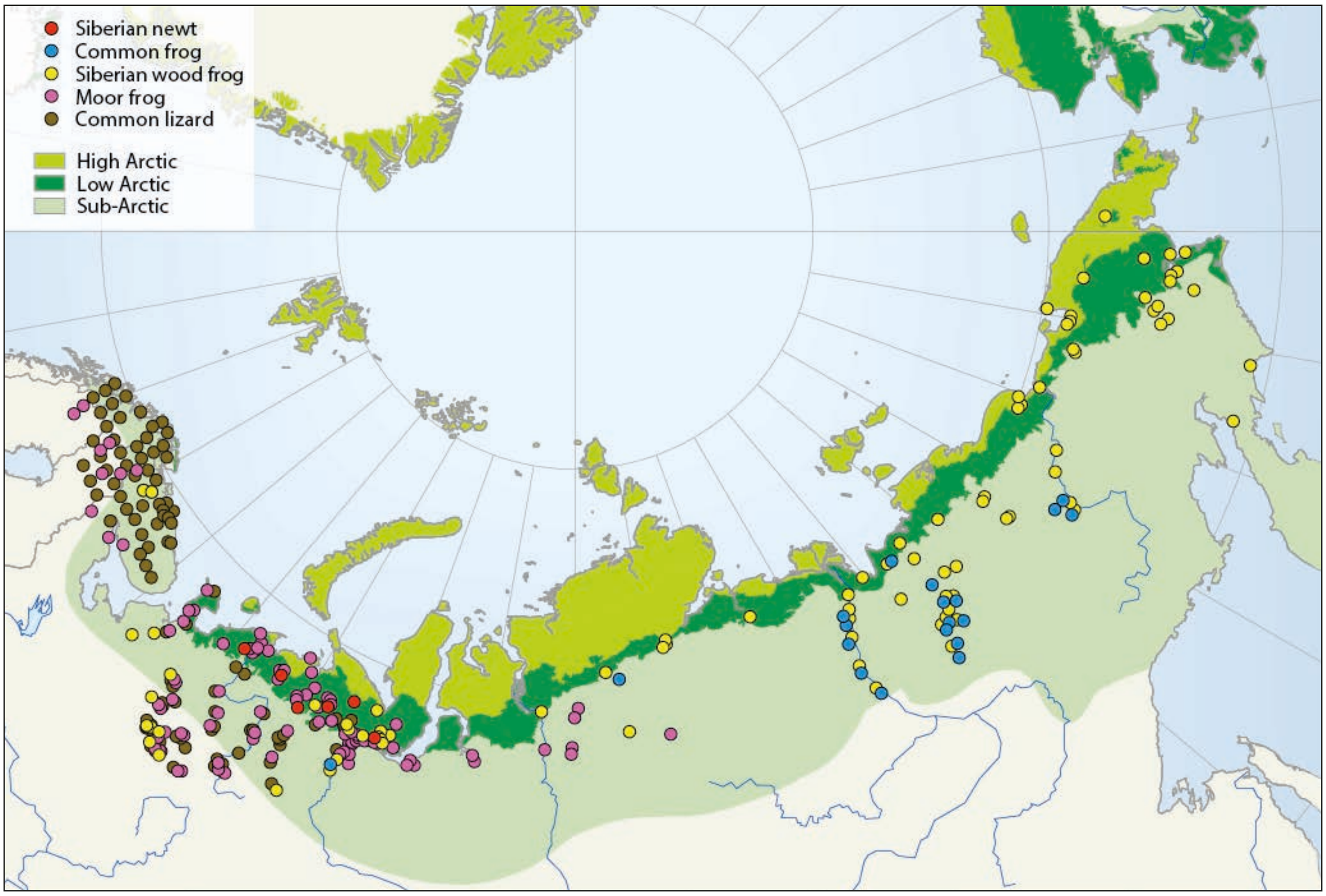

**Figure 5.1.** Known locations of Eastern Hemisphere Arctic amphibian and reptile species. Colored dots indicate known locations: Red dots represent Siberian Newt; Blue connotes the common frog; yellow signifies Siberian wood frog; Pink indicates moor frog; and brown signifies common lizard. The graphic only includes data from the vicinity of the Arctic and sub-Arctic and is not indicative of the global distribution of these species. Data from Amphibians of the former USSR, Databank ® 0229803415 and Gasc *et al.* 1997.

from a number of high-latitude refugia in what is now the northeastern United States, while most amphibians currently found in western and northwestern North America appear to have radiated from lower-latitude refugia to the west. Colonization following the last glacial maximum appears to have been rapid, with expansion to the north and northwest (Arctic Alaska and most of sub-Arctic Canada) having occurred from a single putative refugium near the edge of the Laurentide ice-sheet in present-day Wisconsin, while radiation into sub-Arctic Quebec, Newfoundland and Labrador took place from another refugium near the Appalachian Mountains in the vicinity of Pennsylvania.

## 5.3. STATUS AND TRENDS

### 5.3.1. Species richness and distribution

Maximum Arctic amphibian and reptile richness, three species, occurs south of the Yamal Peninsula, where the European common frog and moor frog coexist with the Siberian newt. The moor frog and common frog are sympatric on the Kanin Peninsula and in the Vorkuta region, while the Siberian newt and Siberian wood frog both inhabit the Khaiyr Settlement in Republic of Sakha-Yakutia. Throughout the remainder of the Arctic, species richness of amphibians and reptiles appears to be zero or one.

#### 5.3.1.1. Eastern hemisphere species

The Siberian newt is the most widespread amphibian species in the Arctic and sub-Arctic (Fig. 5.1), and has the widest geographical range of any recent amphibian species, c. 12 million km$^2$. The northernmost habitats of the Siberian newt consist of grass-undershrub-lichen-moss bogs and low shrub-moss and grass-moss tundras. The newt penetrates the Arctic in the area of the polar Urals and eastwards, and is found along the Khatanga River on the Taimyr Peninsula just south of the low Arctic (Kuzmin 1994). It reaches the Arctic Ocean in some areas of the Republic of Sakha-Yakutia, in particular, near Chukochya Guba in Nizhnekolymskii. The Amguema River in the Shmidtovskii District of Chukotka marks the northeastern extent of its distribution.

Frogs *Rana* spp. are more narrowly distributed in the Arctic than the Siberian newt. The common frog and the moor frog are mainly inhabitants of Europe but both range eastwards to the Urals, with the moor frog found into E Siberia. The common frog crosses into the low Arctic only in the northernmost peninsulas of Norway (Gasc *et al.*1997) and along the eastern slope of the polar

Urals at the southern border of the Yamal Peninsula, in the Priuralskii District of Yamal-Nenetskii Autonomous Okrug, Tyumenskaya Province, Russia (Toporkova & Shvarts 1960, Toporkova & Zubareva 1965, Toporkova 1973, Ishchenko 1978). The common frog has been known to occur on the Kanin Peninsula since at least 1902 (Zhitkov 1905).

The moor frog has a broader Arctic distribution than the common frog. It occurs in southern Yamal and the Polar Urals, and as far north as the Khadyta-Yakha River (Shvarts 1959). A few records indicate it is found on the sub-Arctic/low Arctic margin to the east as far as the Malaya Khadyta River in Yamal (Anufriev 1984).

The Siberian wood frog is a widespread brown frog, whose distribution covers a large part of Siberia, far eastern Russia, and northern Mongolia and Manchuria. Nevertheless, this species is known from only one Arctic locality: Khaiyr Settlement in Ust-Yanskii District of the Republic of Sakha-Yakutia (Borkin *et al.* 1984).

The common lizard is the only reptile species found in the Arctic. It ranges from northwestern Spain through Europe and Siberia to Mongolia and eastwards to Sakhalin Island in the Pacific. It reaches the Arctic in Europe in the vicinity of the Kanin Peninsula and around Vorkuta City in the Komi Republic in Russia (Anufriev & Bobretsov 1996). The common lizard is found in the Polar Urals, southwards from the Yamal Peninsula, where it occurs primarily in river valleys (Vershinin 2007). In the area of Taimyr Peninsula the common lizard occurs in the sub-Arctic near the southern boundary of the low Arctic (Bannikov *et al.* 1977).

### 5.3.1.2. Western hemisphere species

The wood frog is the only herpetofaunal species found in the Arctic of the Western hemisphere. This widely distributed North American frog is found throughout the sub-Arctic (in Labrador, Quebec, Ontario, Manitoba, Saskatchewan, Alberta). It extends into the low Arctic in Alaska, and is suspected to do so in portions of Yukon,

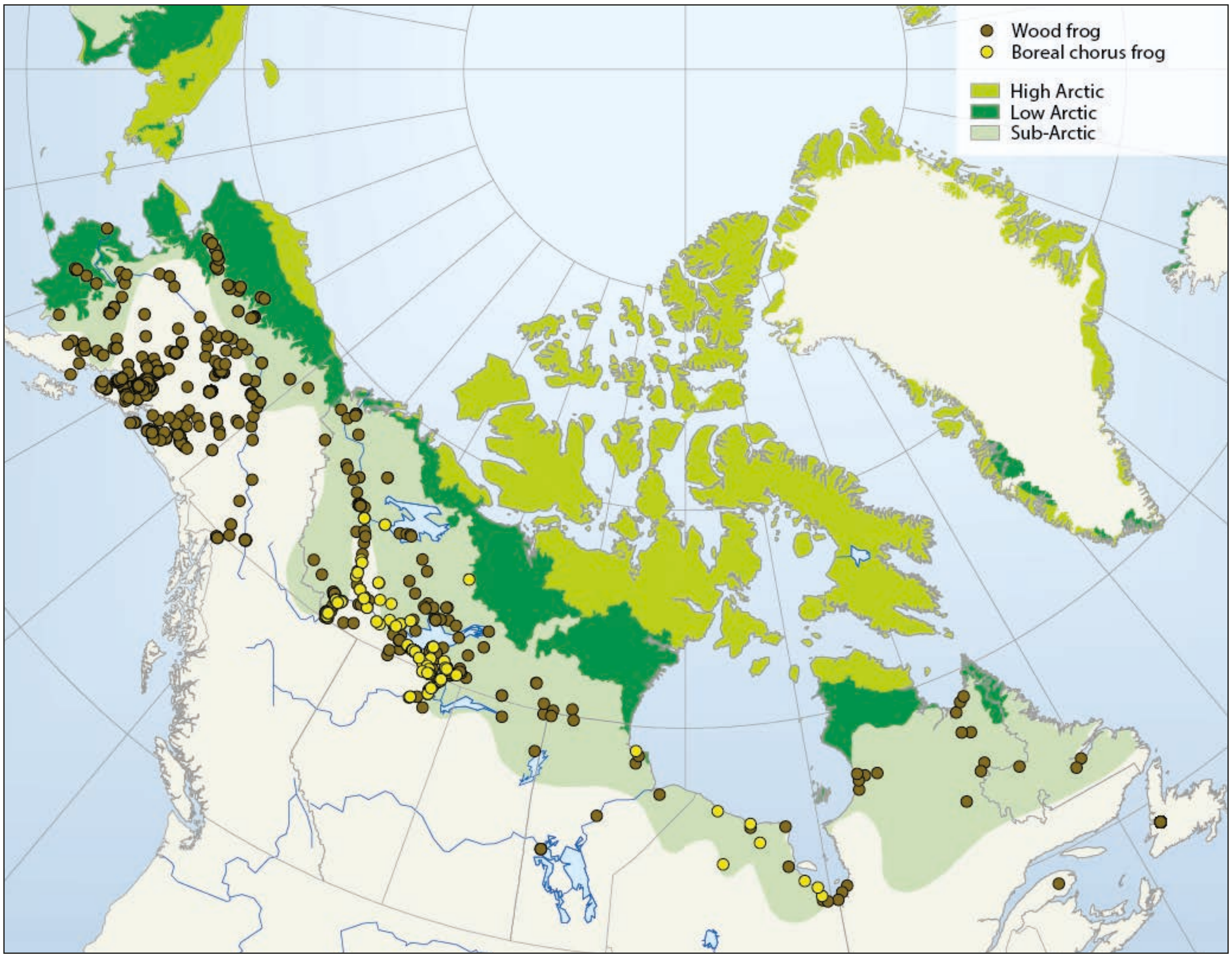

**Figure 5.2.** Known locations of Western Hemisphere Arctic amphibians. Wood frog locations are represented by brown dots. Boreal chorus frog locations are represented by yellow dots. The graphic only includes data from the vicinity of the Arctic and sub-Arctic and is not indicative of the global distribution of these species. Data from Martof 1970, IUCN, Conservation International and NatureServe, 2004, Alaska Natural Heritage Program, 2007, Gotthardt & Pyare 2009, Environment and Natural Resources Office, Government of the Northwest Territories 2010, Frogwatch Database, National Wildlife Research Centre, Environment Canada 2010.

Northwestern Territories, and Nunavut (DeGraaf & Rudis 1983, Cook 1984, Russell & Bauer 1993, Weller & Green 1997, Chubbs & Phillips 1998, Blackburn *et al.* 2001, Trust & Tangermann 2002, Carstensen *et al.* 2003, MacDonald 2003, Anderson 2004, Desroches & Rodrigue 2004, Slough and Mennell 2006, MacDonald & Cook 2007, Lee-Yaw *et al.* 2008, NatureServe 2010). This unique frog ranges at least as far north as the south side of the Brooks Range in Alaska, the Old Crow Flats in the Yukon, and the Mackenzie River Delta in Northwest Territories (Fig. 5.2). Despite its wide distribution and apparent ubiquity, there are only eight confirmed records of wood frogs extending into the Arctic as defined by Geographic Information System data layers developed for the Arctic Biodiversity Assessment (MacDonald 2003, Gotthardt & Pyare 2009, Environment and Natural Resources, GNWT 2010). The species is probably more widespread in the Arctic, and the limited number of records is likely due in part to very limited survey effort.

### 5.3.2. Status

All of the amphibians and reptiles found in the Arctic are considered taxa of 'Least Concern' by IUCN, suggesting their populations are currently stable. However, as a class, amphibians are among the most globally threatened groups, with roughly 32% (1,856 species) considered threatened and 43% (2,469 species) declining. At least 168 species worldwide have become extinct over the last 20 years, and the numbers of threatened and extinct taxa are expected to continue to climb (Stuart *et al.* 2004).

While there are no indications of declines of amphibian and reptile populations in the Arctic, their apparent stability may be a result of the almost complete lack of historic and contemporary abundance data. In a few cases there are some qualitative estimates of local abundance, but these are insufficient to determine the dynamics of even local populations. Overall numbers of amphibians and reptiles in the Arctic appear to be low and populations appear scattered and isolated.

### 5.3.3. Trends

Global population estimates and trend data are largely lacking for all herpetofauna found in the Arctic, and few if any data exist on local Arctic population sizes or trends for any of the taxa.

The Siberian newt has been known as an Arctic species since 1909 (Nikolsky 1918), and is considered to be common and stable throughout its range, with the exception of some small, declining and isolated populations in Mongolia, which are considered threatened (Kuzmin *et al.* 2008a).

The moor frog, though extinct in Switzerland, is considered common, stable and a species of 'Least concern' by the IUCN throughout its distribution (Kuzmin *et al.* 2008b).

The common frog is considered common and stable throughout its range, though local declines have been noted in Switzerland and Spain (Kuzmin *et al.* 2008c), and since the 1970s in Norway along the northern limits of its distribution (Gasc *et al.* 1997).

Globally, the Siberian wood frog is considered common, stable and a species of least concern (Kuzmin *et al.* 2008d), though there is no information on Arctic abundance or trends.

Population size, trend and status data for the common lizard are lacking throughout its large distribution, including the Arctic, but it is classified as 'Least Concern' by the IUCN (2010).

The wood frog is the most widespread amphibian in North America (Martof 1970), the most common amphibian in Alaska (MacDonald 2003), and is considered relatively common throughout most of its range, including the sub-Arctic. There are no data on abundance, status or trends for this species in the Arctic. The global population trend is unknown but is suspected to be stable, and the wood frog is considered a species of least conservation concern (Hammerson 2004).

### 5.3.4. Prospects

In general, the outlook for amphibian persistence in the Arctic is probably good. The species all appear secure globally, with Arctic populations representing the northern fringe of much larger distributions to the south. However, conservation of Arctic reptiles and amphibians will face a number of challenges in the immediate future and over the next century, including contaminants from local and global sources, anthropogenic habitat alteration, emerging infectious diseases, climate change-induced habitat alteration and loss, and the introduction of novel pathogens and predators.

Environmental contaminants originating either from local point sources or from diffuse regional and/or global sources may impact many otherwise undisturbed Arctic wetlands. Ackerman *et al.* (2008) and Landers *et al.* (2008) found concentrations of atmospherically deposited organic and other contaminants in fish from remote lakes in Arctic and sub-Arctic Alaska that exceeded thresholds of health concern for humans and wildlife. Because the study sites were all located in remote areas with no local contaminant sources, their presence was attributed to long-range trans-Pacific transport and to global sources. The risk to amphibians is unclear and undocumented, but due to their aquatic developmental phase, moist and highly permeable integuments, larval diets of zooplankton, phytoplankton and periphyton and adult diets of higher trophic level invertebrates, they may be predisposed to bio-accumulate a variety of contaminants when present in the environment.

As development inevitably proceeds in the Arctic, many wetland habitats will be transformed, and even those that remain intact may be exposed to additional threats as roads and other infrastructure elements are constructed. Research on wood frog breeding ponds at two National Wildlife Refuges in sub-Arctic Alaska documented some of the highest rates of skeletal abnormalities found in amphibians anywhere; as high as 20% of individuals from some breeding sites had pronounced skeletal abnormalities (Reeves *et al.* 2008). The normal background rate for such abnormalities is estimated as either 0-2% (Ouellet 2000) or 0-5% (Johnson *et al.* 2001). The prevalence of structural abnormalities in Alaska was found to increase with proximity to roads, and more recently, the presence of contaminants (both organic and inorganic) and odonate larvae were identified as predictors of the frequency of skeletal abnormalities at these sites (Reeves *et al.* 2010).

As climatic conditions in the Arctic continue to ameliorate, we might expect the amphibians already present to expand their current distributions and colonize previously unoccupied areas. However, a warming climate will also catalyze a suite of interconnected changes in the physical and biological environments of the Arctic, the ramifications of which are poorly understood for Arctic amphibians. Warmer winter and summer temperatures, alteration in both the rates and the timing of snow deposition and melt-off, and permafrost thaw will have profound effects on hydrology and hydroperiod across the Arctic. Both the total volume of water and the timing of its availability to plants and animals may be significantly altered (McDonald *et al.* 2004, Borner *et al.* 2008; see Wrona & Reist, Chapter 13) resulting in shifts in the composition of the biotic community. Permafrost thaw, which is forecast to continue at an accelerated rate, is already causing the draining of Arctic wetlands in Alaska (Yoshikawa & Hinzman 2003). In regions of thawing discontinuous permafrost in Siberia, the number of large lakes declined by 11% and overall wetland surface area declined by 6% since the 1970s (Smith *et al.* 2005). These changes in hydroperiod and hydrology, and their attendant impacts on the biotic community, have the potential to disrupt many facets of amphibian ecology, including: (1) breeding phenology relative to the timing and availability of algae and the emergence of important aquatic invertebrate prey (and predator) species, (2) habitat connectivity, (3) dispersal movements, (4) juvenile and adult survival, and ultimately (5) the persistence of local populations.

Emerging infectious diseases are also likely to play a greater role in the ecology of Arctic amphibians. Warming climatic conditions may aid the spread and survival of deadly new pathogens, and infrastructure development may provide new vectors for transmission across the landscape. The amphibian chytrid fungus, *Batrachochytrium dendrobatidis* (*Bd*) is a recently recognized pathogen widely believed to be expanding due to climate change and implicated in a number of amphibian declines and extirpations (Berger *et al.* 1998, Pounds *et al.* 2006). A number of ranaviruses (genus *Iridoviridae*) are also associated with recent amphibian declines (Stuart *et al.* 2004). There has been little surveillance for *Bd* in the Arctic to date, but the fungus has already been detected in sub-Arctic Alaska, and both *Bd* and ranaviruses have been detected in Canada's Northwest Territories (Reeves & Green 2006, Schock *et al.* 2009, T. Chestnut pers. com.). Infrastructure development and increased human presence in the Arctic may contribute to the spread of these pathogens: Both ranaviruses and *Bd* may be translocated between water bodies via transport of contaminated water or sediments by humans (on footwear and equipment), birds (e.g. on feathers), or other animals (Johnson & Speare 2005, Harp & Petranka 2006, Phillot *et al.* 2010).

Warmer temperatures and expanded human industry and infrastructure will increase the risks of introducing exotic or novel species into Arctic environments. Arctic amphibians breed primarily in fish-free water bodies, including ephemeral pools and small lakes and ponds, and it is widely believed that this preference is an adaptation to avoid predation. Fish are successful predators on the eggs and aquatic larvae of amphibians (Semlitch 1988), and many amphibians have few defenses against fish (Grubb 1972). Introductions of non-native fishes have been implicated as one of the major causes of amphibian population declines (Kats & Ferrer 2003), and even native fish introduced into previously fish free habitats have the potential to extirpate local amphibian populations. Increased human presence may serve as a vector for the spread of native and non-native fish across naïve Arctic wetlands. Amphibian larvae are also preyed on by a variety of birds, other amphibians (Sours & Petranka 2007) and a number of aquatic invertebrates, especially odonates, whose abundance appears related to water temperature (Reeves *et al.* 2010). Trophic webs and competitive interactions among amphibians in Arctic wetlands aren't well understood, but changes in species composition or density can strongly influence the outcomes of competition and predation in these aquatic communities (Relyea 2000, Sours & Petranka 2007). The consequences for Arctic amphibian populations of any new or heightened predatory or competitive interactions are completely unknown.

While most sub-Arctic amphibians are unlikely to colonize the Arctic in the next century (due to their southerly distributions, inherently slow rate of dispersal and less freeze-tolerant physiologies) the boreal chorus frog *Pseudacris maculata* in the Western hemisphere may already have reached it (Fig. 5.2). In 2009 a single un-vouchered observation was recorded in the Arctic in Canada's Northwest Territories near the border of Nunavut in the vicinity of Big Lake (Environment and Natural Resources, GNWT 2010). Very low mitochondrial genetic diversity found in populations occupying regions north of the last glacial maximum suggests the boreal chorus frog colonized its northern frontiers recently and rather rapidly (Lemmon *et al.* 2007). If it is not already, the boreal chorus frog will soon be the second Nearctic amphibian species.

## 5.4. CONCLUSIONS AND RECOMMENDATIONS

### 5.4.1. Sensitive areas and hotspots

Hotspots are difficult to identify because the distributions of Arctic amphibians and reptiles are so poorly characterized. Furthermore, these species are found in small, isolated and patchily distributed populations for a variety of reasons: (1) their Arctic range limits likely represent each species' physiological limitations, (2) amphibians require a number of different microhabitat features to intersect in close proximity due to their limited movement potential, and (3) they may not occupy all suitable habitats within their apparent range due to the susceptibility of small populations to stochastic events and the residual effects of past disturbances (Olson 2009). Nonetheless, a few areas in the Eastern hemisphere appear to be of particular importance: the corridors and deltas of the Khadyta-Yakha River on the Yamal Peninsula, the Chaunskaya Tundra in the lowlands of the Chaunsky Administrative District of the Chukotsky Autonomous Okrug, and the Khalerchinskaya Tundra in the Kolyma lowlands.

### 5.4.2. Key knowledge gaps

The principal knowledge gap is the near complete lack of survey and inventory data for status and population trends of Arctic amphibians and reptiles. Distributions are poorly and incompletely characterized, and are known only in broad general terms.

There are no reliable abundance estimates for local or regional populations for any Arctic herpetofauna, and there are no statistically meaningful monitoring efforts currently in place. General lack of understanding of the factors which limit amphibian and reptile populations in the Arctic is also a principal knowledge gap.

### 5.4.3. Recommended conservation actions

#### 5.4.3.1. Research recommendations

- Establish effective survey and inventory efforts to better define the actual distributions and ecology of these species.
- Construct statistically defensible baselines of abundance data in specific locations against which changes in abundance can be monitored.
- Establish monitoring programs with replicate schema representative of the range of habitats and microhabitats inhabited by each species. Monitoring locations should also be chosen in such a way so as to minimize the effort and expense to reach them in order to increase the likelihood that monitoring will be continued into the future. If practicable, monitoring efforts should be collocated with monitoring efforts for other taxa in order to develop economies of scale for all monitoring, and to improve our understanding of the dynamics of Arctic ecosystems.
- Conduct research into the impacts of climate-induced changes to hydrology/hydroperiod on reproduction, persistence and habitat connectivity for Arctic amphibians.
- Determine the geographic prevalence of contaminant burdens and chief pathogens for amphibians across the Arctic.

These efforts may involve citizen science projects.

#### 5.4.3.2. Conservation action recommendations

- Develop guidelines for human development projects that require land managers and developers to consider amphibian and reptile habitats and populations in their development plans.
- Determine which areas are of special importance for amphibian and reptile species richness and for the long-term persistence of individual taxa. Use data from survey and inventory efforts to identify hotspots and areas of likely significance by modeling species' habitat and micro-habitat associations across the Arctic landscape.
- Establish or strengthen protections for areas of key importance to reptiles and amphibians. Arctic amphibians have complex life cycles, and require a range of habitats throughout their annual cycles and life histories. Conservation of these species will require a landscape-level approach, conserving various vital habitats at appropriate spatial scales and maintaining connectivity between conservation units, while accounting for expected wetland loss and alteration.

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Anadromous (sea-run) male northern Dolly Varden *Salvelinus malma malma* from the Babbage River, Yukon Territory, Canada in pre-spawning coloration; this salmonid is adapted to Arctic riverine habitats in Beringia. Photo: Neil Mochnacz, Fisheries and Oceans Canada.

*Chapter 6*

# Fishes

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## Contents

> » **Local indigenous fishermen from Pokhodsk and Nutendli report that muksun *Coregonus muksun* (a freshwater fish) amounts have decreased. Fyodor Innokentyevich Sokorikov, former head of the fishing sovhoz in Pokhodsk reports that muksun was caught in the amounts of 1,500 tonnes annually in the 1980s but says that in late 1980s and early 1990s there was overfishing of muksun and that is why it has collapsed now.**
>
> Mustonen 2007.

## SUMMARY

Having occupied Earth's waters for about five hundred million years, fishes are the oldest group of living vertebrates. Fishes have radiated to occupy most aquatic habitats on the planet, and estimates of total biodiversity range from 28,000 up to about 35,000 species. Fishes are associated with both marine and freshwater habitats, and some migrate between these biomes. Globally, about 16,000 species occupy marine waters, 12,300 are found in fresh waters, and 225 use both habitats during their lives. It is within this global diversity context that the diversity of Arctic fishes must be assessed.

Freshwater fishes are those confined to low salinity aquatic habitats; diadromous fishes are those which regularly migrate between fresh and marine waters. The latter occur as two major groups – anadromous fishes spend much of their lives in marine waters migrating to fresh water to reproduce, and catadromous fishes do the converse. Anadromous fishes constitute the majority of diadromous fishes in the Arctic. Between 17 and 19 families (3-4% of 515 worldwide) of freshwater and diadromous fishes occur in Arctic waters with about 123-127 recognized species (1% of 12,547 extant freshwater and diadromous species globally). Many of these taxa are unresolved species complexes, consist of multiple types that have differentiated in separate glacial refugia and/or exist as multiple life history and/or ecophenotypic forms. All these forms tend to function as, and may be the equivalent of, taxonomic species. Accordingly, an estimate of simple parameters such as species richness and taxonomic and phylogenetic diversity is fraught with problems and generally under-estimates the true diversity present. To facilitate this, we will use the upper estimate (127 species) herein.

Five families (salmonids – 50+ species of chars, whitefishes (*sensu Coregonus*), salmons; cyprinids – 25 minnows; cottids – nine sculpins; percids – eight perches; and petromyzontids – six lampreys) account for most of the freshwater taxonomic diversity present. Ecotones, areas where distinct habitats or physiographic realms meet, exhibit high local diversity, particularly in lake and river deltas and the estuaries of the large Arctic river basins. Similarly, large water bodies with complex habitats (e.g. deep lakes, large rivers) exhibit high diversity that may be manifested at sub-specific levels. Geologically young landscapes experiencing active disturbance, taxonomically labile fishes, generalist biological strategies and inherent capacity for rapid change in many key groups result in the Arctic being an area where rapid evolution of these fishes appears to occur. This underscores their significance in a global context.

Spatially, freshwater fish diversity decreases with latitude (e.g. in North America species richness is 40 at 60° N, 31 at 70° N along the mainland margin, three at 74° N and one farther north to the maximum extent of fresh waters on land at about 84° N). Longitudinally, the greatest diversity is present in areas that were unglaciated during the last ice age (i.e. much of Siberia and Beringia; see Fig. 2.2 in Payer *et al.*, Chapter 2), declining to low levels in the eastern Canadian Arctic and Greenland that were deglaciated last and still retain large ice sheets. Time lines are too short and monitored sites too few to document temporal trends in species diversity in the Arctic. However, recent evidence suggests northward colonizations by freshwater fishes along river corridors and diadromous species into marine environments where climatic constraints have recently decreased. At present, no documented local extirpations or extinctions of taxa are known in the Arctic, although local population declines have occurred. Anthropogenic stressors are increasing in importance as risk factors both locally and throughout the Arctic. Local 'hotspots' of diversity and several globally significant water bodies are present.

Arctic freshwater and diadromous fishes are of particular importance to humans both inside the Arctic and elsewhere. Food fisheries by indigenous peoples (i.e. subsistence fisheries) are extensive throughout the Arctic and historically always have been.

Pervasive stressors such as climate change result in significant and rapid habitat alterations (indirect effects) as well as direct effects (e.g. thermal stresses) which challenge these fishes. Productivity shifts associated with climate change may create new opportunities (i.e. increased population sizes, growth potential) for freshwater and diadromous fishes.

Localized stressors (e.g. fisheries, hydrocarbon development, industrial activities, mining, water withdrawals, hydroelectric dams) affect populations either directly (fisheries) or through habitat impacts.

Marine fishes reproduce and spawn in seawater although juveniles and adults may occur also in the low salinity waters of fjords, coastal areas and river deltas. Here, we review the marine fishes across the Arctic Ocean and adjacent Arctic seas (AOAS). Altogether 16 regions and seas are examined for species richness, including the main entrances i.e. 'Arctic gateways' that connect the Atlantic and Pacific Oceans with the Arctic Ocean and Arctic shelves. While nearly 250 marine fish species are known from Arctic waters *sensu stricto*, the AOAS encompass *pro tem* 633 known fish species in 106 families. Cartilaginous fishes such as sharks and skates are well represented with about 8% of the species, whereas 92% are bony fishes. From a zoogeographic point of view, only 10.6% of the bony fishes are considered genuinely Arctic and 72.2% are boreal.

The fish faunas of the Arctic gateways are relatively well known compared with the Arctic seas as they support some of the largest commercial fisheries in the world. They are undeniably also the most species-rich regions of the AOAS and include 385 species in the Bering Sea, 204 species in the Norwegian Sea and 153 species in the Barents Sea. This is in stark contrast to the Arctic

Ocean and Arctic shelves where only 13-87 species are recorded to date.

Fishes of the AOAS may display extraordinary phenotypic variation, and the taxonomic status is still unsettled and controversial for several fish species, particularly within the most species-rich families: snailfishes (Liparidae), eelpouts (Zoarcidae) and sculpins (Cottidae). Moreover, new fish species are described regularly, mainly due to recent efforts in Arctic marine research, whereas others are synonymized and lose their taxonomic rank following molecular and genetic studies.

Species richness increases with sea-surface area for the relatively well studied Arctic gateways, which is to be expected. By contrast, there is no species-area relationship for the understudied Arctic seas, and they display disproportionately low numbers of species. The paucity of credible data and lack of time-series for fishes in the Arctic Central Basin and Arctic shelves clearly preclude trend analyses and elaborate studies on biodiversity.

Ocean warming in the marine Arctic has become increasingly critical for the fish fauna native to Arctic waters. The marked shifts in distribution patterns for many targeted fishes, from sub-Arctic to high latitude seas, will inevitably attract modern fishing fleets into hitherto pristine areas, and may conflict with extant subsistence livelihoods among indigenous peoples along the Arctic coasts. Fishes native to Arctic marine waters are mainly associated with the seabed, and they are particularly vulnerable to conventional bottom trawling as they end up as unwanted and unprecedented bycatch. Although of no commercial value, bycatch fishes include species that are indispensable to structuring and functioning of Arctic marine ecosystems.

Credible assessments are the scientific link to legitimate conservation actions. Scientific uncertainty is at present a hallmark for the conservation of Arctic marine fishes, and precautionary management policies are urgently needed for future Arctic fisheries.

Significant gaps exist in the knowledge base for diversity of Arctic fishes. Practical measures to document trends and conserve diversity are thus compromised.

## 6.1. INTRODUCTION

This chapter provides an up-to-date overview of the fish species for which occurrence is scientifically confirmed within the borders of the Arctic mainland and the Arctic Ocean and adjacent seas. We use ‘fishes’ in the wide sense of the word and include four fish and fishlike vertebrate classes: the hagfishes (Myxini), the lampreys (Petromyzontida), the cartilaginous fishes (Chondrichthyes) and the bony fishes (Actinopterygii) (Nelson 2006). In the Arctic, the four classes show some notable differences in habitat choice: the lampreys are confined to freshwaters for reproduction, the hagfishes and the cartilaginous fishes are exclusively marine, whereas the bony fishes inhabit all aquatic environments.

The genuine freshwater fishes and most diadromous fishes require freshwater for reproduction. Diadromous fishes are those species that undertake regular migrations between freshwater and marine habitats, either for refuge, feeding or reproduction (McDowall 1992). Among these are the well-known fish families: lampreys (Petromyzontidae), and whitefishes and salmonids (Salmonidae) as well as some lesser-known groups.

The marine fish fauna, on the other hand, encompasses species that spawn at sea: in the littoral zone along the coastlines, in estuaries and fjords, on the shelves and seaward. Several habitats are oligohaline (salinity < 5 practical salinity units (psu)), such as estuaries, but they are still considered within the geographic realm of the marine Arctic.

In the Arctic, the freshwater and diadromous fishes are significantly molded by glaciation, deglaciation and geological events during the late Pleistocene and Holocene epochs (i.e. ~ 126,000 and 12,000 years ago, respectively). The evolutionary history of the marine fish fauna, on the other hand, dates back to the Neogene period as the modern circulation in the Arctic Ocean began to form some 14-17 million years ago (Krylov *et al.* 2008, Polyak *et al.* 2010). For reasons of clarity and because of the marked differences in habitat choice and evolutionary history, this overview of Arctic fishes is organized into two separate subchapters: (1) freshwater and diadromous fishes of the Arctic and sub-Arctic (J.D. Reist), and (2) marine fishes in the Arctic Ocean and adjacent seas (J.S. Christiansen).

## 6.2. FRESHWATER AND DIADROMOUS FISHES OF THE ARCTIC AND SUB-ARCTIC

### 6.2.1. Focus of this section

Fishes are fundamental vertebrate components of most aquatic ecosystems. Those found in fresh waters or that move between fresh and marine waters (i.e. freshwater and diadromous species; see Box 6.1) are prominent components of northern aquatic ecosystems (e.g. freshwater ecosystems, nearshore marine ecosystems). The focus of this sub-chapter is on the present diversity of fishes at various levels within the Arctic. We also focus upon key processes that have acted over recent time (i.e. Holocene) and which are still acting to affect that diversity. Patterns of diversity in important groups of these fishes are inextricably linked with these processes that accrue and alter diversity.

### 6.2.1.1. Overview of northern freshwater and diadromous fish diversity

Globally, using a conservative estimate, there are about 515 families, 4,494 genera and 28,000 species of described extant fishes (i.e. more than half of all the 54,711 living vertebrate species; Nelson 2006). Of these, about 12,300 (44%) fish species exclusively live in freshwater areas of the globe (i.e. 1% of the Earth's surface area and only 0.01% of the water volume present). Including diadromous species that occupy both marine and fresh waters during life history, about 12,525 species actually occur in fresh waters. Over 225 species globally are diadromous with most being anadromous (see Box 6.1). These numbers (high diversity in small areas and volumes of fresh water) emphasize the relevance of these fishes in the context of overall biodiversity, ecosystem function and ultimately to humans. Of course, these numbers are estimates that change regularly due to taxonomic synonymy and/or inflation (i.e. subspecific taxa arbitrarily raised to the species level due to adoption of a particular species concept; Isaac *et al.* 2004), descriptions of new taxa and better understanding of taxonomies within groups. Nelson (2006) conservatively estimates that 32,500 species of fishes are extant, but points out that such numbers depend both upon taxonomic effort and how taxonomic levels such as species are defined for fishes; other estimates range as high as 35,000 species.

Freshwater and diadromous fishes experience a fundamental constraint relative to their marine counterparts. That is, the habitats utilized are discontinuously distributed in comparison with marine habitats. In this respect, freshwater ecosystems represent 'islands' embedded within the terrestrial biome and thus have many attributes in parallel with island biogeography. This discontinuity in habitats has profound implications for both diversification processes and the resulting diversity that characterize freshwater and diadromous fishes. Generally, historical discontinuities have fostered evolutionary conditions (e.g. isolation, local adaptation) which promote differentiation from ancestral forms and diversification among contemporaneous lineages. This is particularly so for higher latitude fishes of sub-Arctic and Arctic regions, areas significantly affected by Pleistocene glaciations. These geological events promoted isolation and diversification in glacial refugia for several hundred thousand years in some cases, recolonization and mixing of semi-discrete lineages during deglaciation (which continue today) and highly variable habitats in both space and time (see Wrona & Reist, Chapter 13).

All these underlying processes, coupled with the characteristics inherent in the fish lineages (e.g. genetic diversity, developmental flexibility and facultative responses within and among individuals, populations and lineages) have enhanced diversity in northern freshwater and diadromous fishes, especially at lower taxonomic levels. Furthermore, these processes and diversification are ongoing with two major implications. First, Arctic fish taxa represent a wide range of stages of diversification, much of which is recent, ranging from complete speciation (but often unrecognized as such) to ecological associations that may be the first stage of local speciation. These complicate definition and enumeration of discrete units such as species (see De Queiroz 2007). Second,

## Box 6.1. Definitions and examples of northern freshwater and diadromous fishes

Habitats utilized, associated life histories, and physiological tolerances differentiate three general groups of fishes: (1) *marine fishes* pass their entire life histories in saline waters in Arctic seas, although those tolerant of wide salinities (euryhaline) may be found in estuaries and similar nearshore freshened areas; (2) *freshwater fishes* pass their life histories in non-saline waters (i.e. typical fresh waters including highly freshened areas of estuaries); and (3) *diadromous fishes*, those which during life history migrate between fresh and marine waters. Diadromous fishes exhibit four major patterns (McDowall 1988): (A) anadromous fishes which spend most of their lives at sea and migrate to fresh water to breed (e.g. Pacific salmon *Oncorhynchus* spp.); (B) catadromous fishes which spend most of their lives in fresh water and migrate to sea to breed (e.g. Atlantic eel *Anguilla* spp.); (C) amphidromous fishes which migrate between fresh and marine waters for purposes other than breeding, in turn consisting of (i) marine amphidromy (typically spawn in marine waters with larval or juvenile stages in fresh water; e.g. osmerids, smelts), and (ii) freshwater amphidromy (spawn in fresh water with larval or juvenile stages in marine waters; e.g. salmonids, salmons). The focus of the summary in the main text is on freshwater and diadromous fishes present in the Arctic (i.e. 2, 3A, 3Cii above). Some species such as eels (3B above) are present in some Arctic waters, however, these are not primarily Arctic taxa thus will be addressed only minimally.

Clarification of the species in categories 3A, 3B and 3Cii is required for Arctic waters. Formation of winter sea ice results in the extrusion of salt to the underlying water column (Pease 1980). This and temperature decreases result in the formation of water layers immediately below the ice which are both hypersaline and typically below freezing (i.e. regular salinity sea water freezes at -1.8 °C or lower if higher salt content). Such environments are inhospitable to both anadromous and amphidromous fishes, both of which typically vacate marine habitats during Arctic winters simply to overwinter in freshwater areas. Some Arctic anadromous species may remain in the sea during winter but likely occupy areas (i.e. migrate out of the area) or depths unaffected by surface marine freezing. Amphidromous species appear to emigrate from marine areas to fresh waters and/or to highly freshened the sensitivity of partially distinct taxa and processes of diversification to anthropogenic influences in the Arctic is extremely high (see Section 6.2.9.1), thus of conservation concern. Incomplete understanding and enumeration of the actual diversity present over wide areas of the Arctic exacerbate these issues. Substantive under-estimation of the actual diversity of these fishes is thus the overarching consequence, especially if attempted using standard taxonomy and approaches. These issues further reinforce the deficiencies of current approaches, the lack of consensus among approaches (e.g. standard morphological vs. ecologically vs. genetically based taxonomies) and the absence of a method which incorporates all evidence to delineate species-level taxa.

Geographic differences throughout the Holarctic in geological history, in the timing of major seasonal events and in the suite of fishes originally present (i.e. 'reservoirs' in refugia or source areas), all contribute to high regionality in both the processes and products of diversification. Consequences of the above are relevant to any assessment of diversity and include the following: (1) diversity at both the species and sub-specific levels are relevant themes, (2) common definitions of taxonomic levels and the associated taxa have to be established (and underlying philosophies need consideration), (3) assessment of diversity and trends of change require a common and stable taxonomy, and thus, (4) nomenclature and synonymies of fish taxa over space and time have to be established or assumed. Finally, (5) taxonomic (e.g. unresolved complexes) and zoogeographic uncertainties must be considered. Processes of diversification yielding functionally, and in many cases biologically, distinct entities equivalent to species have been and are pervasive throughout the area. Moreover, many of these processes appear to have occurred over relatively short evolutionary time frames (e.g. since deglaciation, < 6,000 years ago in some cases) and are still occurring. The result is difficulty in delimiting taxa within and among areas that fit within specific taxonomic ranks, thus limiting our ability to calculate meaningful diversity indices, for example. These factors are discussed more fully below.

#### 6.2.1.2. Geographic scope

The general geographic scope of this review includes the Arctic and sub-Arctic as defined in this assessment (Fig. 6.1). The focus is on the circumpolar Arctic. Regions south to approximately 60° N latitude are not included, but are nonetheless important due to the presence of several large northward-flowing rivers in the area, their relevance as past and potential future sources of additional diversity and the difficulty of establishing a strict southern boundary for mobile organisms such as fishes. For example, heat transport and contiguity of habitats within large northward-flowing rivers allows temperate species to penetrate well into areas geographically defined as sub-Arctic and even Arctic. Moreover, some more southerly head-water areas for large Arctic rivers (e.g. Transbaikalia in eastern Siberia) characterized by high elevations have local fish faunas similar to those found farther north and may have been refugia with complex patterns of interchange (e.g. Froufe *et al.* 2003 and Alekseyev *et al.* 2009). Within the Arctic, three latitudinally based sub-divisions are made: sub-Arctic, low Arctic and high Arctic (Fig. 6.1).

estuarine areas during winter, returning in spring to marine habitats. These migrations occur annually at appropriate seasons throughout life, thus Arctic amphidromous species represent special cases and can, perhaps, be more appropriately termed as 'semi-anadromous' (see also Craig 1987, who coined the term). The above definitions are both necessary and relevant for a summary such as this in that first they reflect diversity in life history, which increases uses of habitats (e.g. see Reist & Bond 1988, Harris *et al*. 2012), and, second they reflect underlying functional forms which may ultimately underpin some aspects of taxonomic diversification.

Definitions and the description above imply patterns exhibited are constant. Generally, this is not the case within and among species and is especially not so for these fishes in the Arctic. That is, species that typically exhibit anadromy as a life history mode almost always also exhibit a fraction of individual populations or entire populations themselves that do not migrate to marine waters. Whether this variation has a direct genetic basis (i.e. is obligatory) or whether it is a facultative (i.e. non-genetic) response to environmental variation is unresolved at present (and elements of both forces may influence variation at this level). Life history variation represents increased functional diversity in ecosystems and thus is a significant factor in the overall diversity present in Arctic aquatic ecosystems (Harris *et al*. 2012).

Anadromy as a life history strategy is a relatively widespread attribute (McDowall 1988) and is a common feature of fishes from northern latitudes (Gross *et al*. 1988, McDowall 2008) dominating in the Arctic (e.g. two of 41 amphidromous species exhibit catadromy vs. 39 anadromous taxa; Tab. 6.1).

Anadromy appears to confer growth, maturation and reproductive advantages to species/populations that exhibit it, however, it reflects a balance (or a 'trade-off') between the costs and benefits in terms of fitness (Gross 1987, Jonsson & Jonsson 1993) associated with particular habitats. In northern environments, anadromy appears to predominate allowing individuals to exploit the high productivities of marine environments (Gross 1987), which typically are greater than those encountered in fresh water (McDowall 1987, Gross *et al*. 1988).

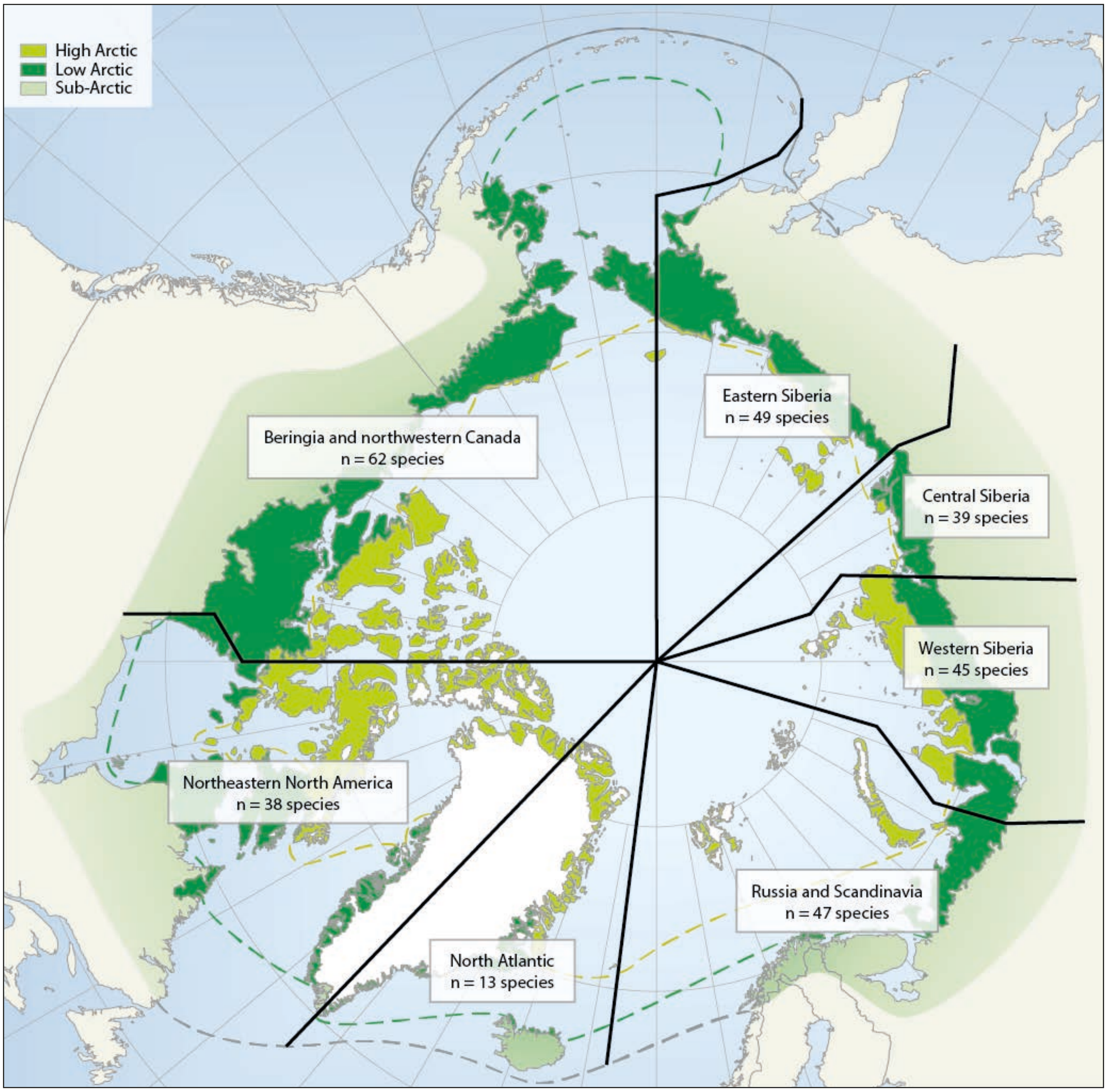

**Figure 6.1.** Sub-regions relevant to freshwater and diadromous fishes within the Arctic and sub-Arctic.

Longitudinally around the North Pole, a wide range of sub-divisions of areas and regionality are possible. These include those used in the Freshwater Ecosystems of the World (Abell *et al.* 2008), which examines patterns on the basis of individual (large) or combined (series of proximate small) drainage basins, to the simple general regionality followed in the Arctic Climate Impact Assessment (ACIA 2004, 2005). Alternatively, a country-based system can be used. Herein, we have divided the circumpolar Arctic into seven regions (Fig. 6.1), each of which is relatively homogeneous at present, has a historical biogeographic basis (e.g. linked by Pleistocene events) and/or represents distinct large-scale drainage basins (see Section 6.2.3.2).

## 6.2.2. Diversity of freshwater and diadromous fishes in the Arctic

### 6.2.2.1. Overall biological diversity of freshwater and diadromous fishes

Seventeen to nineteen (3.3-3.9%) families of fishes (out of 515 recognized living families; Nelson 2006) occur in the Arctic and sub-Arctic (Tab. 6.1). Using a conservative taxonomy (i.e. most diversity considered to be at sub-specific levels thus not enumerated), about 127 species are present (~ 1.0% relative to the global estimate of 12,547). Of these 127 species, 32 (25%) do not occur farther north than the sub-Arctic (Appendix

**Table 6.1.** Families and numbers of species of Arctic and sub-Arctic freshwater and diadromous fishes (see also Appendix 6.1). Endemics are defined as wholly or primarily Arctic in distribution at species or taxonomically distinct sub-specific levels. * indicates a family restricted to the northern hemisphere (Berra 2001).

| **Family** | **Common name** | **N species in the Arctic and sub-Arctic/ endemics** | **N species exhibiting primary life history** | | | **Global N genera/species (Nelson 2006)** | **Arctic and sub-Arctic species as % of global species within families** |
|---|---|---|---|---|---|---|---|
| | | | Fresh water | Anadromy | Catadromy | | |
| Petromyzontidae* | Lampreys | 6/0 | 3 | 3 | - | 8/34 | 17.6 |
| Acipenseridae* | Sturgeons | 5/0 | 2[4] | 3 | - | 4/25 | 20.0 |
| Hiodontidae* | Mooneyes | 1/0 | 1 | - | - | 1/2 | 50.0 |
| Anguillidae | Freshwater eels | 2/0 | - | - | 2 | 1/15 | 13.3 |
| Clupeidae | Herrings | 2/0 | 2 | - | - | 57/188 | 1.1 |
| Cyprinidae | Minnows | 25/0 | 25 | - | - | 220/2820 | 0.9 |
| Catostomidae* | Suckers | 2/0 | 2[4] | - | - | 13/72 | 2.8 |
| Cobitidae | Loaches | 1[1]/0 | 1 | - | - | 26/177 | 0.6 |
| Balitoridae | River loaches | 2/0 | 2 | - | - | 59/590 | 0.3 |
| Osmeridae* | Smelts | 3[2]/0 | - | 3 | - | 11/31 | 9.7 |
| Salmonidae* | Salmonids | 48-52[1,2]/17 | 22[4] | 28 | - | 11/66 | 75.7 |
| Esocidae* | Pikes | 1/0 | 1[4] | - | - | 1/5 | 20.0 |
| Umbridae* | Mudminnows | 1 (3?)[5]/1 | 1 (3?)[5] | - | - | 3/5-8 | 20.0 |
| Percopsidae* | Troutperches | 1/0 | 1 | - | - | 1/2 | 50.0 |
| Gadidae* | Cods | 2[3]/0 | 1[4] | - | - | 75/555 | 0.4 |
| Gasterosteidae* | Sticklebacks | 3[2]/0 | 1 | 2 | - | 5/8 | 37.5 |
| Cottidae* | Sculpins | 9[1]/0 | 9[4] | - | - | 70/275 | 3.3 |
| Cottocomephoridae[6] | --- | 1[1]/0 | 1 | - | - | Not a family | --- |
| Percidae* | Perches | 8/0 | 8[4] | - | - | 10/201 | 3.9 |
| Totals: 18-19 | | ~123-127+/18[2] | 83 | 39 | 2 | --- | --- |

Notes:

1) Some taxa require confirmation of occurrence in the Arctic/sub-Arctic as defined herein.
2) Taxonomic issues preclude accurate counts (i.e. synonymies, species complexes and stable definitions of taxonomic ranks and taxa are all unresolved for many Arctic freshwater and diadromous fishes). Some areas are poorly surveyed as well which adds to taxonomic uncertainty and uncertain diversity estimates. For salmonids, n = 48 if lake whitefish *Coregonus clupeaformis* and humpback whitefish *C. pidschian* in North America, sea trout *Salmo t. trutta* and *fario* forms, and *Salvelinus murta*, *S. thingvallensis* and Arctic char *S. alpinus* are each considered as a single taxon.
3) Only one gadid species (burbot *Lota lota*) is confined to freshwater while all others are marine in habit, however, populations of Atlantic cod *Gadus morhua* occur as isolates trapped in marine layers overlain by fresh waters in some lakes in the Canadian Arctic (Hardie *et al.* 2008).
4) Some freshwater obligate species may briefly enter brackish estuaries but are considered herein to be wholly fresh water because that is their primary habitat. Also, virtually all anadromous species exhibit freshwater-resident populations whereas most catadromous or freshwater species do not exhibit alternative life history variants.
5) Absence of adequate surveys over large areas of the Arctic preclude accurate enumeration within many groups of these fishes. Newer surveys, combined with variable taxonomic philosophies often result in description of new taxa with local distributions. The validity of these requires additional work. Although relevant to most families here, the example is Umbridae – one umbrid (Alaska blackfish *Dallia pectoralis*) is typically considered as the only Arctic member of the family, however, regional work has resurrected two taxa as species (*D. admirabilis*, *D. delicatissima*) (Reshetnikov *et al.* 1997).
6) Nelson (2006) includes Cottocomephoridae with Cottidae; noted here because Russian synopses treat it as a distinct family (e.g. Reshetnikov 2002); counted as one species totalled with Cottidae in appendix materials.

Discrepancies between this table and numbers presented in the appendix materials are attributable to the above causes, widely disputed definitions of taxonomic categories and limited knowledge over wide areas.

6.1.1). As noted, these estimates are almost certainly under-estimates of the true 'species-level' diversity present (regardless of how one philosophically defines the species level), thus the actual diversity is likely much greater. Depending upon the criteria used for delineating species and combined with the huge gaps in surveys, realistic estimates of diversity for this group of species could be double or even triple this number.

Of the 127 species present (Tab. 6.1, Appendix 6.1.1), 83-85 (66.5%) are obligate freshwater forms, although some members may occasionally enter brackish waters in estuaries and along coasts. These are found in 17 of the families present. An additional 39 (30.7%) exhibit anadromous behaviour (found in five families), and two species (1.6%) exhibit catadromy (found in one family); 41 species (~ 18%) of the global total of diadromous species (225) are present in Arctic and sub-Arctic waters (see Box 6.1 for definitions and examples of these fish behavioral types). In many families and even within species (or species complexes) several life history modes are exhibited within and among populations which further contributes to diversity. All typically marine species are excluded from this summary except Atlantic cod *Gadus morhua*, which has been documented as eight isolated populations in several lakes in the Canadian Arctic (Nunavut) (Hardie *et al.* 2008) albeit likely in saline water layers underlying fresh water.

Although there are relatively few freshwater and diadromous fish species in the Arctic, these species are disproportionately important for human activities and aquatic ecosystems. In that respect, four families (trouts and salmons, perches (Percidae), pikes (Esocidae) and cods (Gadidae)) figure prominently with salmonids being by far the most important due to wide geographic distribution throughout many habitats over the entire area of consideration, relatively high local population sizes and ease of exploitation. Salmonids also exhibit many types and high levels of biodiversity below the species level, thus are particularly relevant for biodiversity assessments.

#### 6.2.2.2. Faunistic scope – diversity among families

Overall, of the 17-19 families, five (trouts and salmons, carps and minnows (Cyprinidae), lampreys, sculpins (Cottidae) and perches) account for most of the diversity (Tab. 6.1, Fig. 6.2). Considering diversity of only freshwater species (n = 83-85) distinctly, the greatest diversity (53% of all, or 79% of only freshwater fishes) is represented by the following five families: carps and minnows, trouts and salmons, sculpins, perches and lampreys (Tab. 6.1, Fig. 6.2). For diadromous species, diversity is represented primarily by one family (trouts and salmons) with 22% of all, or 68% of diadromous species). However, many of these species are only marginally present in the area, may not be 'true' Arctic species, or may not be taxonomically valid. Thus, these numbers and percentages are neither fixed nor totally accurate.

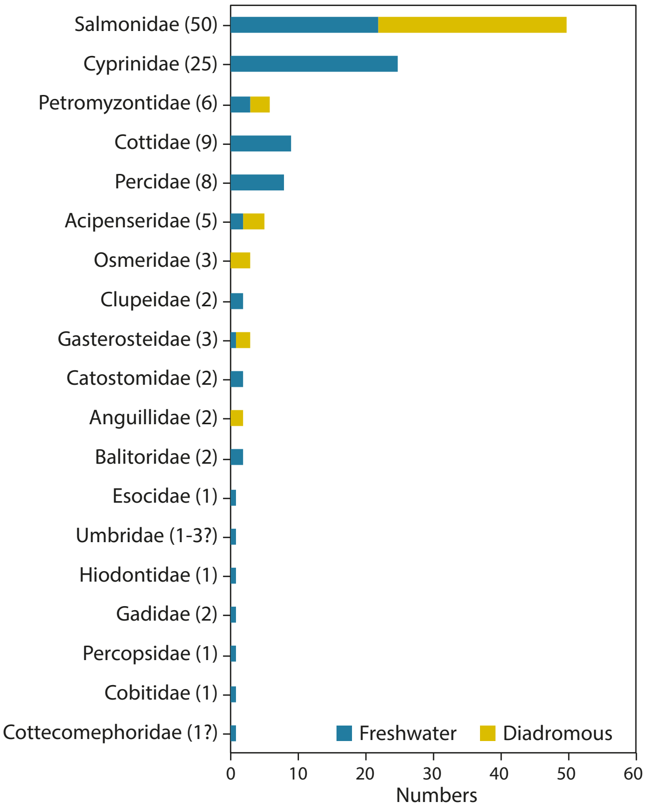

**Figure 6.2.** Numbers of diadromous and freshwater fish species in the Arctic and sub-Arctic by family.

## 6.2.3 Patterns of diversity at the species level

#### 6.2.3.1. Arctic diversity within fish families relative to global diversity

Patterns of distribution and diversity of freshwater fishes are relatively difficult to understand. Particular fish families are associated with particular global regions (Darlington 1957, Berra 2001). However, as with most other faunistic groups, both the diversity and overall abundance generally declines with latitude. This partially explains why some families are represented by many species and others by few in the Arctic. Salmonids, for example, are typically viewed as a northern group. For some families (e.g. carps and minnows, mooneyes (Hiodontidae), river loaches (Balitoridae) and loaches (Cobitidae)) distribution is centred in southerly areas, with some species occurring only at the southern fringes of the Arctic region. Diversity enumerated at the southern limits of the Arctic does not include anthropogenically transplanted taxa, which in some areas may be relatively numerous, particularly in large northward flowing rivers (Wrona & Reist, Chapter 13). These species are, however, of relevance in that they may colonize more northerly locations as conditions change. Colonizing species may affect or supplant Arctic species through competition, predation and/or introduction of parasites or diseases (Reist *et al.* 2006a, 2006b; see also Lassuy & Lewis, Chapter 16). Consequent effects on local fisheries may ensue (Reist *et al.* 2006c).

Arctic and sub-Arctic diadromous and freshwater fish species represent between 0.3% and 75.7% of their respective global family-level diversity (see Tab. 6.1). Percentages greater than 50, particularly for speciose groups, suggest a ‘northern’ aspect to the respective family. Thus, only one family, trouts and salmons with 75.7%, can be considered northern in the context of the Arctic used herein. This rather simple analysis points out the high diversity of salmonids across the Arctic. Of course, most of the families listed represent northern temperate fishes and thus may exhibit relatively higher diversity in the Arctic in the future as conditions change.

#### 6.2.3.2. Spatial patterns of freshwater and diadromous fish diversity

Northern freshwater habitats are geologically relatively young in many cases and have been much disturbed by historical factors (e.g. Pleistocene glaciations and the rates of deglaciation; Pielou 1991; see also Payer *et al.*, Chapter 2). Accordingly, present-day broad-scale patterns are heavily influenced by this legacy. Regional and local factors are superimposed upon these and progressively assume importance as smaller geographic scales are encompassed. Tonn *et al.* (1990) and Heino (2011) provide generalized models of aquatic diversity across various scales. Specific patterns of diversity appear to be related to the following factors: area, spatial criteria and geomorphology (e.g. latitude and altitude), climate, surficial geology of adjacent landscapes (e.g. bedrock vs. tundra and associated nutrient and sediment loadings in fresh waters), nature, complexity and size of the water body which includes depth for lakes and order for rivers, proximity to the marine environment (thus the addition of diadromous species to local faunas and/or additional routes for re-colonization) and diversity and stability of habitats within large bodies of water (Tonn *et al.* 1990, Schlosser 1995, Oswood *et al.* 2000, Griffiths 2006, 2010, Leveque *et al.* 2008, Heino 2011, Oberdoff *et al.* 2011). Generally, greater diversity is correlated with the size of water body globally for freshwater fishes, with larger rivers generally showing higher diversity than smaller rivers (Darlington 1957).

**Overall Palearctic and Nearctic species richness**

Using the classical delineation of the Palearctic and Nearctic realms (Darlington 1957), the associations of the 127 species are as follows. Thirty-two species representing 12 families are present in both realms. The Palearctic exhibits greater species richness than does the Nearctic (88 vs. 68). In terms of species unique to each realm, greater richness is also found in the Palearctic than the Nearctic (56 vs. 36). Two (loaches and river loaches) of the 18 families overall only occur in the Palearctic and two (trout-perches Percopsidae and mooneyes) are unique to the Nearctic. Within most other families there is typically a slight bias towards greater species richness in the Palearctic. One exception to this occurs: salmonids, which are heavily biased towards the Palearctic – of a total of 50 species, 42 occur in the Palearctic and 25 in the Nearctic; 25 and eight of these are unique to the respective realms, and 17 are common to both. The Palearctic occurrence of the shared species is on the extreme eastern margin and reflects Beringian historical associations (see Appendix 6.1.2).

**Regional differences in the Arctic**

To facilitate comparison, the Arctic and sub-Arctic were divided into seven regions on the basis of historical geomorphic processes (i.e. unglaciated areas that shared faunal similarities), current barriers to dispersal and geographic size (Fig. 6.1, Appendix 6.1.3).

Beringia and adjacent areas of northwestern Canada exhibit the greatest species richness (15 families, 62 species) and by far the highest level of endemism (Tab. 6.2). Russia, Scandinavia and western Siberia exhibit the next highest levels of species richness (13 families, 47 species; 12 families, 45 species, respectively) and endemism (10 and three species, respectively), followed closely by eastern Siberia (13, 49 and 3). Central Siberia and eastern North America exhibit similar but lower levels of species richness (12 families each; 39 and 38 species, respectively; one endemic each; Tab. 6.2). The North Atlantic region exhibits the lowest level of species richness (six families, 13 species and no endemics).

These patterns are likely the result of several factors:

- Patterns of glaciation vary widely (e.g. no/little Pleistocene glaciations in much of Siberia, Chukotka and Alaska; Flint 1971, Grosswald 1980, Andersen 1981, Pielou 1991, Dyke *et al.* 2003).
- Time horizons since deglaciation similarly are highly variable (e.g. deglaciation in Canada progressed northeastwards). Thus northwestern Canada has been available for fish colonization approximately

**Table 6.2.** Diversity of freshwater and diadromous fishes by regions of the Arctic and sub-Arctic.

| | Beringia and northwestern Canada | Northeastern North America | North Atlantic | Russia and Scandinavia | Western Siberia | Central Siberia | Eastern Siberia |
|---|---|---|---|---|---|---|---|
| Number of families present | 15 | 12 | 6 | 13 | 12 | 12 | 13 |
| Number of species present | 62 | 38 | 13 | 47 | 45 | 39 | 49 |
| Number/% of Arctic endemics | 10/16.1 | 1/2.6 | 0 | 5/10.6 | 4/8.9 | 1/2.6 | 3/6.1 |

twice as long as has extreme northeastern Canada (i.e. 12,000 vs. 6,000 years) although deglaciation is still ongoing in the latter area.

- Multiple refugia combined with multiple re-colonization pathways (e.g. both marine and several freshwater pathways in some cases) result in increased diversity at present in a region. Diversity in an area is also related to the proximity of refugia, barriers present within pathways and other complexities (e.g. major drainage reversals during deglaciation such as the Peel River area of the Mackenzie River basin in Canada; Lindsey & McPhail 1986). Polar orientation (north-south) of many of the large freshwater drainages has also influenced colonization ease of the North in the past and likely will continue to do so under current climate warming. Additionally, size and habitat diversity within refugial areas also has likely had an influence.
- Distance from refugia combined with intervening barriers (e.g. marine inundations) has also influenced present-day regional diversity. Thus, areas of the North Atlantic described here have been colonized wholly by anadromous species (e.g. Greenland, n = 7; Iceland, n = 13) given that the last land connections among these areas was in Eocene times (~ 40 million years ago; McKenna 1975).
- Climatic parameters, especially thermal regimes and associated productivities, have restricted colonizations of northern locales by many fishes. This is best observed as latitudinal gradients in diversity discussed below.

### Broad-scale latitudinal and longitudinal patterns

Specific studies of fish diversity associated with latitude and longitude are generally lacking, particularly for high northern latitudes. Continental-scale patterns for North America indicate total species richness declines to the north and west (McAllister *et al.* 1986, Griffiths 2010). Compositional similarity across geographic distance changed more slowly for northern areas than for southern areas (Griffiths 2010), indicating greater homogeneity over larger distances in the North. Northerly declines in species richness were more rapid for resident than for migratory species (Griffiths 2010), likely a reflection of both potamodromy (migrations within freshwater) and anadromy, the occurrences of which appear to increase in the North. Diversity in northeastern Arctic North America declines quickly as latitude increases and/or key zoogeographic barriers (e.g. marine straits) are passed. These patterns reflect the effects of glaciations which covered most of Arctic North America, the nature, number and temporal sequence of post-glacial re-colonization routes open to fishes, as well as the time since deglaciation (Crossman & McAllister 1986, Lindsey & McPhail 1986, McAllister *et al.* 1986, Power 2002). Habitat diversity also appears to be a factor in determining present species diversity in particular areas (see below).

In Europe, a similar pattern emerges with species richness declining to the north and westwards from the 'Ponto-Caspian' area, which appears to be the primary refugial source (Griffiths 2006). Multiple routes were available for re-colonizations of northern areas here also. Life history patterns of fishes appear to affect geographical variation with diadromous species exhibiting no trends with latitude, whereas in fresh water, taxa (potadromous and resident fishes) diversity declines towards the north (Griffiths 2006). Note that similar species richness across wide areas (e.g. for diadromous species) does not mean that the complements of species present are similar; simply that the numbers remain similar. European sub-Arctic and Arctic areas are dominated by an Atlantic fauna with overall richness of about 25 or fewer species and with diadromous taxa comprising the majority (Griffiths 2006).

Most regional analyses of Siberian fishes do not differentiate among sub-areas over this vast region nor specifically focus upon the Arctic (e.g. Popov 2009). For all of Siberia including headwater reaches of the large basins and the Baikal area, 96 species and subspecies are present. Eighty of these are native to the area, and 16 are categorized as non-native (i.e. resulting from anthropogenic actions). These represent explicit underestimates – e.g. Arctic char *Salvelinus alpinus* was chosen to represent all char forms found in the area, many of which are likely valid endemic species (and considered as such herein). Excluding endemics to Lake Baikal drainages, the next most speciose group is the cyprinids (carps and minnows). Thus, overall patterns in Siberia are similar to those noted for the Arctic overall and for other regions within the Arctic. Native species are almost equally distributed among the large rivers albeit with a slight decline to the east (i.e. Ob = 37, Yenesei = 38, Lena = 34 and Kolyma = 28 species; Popov 2009). Inclusion of taxa not recognized by Popov (2009) would increase the counts particularly in the western rivers. Western basins also have the greatest influence of anthropogenic introductions (i.e. 15 in the Ob, eight in the Yenesei and none in the Lena or Kolyma; Tab. 6.3).

As noted above, regionally specific high-latitude studies are generally lacking. However, examination of this for the Canadian Arctic reveals that diversity declines from south to north but this depends upon connectivities of freshwater habitats – i.e. 41 species declining to

**Table 6.3.** Numbers of fish species and subspecies reported for Siberian river basins in 1949 and 2009, respectively, including the number of invasive species. Summary of data presented in Popov (2009) that shows both an increase in diversity related to increased scientific study and anthropogenic impacts in the region and a loss of species (Lena) related to probable anthropogenic impacts.

| River basin | Reported in 1949 | Reported in 2009 | Number of invasive species |
|---|---|---|---|
| Ob | 36 | 52 | 15 |
| Yenisei | 39 | 46 | 8 |
| Lena | 35 | 34 | 0 |
| Kolyma | 27 | 28 | 0 |

31 within the continental mainland in the Mackenzie River basin, 16 to four in eastern Nunavut and Quebec (J.D. Reist unpubl.). A further discontinuity is present in the Canadian Arctic Archipelago at ~ 75° N with only one freshwater/diadromous species occurring north of the marine straits in this area. Regional differences between the western and eastern Canadian Arctic areas are also apparent both overall and within families (e.g. 61 vs. 16 species in the west and east, respectively; J.D. Reist unpubl.). No one species occurs throughout the areas, either latitudinally or longitudinally; rather, compositional changes accompany declines in diversity over space. Moreover, at least for the period from 1973 to 2003 and also likely to today, no substantive shifts in overall diversity occurred – rather, the changes from 56 species overall to 61 primarily reflect nomenclatural and/or taxonomic changes and/or introductions. Of three 'new' taxa, two represent uncertain distributional records for southern taxa that require confirmation, and only one represents a new 'natural' occurrence in the area. Similar to the Arctic overall, this regional fauna is dominated by a few families – trouts and salmons, carps and minnows, and sculpins (23 to three species present).

#### Altitude and faunal diversity

Generally, lower diversity is present within drainage basins at higher altitudes (Hammar 1998). This is likely the result of several interacting factors including river order (and size) given that smaller rivers have fewer taxa, presence of barriers (e.g. waterfalls, high-velocity reaches) and historical colonization routes to higher elevations. These are all combined with environmentally rigorous conditions (i.e. colder, lower productivity waters in higher elevations). Few studies exist within the Arctic; however, the following examples illustrate some common features.

In the Ural Mountains, waters draining to Baidaratskaya Bay on the Arctic coast contain 35 freshwater and diadromous fishes overall (Bogdanov & Mel'nichenko 2010). Mountain reaches (1000-1300+ m) contain nine species, foothill areas 17, and 30 are present in tundra plain areas only a few meters above sea level. Coastal areas with direct marine influence house the additional five species. Both lacustrine and riverine environments exhibit parallel diversity shifts, with some populations in higher elevations being isolated (and representing distinct forms). Within this area, species richness is a useful predictor for categorizing lake types thus reflecting habitat qualities relevant to species preferences. Similar circumstances pertain in other areas.

#### Fish diversity with major habitat types

For lentic (standing water) environments, fish diversity decreases with both altitude and depth, thus despite being overall very speciose, deep-water areas of large southern (non-Arctic) lakes in Europe typically have Arctic char as the only or one of a few profundal fish species; similarly lakes at high altitudes at similar latitudes also often have Arctic char as the only fish species. Where comparable conditions exist in the Arctic, similar parallels are present, although the particular species complement may shift (Hammar 1989). These situations exactly parallel the trend in overall latitudinal diversity with Arctic char being the most northerly distributed and only fish species present in fresh waters along the northern edges of Arctic land masses (i.e. the high Arctic; see Fig. 6.1). These observations reinforce the perspective that Arctic char is likely a generalist taxon highly adapted to cold oligotrophic environments and capable of colonizing and persisting in marginal environments (Power 2002, Reist *et al.* 2013; see Section 6.2.4).

#### Regional patterns of distributions of species within families

Species distributions for speciose families generally parallel those noted overall for the families. That is, for salmonids, 28 species are present in Beringian/northwestern Canadian waters compared with 18-24 in Siberian areas and 17 in Russia/Scandinavia. Northeastern North America and the Atlantic regions exhibit the lowest salmonid diversity (10 and 7, respectively). Some families are only represented by species specific to particular regions – e.g. freshwater eels (Anguillidae) in areas bordering the Atlantic only, mooneyes in northwestern North America only, suckers in eastern Siberia, Beringia and North America only, loaches and river loaches in Russia and Siberia only, mudminnows (Umbridae) in Beringia only and trout-perches in Beringia and North America only. This likely represents a combination of historical factors and taxonomic (and/or diversification) patterns. Other species are much more widely distributed, approaching the entire area (see below). Total distribution is independent of species diversity within families. That is, several families represented by only one or two species in the Arctic are widely distributed (e.g. northern pike *Esox lucius* and burbot *Lota lota*, Gadidae).

#### Patterns of diversity below species level (habitat associations)

As noted, considerable diversity is present in Arctic fishes below the species level (e.g. formal subspecies, life history variants and ecologically differentiated forms). Much of this diversity appears to be related to both the size and complexity of the systems (and thus presumably the associated habitat diversity). Thus, within complex aquatic systems (e.g. large rivers) some species exhibit substantive diversity. Broad whitefish *Coregonus nasus*, a significant Arctic endemic distributed from extreme eastern coastal Russia throughout Siberia, Beringia and the North American Arctic eastwards to around the Boothia Peninsula, has been documented as exhibiting three major life-history variants: a typical anadromous (or semi-anadromous) type, a form associated primarily with lakes and a form associated with rivers (Berg 1962, Reist & Chang-Kue 1997, Harris & Taylor 2010). At least in North America (Mackenzie River basin) this differentiation appears to be recent in origin (i.e. postglacial) and directionally developed (i.e. from the presumptive anadromous initial colonizer to local non-anadromous variants; Harris *et al.* 2012). Similar variation likely exists to varying degrees in other Arctic fishes. An additional note of significance is that other than exhibiting this type of variation, broad whitefish is notably invariant throughout its range unlike many closely related congenerics such as the Siberian/lake whitefish group (common whitefish *Coregonus lavaretus,* humpback whitefish *C. pidschian*, and lake whitefish *C. clupeaformis*). Thus, key aspects of diversity manifested at many levels appear to be common characteristics of northern fishes. Intriguingly, high variation appears to exist amongst taxa in the nature by which levels of diversity are exhibited. This topic is also relevant across higher taxonomic levels (i.e. among families) of Arctic fishes (see below).

Diversity at more local scales also exists for many species. This is indicative of adaptability to wide ranges of ecological conditions. For example, the northern form Dolly Varden *Salvelinus m. malma*, typically present in high-gradient rivers of the North American Arctic, exhibits seasonal anadromy as the typical mode of life history characteristic of large-bodied migrating males and females. A residual (non-migratory) resident life history type is also present comprised almost wholly of small males, which remain in rivers throughout life, mimic the coloration of pre-migratory juvenile fish and reproduce with anadromous pairs by 'sneaking' fertilizations. Additionally, in rivers where impassable barriers exist to migration, isolated populations (small size, both sexes) occur in mountain reaches above falls. Dolly Varden and its close relatives also exhibit additional local variants of uncertain status (e.g. Angayukaksurak char *S. anaktuvukensis* of northern Alaska, a variant form differentiated by atypical spawning time; together with putative lake-dwelling populations; DeCicco 1985, Ayers 2010). Similar variants across multiple levels of organization (i.e. distinct subspecies, life history variants) exist within the Dolly Varden complex of species in Chukotka, Kamchatka and drainages to the Sea of Okhotsk (Chereshnev 1983). In some cases, these are recognized at the species level (e.g. neiva *S. neiva*, Levanidov's char *S. levanidovi*), but much debate surrounds their validity as distinct species. Regardless, the presence of wide diversity can not be disputed. Genetic evidence indicates three lake-dwelling forms in Lake Kronotskoye (Kamchatka), where white char *S. albus*, *S. kronocius* and *S. schmidti*, are derivatives of Dolly Varden. Distinct habitat associations suggest species-level differentiation from Dolly Varden whereas the genetic evidence suggests otherwise. Regardless, all forms and Dolly Varden itself are widely differentiated from chars of the Arctic char group (i.e. Taranetz' char *S. taranetzi* from Chukotka and Arctic char). Reference to a taxonomic group as a complex thus reflects incomplete resolution, major disagreements amongst taxonomic experts and/or conflicting results regarding taxonomic delineations. Northern fish groups appear to be particularly prone to this (e.g. complexes present in salmonids, sticklebacks (Gasterosteidae) and lampreys; Vladykov & Kott 1979, Docker *et al*. 1999, Kristjansson *et al.* 2002, Reshetnikov 2002, Reist *et al.* 2013), however, some aspects of this likely also reflect ecological diversification.

In northern lotic systems, Arctic char also exhibits ecologically associated diversity typically referred to as ecophenotypic diversity (Power *et al.* 2008, Reist *et al.* 2013). This diversity appears to be a complex outcome of local habitat diversity, un-filled niches (i.e. low interspecific diversity) and some form of sympatric differentiation (Reist *et al.* 2013). Life history variation and multiple colonizations by allopatrically derived forms may or may not be implicated as well (Alekseyev *et al.* 2009). Regardless, the result is high adaptability (as reflected by high local diversity) in some situations with two to four forms being documented (e.g. Thingvallavatn, Iceland; Snorrason *et al.* 1994). Although the greatest range of this type of diversity is perhaps exhibited by Arctic char, other northern taxa exhibit similar ecophenotypic diversity (e.g. sticklebacks, Kristjansson *et al.* 2002; lake trout *Salvelinus namaycush*, Blackie *et al.* 2003; ciscoes, Vecsei *et al.* 2012).

Based upon the various examples provided above, a wide range of patterns of diversity exist in many groups of freshwater and diadromous fishes throughout the Arctic. These appear to result from a complex intermixing of both contemporary (e.g. life history variation, ecophenotypic diversification) and historical (e.g. allopatric origin) factors. The consequence is relatively high levels of functional diversity present in northern freshwater ecosystems despite seemingly low levels of taxonomic diversity. Accounting for, and the conservation and management of, this diversity represents a widespread challenge throughout the Arctic.

A further complicating aspect is that of hybridization and introgression. This likely occurs among lineages at many of the levels of diversity noted above, although it is poorly understood or documented below that of distinct species. Consequences of this include blurring of lineage boundaries and blending (extinction?) of lineages, taxonomic uncertainty, genomic exchange and replacement, and practical difficulties differentiating taxa, linking them to habitats and establishing conservation goals.

### 6.2.4. Zoogeography of particular taxa

Of the 17 families of fishes found in this area, only members of the Salmonidae are distributed throughout the entire area considered here as Arctic and sub-Arctic. This is likely due to the high numbers of species in this taxon present in the area, the northern nature of this family (Berra 2001) and the extreme adaptability and generalist strategies of some species (e.g. Arctic char), which allow colonization and persistence in marginal northern environments (Power 2002). An additional factor contributing to high salmonid diversity, both generally and in the Arctic, is a genome duplication event between 25 and 100 million years ago (Koop & Davidson 2008). That is, salmonids are tetraploid[1] organisms exhibiting great molecular and accompanying physiologi-

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[1] An individual or cell having four sets of chromosomes.

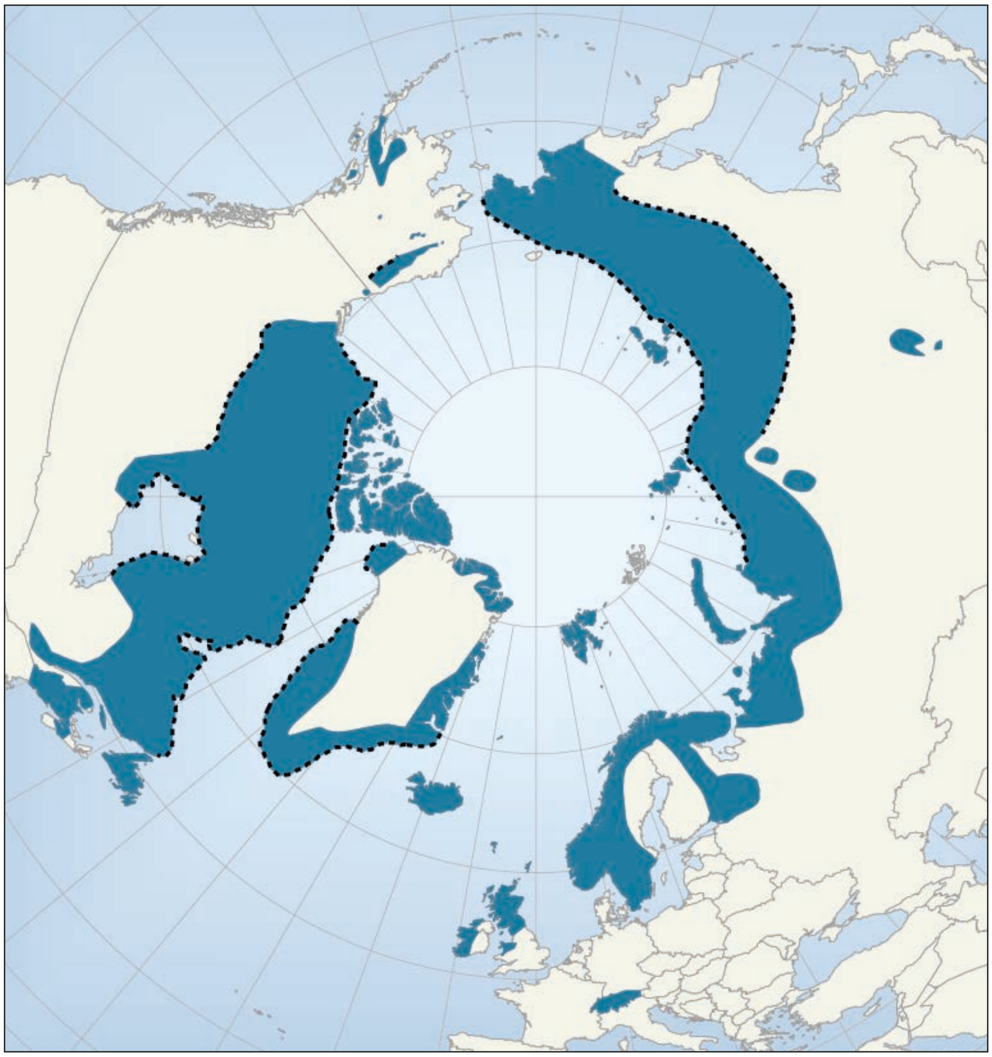

**Figure 6.3.** General distribution of Arctic char. Dotted lines indicate uncertain limits of distribution.

cal diversity. The implications of this with respect to morphological variability and environmental adaptability are poorly investigated and understood, but presumably mutations are enhanced at genetic loci for which selection is relaxed, and diversity and adaptability may thus be increased. Newly available genomic methods may aid in resolving our understanding of the implications of this for salmonid adaptability and for the relationships among genetic, ecological and taxonomic diversity.

Other families widely distributed in the area include speciose ones (carps and minnows, lampreys, sculpins, perches) as well as those of lower taxonomic diversity, but whose individual species are widely distributed (i.e. sticklebacks, suckers, pikes, cods; see Section 6.2.7). No one species of freshwater/diadromous fish occurs throughout the entire area of consideration here (whether delineated narrowly as Arctic, or including the sub-Arctic). Several species, however, are distributed over almost the entire area such as the Arctic char species complex (including Dolly Varden and closely allied Siberian chars) and also Arctic char in a narrower taxonomic sense (Fig. 6.3). The latter taxon is especially important as the only fish present in fresh waters of the extreme high Arctic (see Section 6.2.3.2).

### 6.2.5. Other diversity issues in northern fishes

Diversity in northern freshwater and diadromous fishes has significant species-level components. Embedded within this are the unresolved species complexes noted above. These complexes include most major groups: trouts and salmons – Arctic char complexes at two levels (see Reist *et al.* 2013), whitefishes and ciscoes; lampreys – life history as well as taxonomic complexes; sticklebacks – threespine stickleback complexes. Within this context some additional diversity issues are apparent. These include:

- Why are some species taxonomically conservative (e.g. northern pike, burbot), whereas others (e.g. many salmonids) are highly diverse at many levels?
- Within some groups, why are some lineages highly conservative (e.g. broad whitefish), whereas others (e.g. lake-Alaskan-Siberian whitefishes) are highly diverse both within and among nominal taxa?
- Ecological and morphological variants, particularly chars in lakes (i.e. Arctic char and lake trout) are widespread – are there a few dominant underlying explanations that account for most, or is each situation unique thus worthy of high conservation effort?

What is the functional and phylogenetic significance of this variation?
- Significant philosophical differences underlie species definitions as applied to northern fishes; these are exacerbated by disparities among approaches using different lines of evidence (i.e. classical taxonomic, genetic, functional ecological) – how should these be reconciled so as to yield a stable approach to enumerating and monitoring diversity in northern fishes?

Although extremely complex and difficult to resolve, addressing these questions is of paramount importance in order to adequately understand diversity in these fishes. Failure to address these questions undermines our ability to effectively enumerate this biodiversity and thus to detect change in it.

## 6.2.6. Areas of high diversity, endemism or other significance

### 6.2.6.1. Hotspots

Comprehensive studies documenting high diversity associated with particular areas (e.g. so-called 'hotspots') of Arctic freshwater and diadromous fish species are lacking. Similarly, limited knowledge is available regarding local endemism, and that which is available tends to focus upon groups of importance to humans (e.g. salmonids). General examination of the knowledge base suggests two conclusions.

1. Areas that were not glaciated during the Pleistocene (e.g. Beringia, much of Siberia) generally exhibit higher diversity and local endemism. Often this diversity is manifested as subspecific forms that are widely divergent from basal lineages, with the forms being present only in limited areas. Poor zoogeographic knowledge and limited surveys again tend to prevent generalizations.

2. Ecotones or other zones where both habitat diversity and local species diversity is usually higher tend to harbor greater fish diversity. Of particular note in this context are the deltas and lower reaches of the large Arctic rivers (Ob, Yenesei, Khatanga, Mackenzie, Yukon), which are characterized by mixtures of southern freshwater taxa and northern anadromous species; endemic diversity may be superimposed on this in some systems. Combined effects of northward displacement of temperate taxa along water courses, complex post-glacial histories, mixes of suitable habitat and availability to anadromous taxa all contribute to this enhanced local diversity.

### 6.2.6.2. Endemism

Best estimates suggest that only about 18 (~ 14%) of the 127 freshwater and anadromous species are endemic (i.e. occur only in the Arctic and sub-Arctic; Tab. 6.1). These include one blackfish *Dallia* and 17 salmonids. Endemism generally is higher in parts of Siberia and Chukotka driven substantively by groups such as salmonids (i.e. both freshwater whitefish and *Salvelinus*), which are highly variable. Local endemics, particularly in Arctic Siberia, often occupy a very narrow distribution occurring in only one or two lakes or river systems (e.g. see Reshetnikov 2002) with the Taimyr area being particularly prominent. Low overall endemism is likely due both to widespread geological upheaval of much of the area during Pleistocene glaciations and the broad ecological associations of many Arctic taxa (i.e. most Arctic fishes tend to be 'generalists'). Additionally, Arctic endemism is difficult to define given that high altitude lakes and abyssal areas of deep southern lakes mimic Arctic freshwater habitats (i.e. cold, low productivities; Hammar 1989) and often harbor local populations of northern fishes. Thus, relict populations of fish species typically thought of as 'Arctic', such as Arctic char, also occur well outside the geographic area considered here (Fig. 6.3). As noted elsewhere, resolution of taxonomic issues including the elevation to species rank of taxa considered here to be below that level all affect estimates of endemism. Limited survey information for many areas further hampers estimates.

Endemics can also be defined regionally (i.e. endemism is a conditional parameter defined in terms of the region delimited). Thus, for the regions delimited here, Beringia and northwestern Canada exhibit the highest level of endemism (i.e. 10 of 88 species; 16.1%; Tab. 6.2, Appendix 6.1.3). Other regions exhibit much lower levels of endemism (0-10.6% of local fish faunas specific to that region). Only the Beringian area, however, exhibits its high levels of true local endemism. Most endemism implied for other regions is the result of more widely distributed southerly species at the northern extent of their ranges.

As noted previously, endemism at least at a species level is also contingent upon the taxonomy one uses. Accordingly, given the conservative taxonomy followed here these levels of endemism are under-estimates of the actual levels. Many variant forms within some taxa (e.g. chars, whitefishes, ciscoes, lampreys, sticklebacks) would be endemic under a less conservative taxonomy. In addition to Chukotka, another area of high apparent endemism is the Taimyr Peninsula of central N Siberia (Pavlov *et al.* 1999). Moreover, endemism as an endpoint associated with diversity is also linked to the diversification processes occurring in an area and the length of time over which those processes have occurred unimpeded by geomorphic events (see Section 6.2.6.3).

As noted above, there are approximately 18 wholly Arctic and sub-Arctic endemic species according to the taxonomy and geographical delineation of the Arctic and sub-Arctic used herein. The vast majority are salmonids (17) and particularly chars (12) or freshwater whitefish (4). Species include: Alaskan blackfish *Dallia pectoralis*, Bering cisco *Coregonus laurettae*, humpback whitefish, tugun *Coregonus tugun*, Arctic cisco *Coregonus autumnalis* (nearly so if Irish pollan excluded), Chukot char *Salvelinus andriashevi*, Boganid char *S. boganidae*, Czerskii's char *S. czerskii*, smallmouth char *S. elgyticus*, Drjagin's char *S. drjagini*, Yakutian char *S. jacuticus*, murta *S. murta*, Taimyr Lake char *S. taimyricus*, Taranetz' char, Thingvallensis char *S. thingvallensis*, Esei Lake char *S. tolmachoffi*, longfin char *Salvethymus svetovidovi* and East Siberian grayling *Thymallus pallasii* (McPhail & Lindsey 1970, Scott & Crossman 1973, Chereshnev 1992, 1996, Mecklenberg *et al.* 2002, Reshetnikov 2002, Chernova 2011). Again, these are under-estimates given that some taxa are unresolved complexes likely consisting of many distinct species (e.g. sticklebacks). The distributional ranges of other taxa not listed here as endemic but which are generally considered to be northern or Arctic species (e.g. Arctic char) extend south, outside the Arctic, as well. Often this is in habitats that have characteristics reminiscent of the Arctic (e.g. oligotrophic, cold-water habitats such as high altitude lakes in Europe). In such situations, Arctic char can be considered as a relict species. Similar relicts often occur in profundal habitats of deep lakes.

Local endemism, rarity and regional endemism all contribute to vulnerability of taxa to adverse circumstances (e.g. stochastic environmental events, anthropogenic stressors). Vulnerability is heightened by low population sizes, which often are characteristic of local endemics, especially if they occur only in a limited number of freshwater localities. Accordingly, Chereshnev (1992) argued that many of the regional endemics present in northeastern Asian waters deserved heightened levels of local, regional, national and international protection. The present status, levels of protection and circumstances for many of these are poorly known.

### 6.2.6.3. Significant areas

In the context of both hotspots and endemism, several locations deserve mention. Lake El'gygytgyn is an ancient meteorite crater lake (3.6 million years old) situated in the low Arctic in central Chukotka. Five fish species occur in the lake, three of which are chars – longfin char, smallmouth char and Boganid char (Chereshnev & Skopets 1990, 1999, Skopets & Chereshnev 1991). Other species include Arctic grayling *Thymallus arcticus* and slimy sculpin *Cottus cognatus*. The first two chars are endemic to this lake and represent well-differentiated taxa, with the longfin char being so distinct that it constitutes a distinct genus. Both forms appear to have evolved in the lake, which has not been glaciated since its origin. The Boganid char is found elsewhere only in Taimyr lakes suggesting these may be remnants of a much more widely distributed taxon.

El'gygytgyn represents the endpoint of a long period of isolated evolutionary history relatively undisturbed by Pleistocene events. Accordingly, divergence to generic and species levels has occurred in two taxa, along with colonization by a well-differentiated third char taxon. Other Arctic lakes represent the other extreme, that is, short existence combined with subspecific divergence. Thus, although poorly studied, Pingualuk Lake in northern Quebec (a meteorite impact crater lake formed about 1.4 million years ago but deglaciated about 6,000 thousand years ago) appears to have only a single form of Arctic char present (Gantner *et al.* 2012). Between these two extremes, several examples of differentiation are known. Lake Hazen (northern Ellesmere Island, Canada), again only recently deglaciated, supports three ecophenotypes of Arctic char (pelagic, limnetic, profundal; Reist *et al.* 1995, 2013, W. Michaud & J.D. Reist unpubl.). Thingvallavatn in sub-Arctic southern Iceland supports four ecophenotypes (pelagic planktivorous and pelagic piscivorous forms are likely size morphs of a reproductive population and benthic large and benthic small types differentiated from each other and the pelagic forms; Sandlund *et al.* 1992, Skúlason *et al.* 1999). Taxonomic splitters claim these are three taxa distinct at the species level (Kottelat & Freyhof 2007). Fjellfrosvatn in sub-Arctic northern Norway has two distinct morphs (littoral, profundal) present (Knudsen *et al.* 2006).

In-situ sympatric speciation is strongly suspected as underlying these latter examples of differentiation, all of which are under 10,000 years old. Accordingly, early and rapid differentiation driven by niche expansion (Knudsen *et al.* 2006) of chars when colonizing post-glacial environments seems the norm. In the absence of subsequent widespread disruption, incipient species apparently can complete their differentiation to become distinct species or even genera given sufficient time. This aspect of diversity and the processes that drive it appear to be key attributes of Arctic freshwater systems, thus of conservation importance. It is very likely that many additional examples of differentiation exist throughout the Arctic in salmonids and other families of freshwater fishes exhibiting high diversity; these are likely especially pertinent in unglaciated areas of the Arctic. As noted above, from the perspective of enumerating the diversity the issue is 'when is differentiation of freshwater fish lineages sufficient to warrant taxonomic recognition as species'. This is a fundamental problem for which no adequate resolution has been forthcoming, and the range of char situations above exemplifies the problem.

Ecological (primarily climatological and productivity constraints) and historical (e.g. Pleistocene glaciations, colonization routes and time since deglaciation) factors result in many southern taxa being present in the southern margins of the sub-Arctic. These peripherally distributed taxa are rare (i.e. occur as numerically small populations) in the sub-Arctic but not so elsewhere. Many of the local endemics noted above are also likely rare. Similarly, a unique ecophenotype or taxon that occurs only in a single location can be considered rare, although limited information regarding absolute or limited abundance generally precludes delineation of rare taxa.

Local endemics with limited distributions are likely to be naturally rare, especially if they are habitat specialists. Chereshnev (1996), who considered the majority of species recognized here, indicated 14 were rare in the Arctic (~ 11% of our total of 127); additional taxa not recognized here would be rare if included (e.g. local blackfish taxa – *Dallia admirabilis* and *D. delicatissima*). Families with rare representatives included: lampreys (3 species), sturgeons (Acipenseridae 2), herrings (Clupeidae 1), carps and minnows (1), trouts and salmons (5), cods (1) and sculpins (1). Conversely, using exploitation as a proxy of inherent abundance, 73 (57% of 127) species are fished and therefore very likely not rare. Approximate numbers of species fished by family are: lampreys (1), sturgeons (3), freshwater eels (2), smelts (3), mooneyes (1), carps and minnows (9), suckers (2), pikes (1), trouts and salmons (42), cods (1), sticklebacks (2) and perches (6) (Chereshnev 1996).

### 6.2.7. Taxonomic diversity within families

As noted above, 127 species of diadromous and freshwater fishes are distributed among about 18 families with most of this diversity (n = 98 species) being accounted in five families (trouts and salmons: 50 species; carps and minnows: 25; sculpins: 9, perches: 8; lampreys: 6). These especially diverse families and a few others of relevance (suckers, pikes, cods) are particularly important in the Arctic. Short synopses follow; general references to support this material include: McPhail & Lindsey (1970), Scott & Crossman (1973), Coad *et al.* (1988), Berra (2001) and Kottelat & Freyhof (2007).

Trouts and salmons (11 genera, 66 species conservatively globally): The Salmonidae is the most significant northern fish family and geographically is distributed throughout the entire area considered here (10 genera and 50 species). Collectively, salmonids occupy virtually all fish-bearing fresh waters of the sub-Arctic and Arctic from the deepest lakes (e.g. pygmy whitefish *Prosopium coulteri*) to the northernmost extent of land (e.g. Arctic char; Fig. 6.3). Anadromous species occupy coastal and offshore marine surface waters also. Multiple ecological forms that function as species and multiple life history types add to this diversity. Moreover, due to limited taxonomic surveys over wide areas of the Arctic, it is very likely that additional diversity is present but is currently inadequately documented.

Major widespread lineages (recognized mostly as genera) are chars (*Salvelinus* – 18 species), whitefishes and ciscoes (*Coregonus* – 13, *Prosopium* – 3, *Stenodus* – 1) and graylings (*Thymallus* – 3). Regionally, additional lineages include Atlantic salmons (*Salmo* – 3), Pacific salmons (*Oncorhynchus* – 6), taimen (*Hucho* – 1), longfin char (*Salvethymus* – 1) and lenok (*Brachymystax* – 1). The genus *Coregonus* is recognized as a polyphyletic taxon consisting of several lineages (i.e. whitefishes, Old-world ciscoes, New-world ciscoes), thus levels of difference within taxa are greater than implied by nomenclature.

The majority of salmonids are migratory within fresh water (potadromy) or to and from the sea (anadromy), thus all life stages figure prominently in ecosystem structure and function and in linkages among ecosystems. High local abundances and large migratory runs of salmonids form the basis of Arctic fisheries in coastal marine and freshwater areas. Additional importance of salmonids with respect to scientific principles of evolution and diversification results from their high diversity, adaptability and apparently rapid evolution in and occupancy of marginal aquatic environments in extreme locations. Some species grow to a large size (~ 200 cm in taimen *Hucho taimen*) and are long-lived (e.g. >45 years in Arctic char and lake trout).

Carps and minnows (210 genera, > 2,000 species globally): 25 species are found in sub-Arctic and Arctic waters, all of which are obligate residents of fresh waters. Individual species typically have narrow tolerances for environmental conditions and in our region of interest are mostly sub-Arctic, although several penetrate into the Arctic along large northward-draining rivers. The significance of the remaining species is their potential for northward colonizations as the climate warms. Most cyprinids (carps and minnows), especially small-bodied species, are essential components of lotic and lentic ecosystems as primary (algae) and secondary (benthos, zooplankton) consumers and as primary detritus feeders. In turn, cyprinids are prey for larger fishes such as northern pike and salmonids. Larger species, particularly carps, are commonly fished, although smaller species may also be locally fished for use as bait.

Lampreys (8 genera, 34 species globally): Six species are found in sub-Arctic and Arctic waters, three are wholly freshwater and three anadromous in habit. Lampreys are primarily found in Beringian, Siberian and northern European Arctic waters. Some species are parasitic on other fishes as adults; ammocoetes (untransformed young) are benthic detritivores. Taxonomic issues are apparent, particularly the relationships of non-anadromous and anadromous congeners (i.e. distinct species or life history variants of the same taxon?). Usually lampreys are small and short-lived (< 30 cm, 7 years); they are not normally captured with typical fishing gear (unless attached to other fishes), thus are not often encountered. Lampreys are locally fished in Eurasian Arctic waters.

Sculpins (70 genera, 300 species globally): Nine species occur in sub-Arctic and Arctic fresh waters distributed throughout much of the Holarctic. All are small (< 25cm), generally short-lived (< 7 years) and prefer benthic habitats of both lakes and rivers. Diet is primarily benthic invertebrates and eggs of bottom-spawning fishes. Higher trophic-level predators such as burbot, northern pike and lake trout consume sculpins, thus they are pivotal in linking benthic and pelagic portions of aquatic ecosystems. Taxonomic issues are problematic in southern taxa but northern taxa appear to be mostly resolved.

Perches (10 genera, 195 species globally): Eight species occur mostly in southern portions of the sub-Arctic and Arctic fresh waters. They are generally tolerant of a wide range of conditions, and their northernmost extent is limited by thermal and productivity constraints. Paired counterparts of perches and walleye/pike-perch recognized as distinct species occur in North American and European waters. One species (ruffe *Gymnocephalus cernuus*) is widely distributed in Europe and Siberia. Fisheries occur for all the larger-bodied species. Zooplankton and other fishes form the diets of most, thus combined with habitat associations (perches are nearshore generally whereas walleyes and pike-perches are demersal in large rivers and lakes), these fishes are central components of aquatic ecosystems.

Suckers (13 genera, 72 species globally): Two species confirmed as present in the Arctic (longnose sucker *Catostomous catostomous*, white sucker *C. commersoni*) are distributed in mainland northeastern Siberia, Chukotka and northwestern North America. A third taxon (largescale sucker *C. macrocheilus*) requires confirmation of presence in the Arctic. No taxonomic complexities or significant sub-specific diversity are present. Suckers are benthic feeders preying upon detritus, aquatic insects, crustaceans and molluscs, thus, likely function in coupling benthic lower trophic levels of the ecosystem with higher predators (e.g. freshwater fishes and mammals, piscivorous birds). Suckers may reach 75 cm in length and live to age 25. They are often captured as a local food fish, thus are important in subsistence fisheries.

Pikes (1 genus, 5 species globally): The only Arctic representative, northern pike, is widely distributed in freshwaters of the mainland of the Holarctic including temperate areas. No taxonomic complexities exist, and sub-specific diversity appears to be limited. Commonly found in weedy slow areas of rivers and lake embayments, pike are voracious pelagic ambush predators at all sizes (to 130+ cm) and ages (to 26+ in the North). Thus, they are pivotal components of aquatic ecosystems. Pike are easily captured, thus supporting all types of fisheries where they occur.

Cods (Gadidae) (one genus and species, burbot, in freshwater; remainder marine, but a relict population of one marine species, Atlantic cod, occurs in eight fresh water lakes in northern Nunavut; McLaren 1967, Patriquin 1967, Hardie *et al.* 2006, 2008): Burbot is the only freshwater cod distributed throughout much of the mainland Holarctic. Similar to northern pike, neither taxonomic complexities nor substantive sub-specific diversity is present, but local habitat specialists appear to occur. Burbot are primarily benthic and epibenthic feeders upon any food types present including fishes. Burbot are thus a key component of freshwater ecosystems. As with most higher-trophic level predators which are large (i.e. 1.2 m, > 20 years of age), burbot are prominent in local freshwater fisheries wherever they occur.

Remaining families: The remaining 10 families (sturgeons, mooneyes, freshwater eels, herrings, loaches, river loaches, smelts, mudminnows, trout-perches and sticklebacks) have few representatives in the Arctic, occur only in the southern geographic margins of the area defined here, are small-bodied forage fish, or are otherwise less relevant to Arctic freshwater systems. However, this does not mean that they are locally unimportant, especially the large-bodied groups (sturgeons, goldeyes, eels).

## 6.2.8. Importance of biodiversity of Arctic freshwater and diadromous fish

### 6.2.8.1. Ecosystems

Generally, Arctic freshwater fishes are significant components of their ecosystems, exhibiting relatively high local diversity, and also often attaining substantive population abundances. Virtually all freshwater habitats present are used throughout the year; exceptions being seasonally ephemeral habitats to which no access is possible (e.g. tundra ponds < 2 m depths or those isolated over the landscape). Generally, the larger the water body (i.e. area of lakes or order of rivers) the greater the complement of freshwater fish species, however, this is mediated in many areas by Pleistocene glacial histories, thermal regimes and various landscape filters (Tonn *et al.* 1990). Thus, overall diversity decreases with latitude such that north of about 75° N latitude the only fish found in fresh waters is Arctic char. An additional factor is that of habitat complexity of the water body with more species (or ecological forms) being present in structurally more complex systems. Local ecological significance of many taxa occurs due to pivotal ecological roles in ecosystem structure and function (i.e. key forage or predatory species) associated with key types of habitats.

Ecosystem trophic structure, functional relationships that transfer nutrients among ecosystem components and different ecosystems, stability, resistance and resilience of Arctic freshwater and nearshore marine ecosystems are all enhanced by diversity within and among components (Hooper *et al.* 2005). In southern freshwater systems, individual fish species specialize with respect to different ecosystem functions. In relatively depauperate Arctic systems, it appears that the various sub-specific components and levels of diversity act as functional equivalents to species. Accordingly, life history variants, ecological morphs and other diversity below the species level are disproportionately important in northern ecosystems (Reist *et al.* 2013). Taxonomic, functional and ecological response afforded by this diversity enhances resistance (i.e. ability to withstand perturbation) and resilience (i.e. recovery rate and potential) (Hooper *et al.* 2005, Vallina & Le Quéré 2011). This is particularly relevant in situations of high rates and degrees of change such as now pertain to the Arctic. Management and conservation efforts thus require re-focusing to include the wide scope of sub-specific diversity present in Arctic freshwater and diadromous fishes as part of the overall whole of the managed aspects of biota. Initial efforts must also include increased documentation of the range and nature of the diversity present in an integrated fashion, particularly in poorly surveyed areas. Existing efforts to develop and implement 'ecosystem-based management' represent appropriate steps in this direction (Essington & Punt 2011, Berkes 2012), but better understanding of sub-specific diversity is required in support.

These fishes are also keystone components (Jordán 2009) of Arctic aquatic ecosystems. Life stages of most fish species undertake substantive movements among habitats during ontogeny; sub-adult and adult individuals also migrate among habitats seasonally both within fresh waters and between fresh and marine waters. Thus, fishes are responsible for both material and energy transfers among aquatic habitats. Transfer of marine-derived energy and nutrients is perhaps best known for semelparous (i.e. reproduce only once throughout life) Pacific salmons, which grow in marine systems but die upon reproducing in fresh waters (Naiman *et al*. 2002, Jonsson & Jonsson 2003, Petticrew *et al*. 2011). Iteroparous species (i.e. reproduce several times during life) such as chars, whitefishes and ciscoes also transport nutrients (e.g. as eggs) thus may substantively influence ultraoligotrophic northern freshwater systems. Sequestered long-lived contaminants may also be transported coincidentally. Many freshwater species are ecological specialists. For example, northern pike link terrestrial and aquatic ecosystems through shoreline occupancy and predation of organisms from both environments. Similarly, burbot, a benthic predator and scavenger, links benthic, limnetic and pelagic habitats within both lotic and lentic systems (Cott *et al*. 2011).

### 6.2.8.2. Relevance to humans

Despite their relatively low diversity, freshwater and diadromous Arctic fishes are extremely important as food to humans both within the Arctic and also outside it. Four themes are relevant in the human context: fisheries, cultural importance to indigenous peoples, aquaculture and aesthetics.

Three types of Arctic fisheries can be delineated: those for profit with product being sold (commercial), those for sport (recreational) and those conducted by indigenous peoples (variously food, subsistence or artisanal) (Clarke 1993, Reist & Treble 1998). Of these, subsistence fisheries are by far the most important because they contribute both food and cultural services for indigenous peoples. Management requirements to report catches vary widely across Arctic jurisdictions and generally are limited in nature, thus leading to false impressions that these fisheries are relatively insignificant (Zeller *et al.* 2011). Species harvested are typically large-bodied, locally abundant in space (e.g. migratory corridors) and time (i.e. seasonally concentrated) and accord with the diversity present in a particular area. Many species are long-lived, reproduce episodically and may have low survival of young, thus vulnerabilities to overfishing exist. Species from most families are harvested – exceptions are sticklebacks, sculpins, river loaches and trout-perches. Salmonids account for both the greatest diversity of fish species harvested and the largest overall harvests, figuring prominently in all types of fisheries and areas (Zeller *et al.* 2011). Arctic-wide statistical summaries are not available, but reconstructed estimates are (Zeller *et al.* 2011) and together with regional summaries will be used to illustrate key points.

Diadromous species (or life history types) generally support extensive commercial fisheries, and large local migratory stocks predictably returning from summer marine foraging support subsistence fisheries over large areas of the Arctic (see also Huntington, Chapter 18). Reconstructed catch estimates in FAO statistical area 18 (i.e. EEZ's of Canada, USA and the Russian Federation bordering the Arctic Ocean proper) revealed the following (Zeller *et al.* 2011):

- Virtually no harvesting of marine species occurred (i.e. marine fisheries are all in gateway areas of sub-Arctic seas); rather the focus of fisheries were species harvested in coastal or estuarine areas;
- Reconstructed catches for the 1950-2005 period in total were 950,000 tonnes (770,000 + 89,500 + 94,000 tonnes respectively for Russia, USA and Canada);
- Annual catches of 24,000 tonnes per year in the 1950s declined to 10,200 tonnes per year by the mid-2000s, likely reflecting underlying demographic (i.e. human emigrations in Siberia) and cultural (i.e. switch from dog teams to snow machines for personal transport) changes; and
- High regionality occurred in species harvested, however salmonids dominated in every sub-area with whitefishes, ciscoes, salmons and chars predominating (e.g. freshwater whitefish constituted 65% of the total catch for the 50+ year time period).

Species-specific migratory idiosyncrasies often result in these fisheries occurring well inland, where catches may be substantive (e.g. for broad whitefish in the Mackenzie River of Canada historically to 400 tonnes per year) and also may be a mixture of commercial and subsistence fisheries (Reist & Treble 1998). Substantive fisheries also target chars, particularly Arctic char wherever people encounter them both as anadromous migratory populations and those restricted to fresh waters (e.g. Born & Böcher 2001, Gudmundsson 2002). As noted previously, adults of many fish species exhibit both migratory and non-migratory co-occurring population components. The basis for this diversity is unknown but may be genetic, facultative (e.g. based upon growth rates) or some mixture of both. Fisheries as described here select for larger, faster growing and migratory individuals. This is likely a general aspect of all exploitation on these fishes, thus long-term alteration of local fish biodiversity may result (see below).

Inland fisheries on wholly freshwater species are also widespread throughout the Arctic (e.g. Bodaly *et al.* 1989), but disentangling those specific to Arctic waters is problematic, as overall statistics are typically examined on a country basis (e.g. Lehtonen *et al.* 2008), or their importance is de-emphasized in comparison with other fisheries (e.g. Andrews 1989). Regardless, inland fisheries are important components of the overall economy of the North.

Economic valuation, similar to quantification of fishery statistics, is problematic for Arctic resource use, but relative valuations are apparent. For example, in developing a fisheries strategy, the Government of Nunavut in Canada estimated the annual value of Arctic char to subsistence use at 4.4 million CAD, and that of commercial sales at 1.4 million CAD. Commercial quotas of 523 tonnes were set in 2005 for sea-run char and 160 tonnes for land-locked char. An additional 400 tonnes is harvested for domestic (subsistence) use. Relative valuations of char in various types of fisheries indicated that recreational fisheries yielded about 55 CAD per kg of harvested fish, subsistence food replacement value was about 11 CAD per kg, and commercial value was about 3.30 CAD per kg. Sport fisheries also relied upon very small numbers of harvested fish. Thus, from perspectives of overall conservation (limiting adverse selective effects on biodiversity) and economics, sport fisheries in the Arctic are a preferred strategy relative to commercial exploitation.

Benefits of fish biodiversity accrued to humans in the Arctic, particularly indigenous peoples, also include those associated with culture (e.g. shared experiences on the land, food sharing with elders; Kristofferson & Berkes 2005, Nuttall *et al.* 2005). Although difficult to value and to distinguish from similar benefits accrued from other biodiversity components and the overall Arctic environment contributing to cultural well-being, positive effects of freshwater and diadromous fisheries in a cultural context are estimated to be extremely high (see Huntington, Chapter 18).

Some species of Arctic freshwater and diadromous fishes are extensively cultured particularly in Norway (Arctic char and Atlantic salmon *Salmo salar*), Russia (northern whitefishes), Alaska (Pacific salmons) and to a lesser extent, Canada (Arctic char) (Johnston 2002, Vilhjálmsson *et al.* 2005, Paisley *et al.* 2010, FAO 2012). Operations occur in both fresh and coastal marine waters and involve hatchery supplementation of wild stocks as well as rearing of penned fishes to marketable sizes, though the activities that are allowed vary by jurisdiction. Aquacultural operations also often focus upon non-native species and/or lineages not natal to the area, thus accidental releases and establishment of populations in an area are a threat to local diversity. Reliance upon wild populations and their inherent diversity underscores the linkage of biodiversity in providing human benefits in the Arctic. Regardless, aspects of these activities represent threats to native Arctic biodiversity if not properly managed (see Section 6.2.9.2).

Although less well known than many Arctic iconic species, some Arctic fish species can be considered as Arctic icons. Arctic char in particular has high aesthetic value globally, and while direct appeal to southern tourists is low, its appeal to recreational fishers and as a northern delicacy is considerable. Arctic char also serves as a sentinel species useful in documenting and understanding changes in the Arctic system (e.g. Sawatzky & Reist 2008, 2009, Reist & Sawatzky 2010, Culp *et al.* 2011).

## 6.2.9. Drivers, stressors and threats to Arctic freshwater and diadromous fishes

### 6.2.9.1. Vulnerabilities of freshwater fishes in the Arctic

Freshwater fishes are often tightly associated with particular habitats both as species and during various life history stages. Thus, stressors that affect their habitats will inevitably affect the fishes. Lakes can be considered ‘islands’ of appropriate habitat within which effects may be focused; as such, lacustrine fishes may be unable to emigrate or move to avoid the effects of stressors. Rivers act differently in that they ‘export’ effects downstream, thus stressors that are spatially remote may affect Arctic fishes particularly in large northward flowing river basins. Moreover, many stressors typically cumulate over the course of the river, thus the total effects may be greater on fishes occurring in downstream areas. Given the number and size of northward flowing rivers in the Arctic and the significance of freshwater and diadromous species to both ecosystems and people in the area, cumulative impacts represent real and present threats to fishes (see also Wrona & Reist, Chapter 13). Moreover, impacts of cumulative stressors are exacerbated by the following: iteroparous[2] nature of life history of most of the very important fishes, greater ages/longevities (e.g. Spromberg & Birge 2009), differential habitat usages (typically seasonal) which may involve several different stressors (e.g. Reist & Bond 1988), and differential ecological roles (e.g. planktivores vs. piscivores) associated with multiple ecophenotypes within populations that may also act to cumulate some stressors (e.g. bioaccumulating contaminants; Kallenborn *et al.* 2011) and migratory aspects of life history.

Arctic freshwater fish species differ with respect to their sensitivities to perturbations, but many populations are adversely affected by anthropogenic activities. This is especially so with respect to local habitat disruption or disturbance. Hydrocarbon development activities including physical disturbances (e.g. seismic, construction and production activities; temporary or permanent blockages), direct habitat impacts (e.g. spills into fresh waters) or indirect habitat impacts (e.g. sediment, toxicant inputs) will all ultimately affect aquatic biota including fishes. Vulnerability to such effects depends upon species or life stage sensitivities, the nature, duration and severity of stressors (usually a function of proximity to sources), biomagnification factors (e.g. propagation of increasing effect through trophic processes) and barriers to (or the ease of) movements or emigrations coupled

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[2] An organism that produces offspring more than once during its lifetime.

with the ability of the fish to do so. An additional, often under-appreciated factor associated with hydrocarbon development on land results from the necessary construction of access corridors and roads. Thus, increased access to fresh waters afforded by seismic lines, road development and pipeline construction all may have their own direct consequences to freshwater fishes (e.g. dewatering of habitats for winter ice road construction) but may also result in additional stressors (e.g. exploitation, sediment loading from poor crossings) upon previously pristine populations.

Effects from hydrocarbon development as outlined above are, of course, integrated into the milieu of other stressors affecting northern freshwater ecosystems and fishes. These include effects from climate change (e.g. productivity shifts, habitat changes, effects of colonizing species; Wrona *et al*. 2005), contaminant loadings (e.g. metals, persistent organic pollutants, acidification; see Moles *et al*. 1979), exploitation and barriers to migration (e.g. dams, thermal effluents). Thus, potential effects of hydrocarbon development on Arctic freshwater fishes must be viewed in a context of cumulative effects scenarios resulting from multiple stressors additively and synergistically impacting the populations.

Within the above context, the following generalizations can be made with respect to vulnerabilities of Arctic freshwater fishes. Species which mature late, live longer, exhibit habitat specializations, have low survival of young (or produce fewer young) and migrate among wide ranging habitats will likely be more vulnerable to anthropogenic activities than species which exhibit the converse traits. Species that do not move widely during life may be vulnerable to local point source impacts. Conversely, migratory behavior results in increased probability of exposure to multiple stressors. Migratory behavior also typically results in fish being concentrated both spatially and temporally into a few key habitats. Such concentrations increase vulnerability to some anthropogenic impacts (e.g. exploitation, local industrial development).

Because fishes are central to the functioning of Arctic aquatic ecosystems and to the well-being of northern peoples, it is essential to ensure that a healthy diversity of fishes remains in these freshwater environments.

### 6.2.9.2. Stressors and threats

Anthropogenic stressors constitute threats to Arctic freshwater and diadromous fishes in four linked ways.

- Large-scale pervasive stressors delivered over wide areas to large degrees – e.g. climate change and pervasive persistent contaminants delivered atmospherically and/or via northward flowing water courses may affect fish biodiversity at many levels.
- Local-scale stressors scaled up through numerous delivery events – e.g. exploitation of many populations spatially, sequentially and/or temporally alters populations locally, and the collective effects can be substantive and integrated over space and time.
- Local-scale stressors delivering limited, mostly local effects – e.g. many industrialization activities (e.g. hydroelectric, oil and gas and mining developments; aquaculture and introductions), although mitigated locally, have many residual effects. Similarly, increase of human populations in the Arctic, whether ephemerally associated with industrial developments or more permanently through demographic processes or immigration will accompany and interact with both exploitation and developmental activities. In some areas, aquaculture – i.e. 'farmed' biota, introductions of species and/or artificial supplementation of natural populations (e.g. Pacific salmon in western Siberia; Gordeeva & Salmenkova 2011) – is a stressor. Non-native species, genotypes or forms typically have detrimental influences on native biodiversity.
- Cumulative stressors and concomitant effects from multiple exposures and/or multiple stressors – e.g. overall human development and population growth in the Arctic.

Of course, some stressors may affect targeted organisms through multiple pathways to also cumulate consequences.

A detailed analysis of these stressors and their threats/effects on Arctic fish biodiversity requires extensive study beyond the scope possible here. Thus, an overview of threats and possible effects on Arctic freshwater and diadromous fishes includes the following:

#### Climate change

Both direct (e.g. thermal and hydrological changes) and indirect (e.g. habitat changes, colonizing species) effects are highly likely to affect diversity of these fishes at many organizational levels. Differential effects on different diversity levels are likely (e.g. shift in balances of life history types), as is the scale and significance of this stressor. Over time, population extirpations and ultimately extinctions of vulnerable Arctic endemic fishes are possible. Overall local diversity, however, is likely to increase through northward range extensions of sub-Arctic taxa (i.e. natural colonizations and range extensions). Conversely, many aspects of sub-specific diversity associated with key northern fishes (e.g. Arctic char; Reist *et al.* 2013) are very likely to be adversely affected by all aspects of climate change. For chars, these may include population extirpation at southern margins of the range, switching from anadromy to resident life histories and loss of ecophenotypic forms (see Reist *et al.* 2013 and references therein).

One of the over-arching consequences of climate change upon Arctic freshwater ecosystems and by extension the fishes which occupy them will be increased heating, which, if accompanied by increased nutrient inputs, will likely result in overall increased productivity of all levels of the ecosystem (Reist *et al.* 2006a, 2006b, 2006c, Finstad & Hein 2012). This will be manifested as increased growth and perhaps population abundance of Arctic fishes, but how this will be explicitly observed for particular locations or for levels of diversity below that of species remains uncertain. Eutrophication in southern latitude lakes mimics these productivity effects of climate change, thus understanding of the effects of eutrophication on functional (and taxonomic) diversity offers insight to potential impacts in northern ecosystems. Vonlanthen *et al*. (2012) document the loss of ecological opportunity (which drives diversification within lakes) associated with eutrophication in Swiss high altitude lakes and in turn, associate that with patterns of lost diversity in freshwater whitefish forms unique to individual lakes. Accordingly, a likely direct but hidden effect of climate change on diversity of key northern fishes (e.g. salmonids) will be to truncate or reverse existing processes and products of diversification. This will be in addition to other effects, which may include altered patterns of life history, extirpation from particular areas, changes in geographical ranges and/or timing of habitat usages (phenological shifts). Eutrophication effects on fish biodiversity analogous to those examined here and documented for southern lakes serve as analogues of likely long-term shifts for Arctic fishes and ecosystems (Vonlanthen *et al.* 2012). Effects of this stressor on Arctic fishes, their ecosystems and fisheries are further documented in Wrona *et al.* (2005), Reist *et al.* (2006a, 2006b, 2006c), Furgal & Prowse (2008), Moss *et al.* (2009), AMAP (2011) and Wrona & Reist (Chapter 13).

Climate-change driven alteration of the cryosphere affects aquatic habitats through decreased durations and coverage of ice, altered break-up and ice formation regimes, altered water delivery (more snow fall, greater melting of glacial ice stores) and permafrost degradation with concomitant alteration of drainage patterns (AMAP 2011). Cryospheric change also alters contaminant storage, pathways and mobilization in biota (AMAP 2011). These indirect effects of climate change will have substantive ecological effects on aquatic ecosystems and their biota (Reist *et al.* 2006c). Many of these will also cumulate with other stressors to exert greater effects; some effects are likely to be positive with respect to population abundances and growth, persistence and thus overall diversity. Many, however, are likely to be negative. For example, although detailed documentation is sparse, the existing productivity differential (low in Arctic fresh waters, relatively high in adjacent marine waters) is believed to underlie the behavior of facultatively migratory species such as Arctic char. Increased freshwater productivity weakens this differential, thus may result in greater tendencies towards non-anadromy (Finstad & Hein 2012, Reist *et al*. 2013). Follow-on effects on fisheries may then ensue.

#### Contaminants

The Arctic is characterized by the long-range transport and deposition of many long-lived contaminants originating from southern areas (MacDonald *et al*. 2005, MacDonald 2006, Kallenborn *et al*. 2011). Persistence of these and their mobilization in ecosystems often leads to biomagnification (i.e. increase in relative concentrations in target tissues) at higher trophic levels in Arctic foodwebs. Accordingly, fishes such as chars that feed at higher trophic levels bioaccumulate these contaminants which may represent threats to both humans (from consumption) and the health of the individual fish. The effects of contaminants as stressors at the organismal level and subsequent effects on biodiversity are virtually unstudied, especially so for Arctic fishes, and thus represent a gap in knowledge. Similarly, although documented in boreal regional contexts as an industrial impact, acidification of Arctic fresh waters is poorly understood. Thus, effects might be possible on native biodiversity, so that lake-specific stocks of northern fishes are at risk and some even being lost (e.g. see Tammi *et al*. 2003). Fish diversity in combination with the nature of the aquatic habitats, however, is known to affect bioaccumulation processes and thus contaminant concentrations. For example, for mercury within Arctic char, lacustrine (non-migratory) forms exhibit higher concentrations than do anadromous (migratory) forms (Swanson *et al.* 2010). This appears to result from exposure (greater in freshwater) and perhaps chemical processes that make mercury biomobile.

#### Exploitation

As noted above, Arctic freshwater and diadromous fishes are widely exploited throughout the Arctic and sub-Arctic. In the case of highly migratory diadromous species, this may be in marine areas well outside the Arctic or in Arctic 'gateway' seas. Harvesting results in genetic changes that affect biodiversity (Allendorf *et al.* 2008). Sequential and cumulative harvesting of the largest individuals and anadromous life history types may thus alter population levels of biodiversity for Arctic fishes particularly if commercial quantities are taken. Populations of key species (e.g. Arctic char) are vulnerable to overexploitation and in some local situations have been heavily and perhaps overexploited. However, management of these fisheries is often hampered by lack of detailed harvest data, complex stock structures, wide distributions and high levels of diversity below the species level. These factors similarly complicate the demonstration of significant overexploitation. Management protocols that do not consider biodiversity implications of harvest at all levels of biodiversity require appropriate alteration.

#### Industrialization

The wide range of industrial development and associated human activities in the Arctic is well documented elsewhere, thus will not be addressed here (e.g. AMAP 2004, 2009). The vast majority of effects are upon habitat attributes relevant to Arctic fishes (e.g. sedimentation, water withdrawals, shift in flow regimes and fragmentation of habitats). Altered habitats, in turn, affect biodiversity in ways parallel to those discussed above for climate change (e.g. local shifts in species complements, life history types, population viability and altered productivities). While most industrial effects on biodiversity are local in scope and scale, widespread and increasing occurrences may collectively affect diversity at large scales. Strengthening of the documentation and control of impacts is required.

### Habitat fragmentation

As noted above, many Arctic freshwater and diadromous fishes are highly migratory. For many species this is an obligatory, mostly genetically encoded strategy essential to life (e.g. Pacific salmon), whereas for others, it appears to be facultative and to depend upon local environmental and phenotypic drivers including individual fish growth (e.g. Arctic char). Regardless, sequentially displaced habitat use by different ontogenetic components within populations is a norm for fishes in both lotic and lentic ecosystems (and reaches its epitome in anadromous species). Factors that isolate habitats thus fragment overall habitat usage and affect population abundance and viability. These factors include direct interference with migrations (e.g. physical barriers), as well as those that fragment habitat in more insidious ways (e.g. dewatering of river reaches, chemical or thermal barriers from contaminants or sediments). Habitat fragmentation overall in the Arctic is likely low at present, albeit somewhat more substantive in the sub-Arctic, but industrial development and climate change will tend to increase this stressor in the future.

### Introduced species as threats

Popov (2009) lists 96 species of fishes present in Siberian waters (including temperate Lake Baikal), 38 of which occur within the ABA sub-Arctic and Arctic boundary. Overall, 80 species are native to the area with 16 being introduced through human activities (15 to the Ob River basin, eight to the Yenesei and none to Lena and Kolyma river basins; Tab. 6.3) with some species being introduced to multiple Siberian basins. Two additional Siberian species have been moved among basins. Of the 38 northern species, 34 are native and four are introduced from Europe. The extent of introductions overall (20% of native fauna, 11.8% of northern fishes) belies the high potential for negative effects on native species. Although many of these introductions were presumably into the non-Arctic portions of the respective basins, warming climates make northward invasions possible in the future. Given that many northern fish species are generalists and tend to be poor competitors, heightened concern is merited. Introduced and/or colonizing species may also introduce new parasites or diseases to native faunas and may also become predators in addition to competitors (Reist *et al.* 2006a).

### Threats to native species – introduced populations

Another aspect related to introductions is that of the introduction of non-native lineages or genotypes. This is most commonly associated with aquaculture efforts either to introduce new or to supplement existing native populations. Extensive coastal aquaculture in N European boreal fjords (e.g. Norway) and escapees of, for example, Arctic char are an unknown overall threat to native Arctic fishes (e.g. Naylor *et al.* 2005, Hutchings & Fraser 2008). Stocking manipulations in fresh waters are also significant in some areas (e.g. > 52,000 lakes in Fennoscandia; Tammi *et al.* 2003). Artificially increased species diversity, often with undocumented or unknown effects on native diversity, represents a greater threat than does acidification (Tammi *et al.* 2003).

### Cumulative effects

Perhaps the greatest unstudied and unknown threat to Arctic fish biodiversity is that associated with the cumulation of the above stressors. Cumulative effects may be additive as described for both industrial development and sequential exploitation above. Alternatively, stressors can interact to result in multiplicative cumulative effects (i.e. the total is greater than the sum of the parts). It is highly likely that in many areas of the Arctic many of the stressors discussed above are cumulatively affecting fish biodiversity in unknown and undocumented ways. Appropriately designed and implemented monitoring programs are thus required to document this and where possible disentangle the various stressors and their effects.

The vulnerabilities, the suite of individual and cumulative stressors and thus the effects on biodiversity of freshwater and diadromous fishes in the Arctic are unevenly distributed. It is reasonable to assume that most local stressors (e.g. exploitation, mining) are concentrated near human settlements, whereas others (e.g. all aspects of hydrocarbon development) are distant and widespread. Still other stressors (e.g. contaminants, acidification, climate change) are pervasive throughout the Arctic. It is further highly likely that most populations of Arctic fishes are affected to some degree; however, the effects, resistance and resilience of the recipient ecosystems and the responses by the diverse forms of fishes are virtually unknown. Research and monitoring programs to address these knowledge gaps are required throughout the Arctic.

## 6.2.10. Present status and trends

Overall formal assessments of status are available on a country basis and, in some cases, by political regions within countries. These generally, however, do not differentiate Arctic regions from those farther south. Accordingly, the synthesis of a taxon-by-taxon search of the status is presented in Appendix 6.1.4.

Two taxa, European eel *Anguilla anguilla* and sturgeon *Acipenser sturio*, are critically imperiled throughout their areas of distribution within the Northeast Atlantic Arctic nations including European Russia (i.e. listed as such on one or more of the International Union for the Conservation of Nature (IUCN) or European Red lists). The sturgeon has actually been extirpated from most of its historic range (which extended into the sub-Arctic), with only one small population remaining in the Gironde River (France) (Williot *et al.* 2002). Although not assessed nationally, two additional Arctic taxa are locally critically imperiled in the Yukon Territory (humpback whitefish, Arctic char) due primarily to their very restricted occurrence in the area. Four Eurasian taxa are listed as imperiled in sub-Arctic Finland (Atlantic salmon) and the Arctic and sub-Arctic of the Russian Federation (Siberian sturgeon *Acipenser baerii*, Esei Lake char and taimen). Locally in the Arctic and sub-Arctic of Yukon Territory, three species (white sucker *Catostomus commersonii*, Arctic cisco and ninespine stickleback *Pungitius pungitius*) are imperiled. One species in sub-Arctic Sweden (burbot) and three species in sub-Arctic Finland (brown trout *Salmo trutta* (both forms), Arctic char and grayling *Thymallus thymallus*) are ranked as near threatened. Twenty-four species, 19 of which are not regionally included in the above categories, are assessed as vulnerable in Russia, Siberia, Chukotka, Alaska or Canada.

Thus, of 127 taxa in total, 36 (approximately 28%) are assessable at some level of risk in at least one jurisdiction in the Arctic. Notably, all five sturgeons, several endemic forms of chars and whitefishes and two lampreys fall into these categories. Some taxa are undoubtedly so listed due to their restricted occurrence in particular regions; similarly, some may be listed based on their occurrence in the Arctic (but may be secure in southern areas). Regardless, in terms of overall diversity it appears that the 'at risk' status of Arctic and sub-Arctic freshwater and diadromous fishes is proportionately relatively high given the species-level diversity of the fauna. Natural rarity and marginal distributions within jurisdictions aside, it is likely that many of the stressors noted previously are significantly impacting the overall diversity of those fishes. Many of these species are exploited and exhibit vulnerabilities during extensive migrations, thus likely cumulate stresses over space and time and/or exhibit life history traits making them vulnerable. Moreover, as noted previously, the taxonomy used herein is conservative at the species level. Recognition and assessment of additional taxa would likely increase the number of 'at risk' forms simply as a result of incrementing the numbers of local endemics. Conversely, most species are secure or apparently so, although approximately 20% have not been assessed in any fashion.

### 6.2.10.1. Trends

As with many of the topics already considered, information on trends over time in diversity of Arctic freshwater and diadromous fishes is limited at best. This appears to be primarily the result of limited effort exerted to collect necessary information particularly in circumstances that appear to be problem free. Accordingly, in many cases trends are directly associated with stressors, thus addressed in that section. Two aspects of temporal trends are addressed here: biodiversity itself and trends within key species; that associated with conservation status is addressed above.

#### Biodiversity

Given high taxonomic uncertainty and varying philosophies (e.g. taxonomic 'splitters' vs. 'lumpers'), as well as poorly surveyed regions, temporal shifts in biodiversity may be superficially apparent. These are, however, likely the result of increased accrued information, taxonomic revisions and/or shifts in taxonomic philosophies. Accordingly, apparent increases in Arctic diversity are likely to be falsely implied (e.g. Canadian Arctic; see Section 6.2.3.2), thus root causes should be determined with care. This issue aside, real shifts in Arctic diversity are becoming apparent. First, as climatic constraints are lessened, limits on taxa relax, and distributional and/or abundance changes ensue. Thus, Pacific salmon species in the western Canadian Arctic (i.e. west of Hudson Bay) are currently more frequently encountered than in the recent past (Babaluk *et al.* 2000, Nielsen *et al.* 2012), which likely represents both increased local abundance of natal species (i.e. chum salmon *Oncorhynchus keta*), as well as increased exploratory behavior and vagrancy by non-natal anadromous species. Due to generally poorly detailed distributional data to date, no clear documentation exists of northward colonizations of the Arctic by freshwater species within the large northward flowing river basins; however, this is anticipated and may become apparent as studies are initiated. As noted previously, however, human actions such as introductions are affecting local fish diversity.

#### Key species

Virtually the only information available on trends in key fish species results from studies on exploitation or other stressors. For example, temporal assessment of lake trout prior to and following a period of angling indicated reduced median lengths and weights and a reduction in size at reproduction (McDonald & Hershey 1989). Given that large lake trout 'control' recruitment and community structure (particularly relative abundances of prey taxa as well as conspecifics; Johnson 1975, 1976, McDonald & Hershey 1989), continued exploitation will alter lake trout population parameters, dynamics of co-occurring species and thus fish community structure.

Long-term habitat alterations appear to effect shifts in the trophic ecology of Arctic char in alpine Lake Windermere, temperate northwest England (Corrigan *et al.* 2011), which may alter relative abundances of particular ecomorphotypes (i.e. shift subspecific diversity within highly variable taxa). Time frames associated with these shifts are multi-decadal (i.e. 60 years in this example), thus within the temporal horizons of recent anthropogenic impacts on the Arctic. Longer-term monitoring reveals declines in char population abundances and catches of Arctic char in sub-Arctic Lake Mývatn (Iceland) over 100 years proximately related to shifts in prey species (Gudbergsson 2004), but ultimate cause-effect relationships remain uncertain. Although documentation is limited, early findings for a Svalbard population of Arctic char suggest that life history diversity is being altered (i.e. shift away from anadromy to residency), and this may accompany climate-driven ecosystem shifts (Reist *et al.* 2006a, M. Svenning unpubl.). Finstad & Hein (2012) documented this in Norwegian Arctic char.

Numerous, discrete and often small population sizes of diadromous species of fish permits analyses of trends in status and, indirectly, diversity (i.e. through numbers of populations over time; Limburg & Waldman 2009). Documented findings indicate that most Atlantic species lost populations, abundances (or harvest proxies) declined and conservation statuses increased (i.e. more assessed as 'at risk'). Factors which contributed to these changes include habitat loss, overfishing, pollution, climate change, invasive species and/or aquaculture (Limburg & Waldman 2009). Although some Arctic species are represented in this study, widespread similar documentation for Arctic taxa is generally lacking. It is likely though that at least some Arctic taxa are relatively resilient as, for example, centrally located Arctic char populations exhibited high resilience to both intense exploitation and climate-induced habitat shifts (Dempson *et al.* 2008).

Traditional knowledge studies by the Snowchange Cooperative and local indigenous communities of Northeastern Sakha-Yakutia, Siberia have also documented trends in Arctic freshwater and anadromous fishes. For example, in the Kolyma River inconnu are reported to be decreasing in both abundance and size, the Siberian sturgeon *Acipenser baeri* and muksun *Coregonus muksun* subsistence fisheries have reportedly collapsed, while chum salmon abundance has increased significantly (Mustonen 2007). Causation was not investigated and is therefore unknown and may be ambiguous.

As noted above, much of the diversity present in northern freshwater and diadromous fishes appears to be functionally relevant and linked to ecology. Accordingly, altered abundances of particular ecophenotypes, life history types and/or other sub-specific levels of diversity are likely occurring but poorly documented. The importance of addressing this gap in the context of increasing rates of change is obvious.

Other than the comprehensive baselines of status of taxa summarized above and elaborated in Appendix 6.1, no information is available regarding trends in the status of Arctic fishes. Taxonomic lability, philosophical disagreements and poor geographical and temporal coverages exacerbate this, thus precluding effective analyses of trends. Redress of this gap and underlying factors is required; this should include development of relevant circumpolar monitoring networks.

## 6.2.11. Gaps and issues

Specific gaps in knowledge and issues that preclude or affect assessments of Arctic freshwater and diadromous species are noted in several places in the text. Here, the most significant of these will be emphasized.

1. Unresolved taxonomic issues are present in many taxa at many levels (Reist *et al.* 2013). Recent declines in disciplinary experts will impede the resolution of these.
2. Linked to 1) above are underlying philosophical disagreements as to both the approach and the relevance of particular types and degrees of variation (i.e. an agreed-to taxonomy that identifies taxa to a common level and standard).
3. Widespread gaps in surveys and documentation of diversity exist throughout much of the Arctic (e.g. Canada, Siberia). This lack of knowledge links to both 1) and 2) above.

In combination, the above three issues result in a significant under-estimation of the true diversity present in this group of fishes in the Arctic. These are exacerbated by the following:

4. The absence of comprehensive monitoring regimes for Arctic fish biodiversity further precludes effective documentation or timely warnings regarding shifts in fish diversity. This gap includes both spatial components as well as temporal monitoring of diversity at key locations or for key populations.
5. Synoptic re-assessments of the status of taxonomic groups are necessary. These should be developed within jurisdictions on the basis of common criteria but should also be applied in a pan-Arctic context to gather an accurate understanding of the true status.
6. Aspects of all the points above affect the comprehensive development of trend information from which understanding of proximate causation and remedial actions can be developed.

Redress of these gaps and issues is necessary to underpin effective future assessments.

## 6.2.12. Conclusions and recommendations

### 6.2.12.1. Conclusions

1. The documentation, delineation, synonymization, uniqueness and nature of taxonomic, functional and biological types of diversity are poorly known throughout much of the Arctic and sub-Arctic for freshwater and diadromous fishes. Remote and geographically large diverse areas are particularly poorly studied. Basic information such as specific occurrences and distributional limits is generally lacking for most areas. Taxonomic confusion and unresolved complexities of diversity are apparent in many groups of these fishes and across all levels from local population structuring to that of the species.
2. Similarly, both natural and anthropogenic factors that maintain (or promote), truncate or differentially affect diversity within and among these levels are poorly known. Generally, anthropogenic factors appear to affect diversity directly (e.g. specific taxa or forms exploited in fisheries) and indirectly by altering processes by which diversity is maintained (e.g. climate change affecting productivities of water bodies). Effects of cumulative interactions are particularly problematic.
3. Association of various types and levels of diversity with particular ecosystem types, specific 'hotspots' and/or geographic scales is somewhat better understood, but large gaps remain. Additionally, although some distinctive types of diversity have been documented and/or locations with unique diversity are known, it is likely that many undocumented situations exist.
4. Rates of anthropogenically driven change (e.g. resource extraction, climate variability) in the Arctic suggest that much diversity will likely be lost before it is adequately understood or documented.

5. Understanding of roles and relative importance of both the types of diversity and the various levels within those types is generally required.
6. Documentation of the nature and consequences of anthropogenic effects on diversity is required.
7. Documentation of ecosystem roles (e.g. stability/resiliency) and services that accrue from these fishes and their varying levels of diversity are required in terms of those directly accrued by humans (especially indigenous peoples locally) and for other valuable ecosystem components (e.g. as key prey items for marine biota).
8. Better documentation of cultural and traditional uses and relevance of fishes to indigenous peoples is required. These, and levels of use for food (7 above) and selectivity for particular forms, require better documentation.
9. Better documentation is required of local commercial and sport fisheries, both of which are often underreported.
10. Development of protected areas for aquatic biota, particularly for areas where unique or highly diverse groups are present, is in its infancy (in comparison with that for terrestrial biota). Most efforts at conservation are directed towards taxonomic diversity, rather than to functional diversity or dynamic habitats, which might change over time, or to key processes which maintain diversity. Adapting existing models to a dynamic, more variable and changing world is required.
11. Development and implementation of relevant and rapidly assessed indicators of effects of change on fish biodiversity are required.
12. A multitude of definitions of species coupled with highly variable taxonomic philosophies result in wide inter-regional disparity of practical definitions at the species level. This undermines spatial and temporal assessments of diversity, changes therein and linkages to causation.
13. Although many species of Arctic endemic or Arctic-centric fish species can be considered iconic, this diversity is unknown and/or under-appreciated by most.

#### 6.2.12.2. Recommendations

Based upon the above conclusions, the following five recommendations are made regarding research and management of Arctic freshwater and diadromous fishes:

1. Concerted and coordinated effort to document and understand the roles of diversity of Arctic freshwater and diadromous fishes is rapidly required throughout much of the Arctic, at a wide range of geographic scales using a range of techniques. This includes active research to resolve taxonomic complexes and relationships among levels of diversity, issues which are especially prevalent in these fishes.
2. Development and implementation of comprehensive circumpolar monitoring of freshwater and key diadromous fish populations and their supporting ecosystems (e.g. through a dispersed observatory network) is required across the range of ecosystem and diversity types present. This needs to include parallel monitoring of key locally originating and pervasive anthropogenic stressors.
3. Ecosystem-level research programs are required across the Arctic, and these must include all aspects of human interaction with the fishes and their ecosystems. Programs should be explicitly linked with stressors impinging upon biodiversity, key ecosystems and processes which maintain biodiversity, endemism or areas of high diversity. Research linking ecosystem processes to diversification of forms is a priority given the overall relevance of such understanding to global issues.
4. Alternative approaches are required which realistically reflect conservation of diversity, habitats currently used (and those possibly used in the future as change is effected) and processes relevant to maintaining and/or promoting diversity.
5. Development of clear, workable circumpolar definitions of taxonomic diversity at various levels for these fishes and their relevance to human activities is required. Communication and outreach both among taxonomic experts and between these experts, users of their information and the public (both within and outside the Arctic) is required to enhance awareness, importance and conservation actions for this group of fishes.

## 6.3. MARINE FISHES IN THE ARCTIC OCEAN AND ADJACENT SEAS

Here, we address biodiversity and conservation issues for the entire marine fish fauna in the Arctic Ocean and adjacent seas (hereafter AOAS). Further, we touch upon the status and prospects for species targeted by industrial fisheries and the role of management in Arctic fisheries. This overview is largely based on a recent synthesis by Mecklenburg *et al.* (2011) together with annotated fish checklists for specific AOAS regions, for example Alaska (Mecklenburg *et al.* 2002), Canada (Coad & Reist 2004), Greenland (Møller *et al.* 2010), parts of the Greenland Sea, including the waters off Jan Mayen Island (Wienerroither *et al.* 2011a, Christiansen 2012), the Barents Sea (Byrkjedal & Høines 2007, Karamushko 2008), the Norwegian Sea (Pethon 2005) and the seas of Arctic Russia (Andriashev & Chernova 1994, Karamushko 2012). A recent biogeographic overview of northern fishes at large was also consulted (Chernova 2011).

To date, nearly 250 marine fish species are known from Arctic waters *sensu stricto*, i.e. excluding larger parts of the sub-Arctic Bering, Barents and Norwegian Seas (Mecklenburg *et al.* 2011). However, if one includes the adjacent sub-Arctic seas the number of species rises considerably. The marine fish groups (i.e. taxa) assessed here are listed in a species inventory (Appendix 6.2) that covers the AOAS with 16 regions (Fig. 6.4 and Section 6.3.3). Altogether, we evaluate 633 marine fish species in 313 genera, 106 families (suffix: -idae), 31 orders (suffix: -iformes) and three classes. Subcategories, including

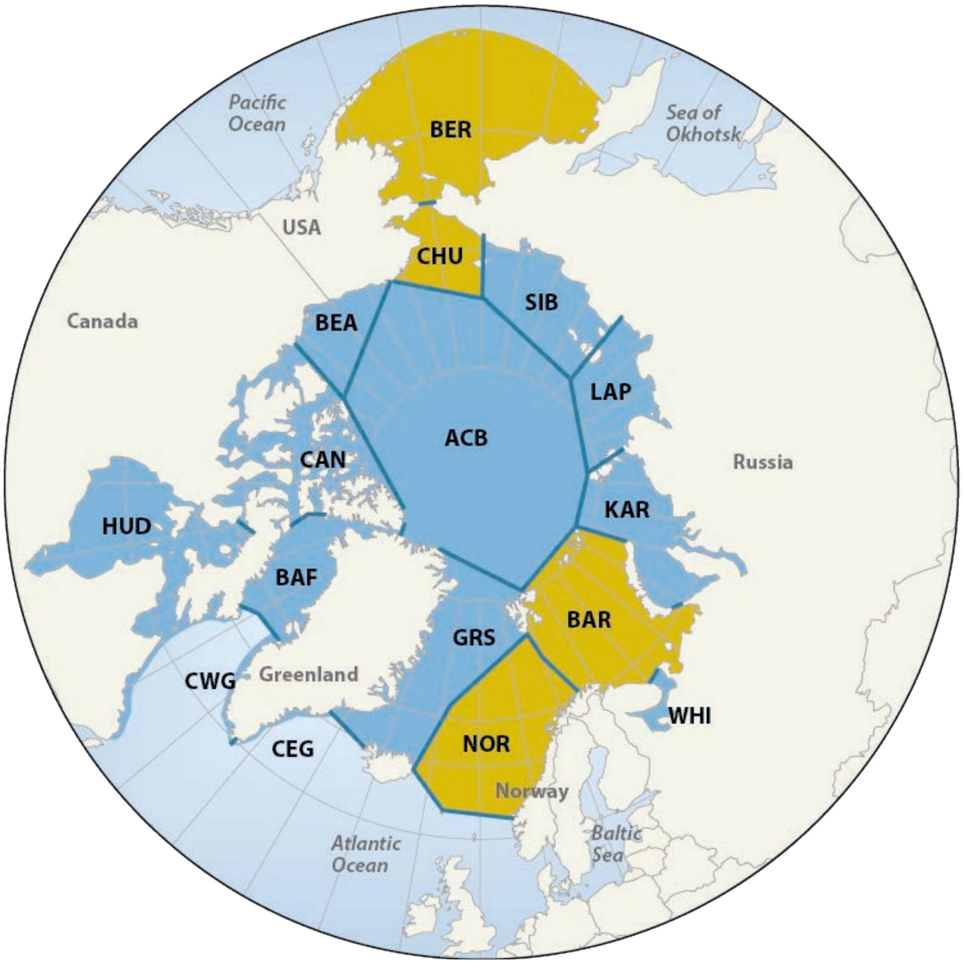

**Figure 6.4.** The Arctic Ocean and adjacent seas (AOAS) with the approximate delineation of the 16 regions examined for the occurrence of marine fish species. The Arctic gateways are shown in yellow and the Arctic seas in deep blue.

Regional codes are:
ACB = Arctic Central Basin
BAF = Baffin Bay
BAR = Barents Sea
BEA = Beaufort Sea
BER = Bering Sea
CAN = Canadian Arctic Archipelago
CEG = Coastal E Greenland
CWG = Coastal W Greenland
CHU = Chukchi Sea
GRS = Greenland Sea
HUD = Hudson Bay complex
KAR = Kara Sea
LAP = Laptev Sea
NOR = Norwegian Sea
SIB = East Siberian Sea
WHI = White Sea.

Physical properties for the specific regions are given in Tab. 6.4 (cf. Section 6.3.3). Note that a stricter definition of Arctic waters, which excludes larger parts of the sub-Arctic seas, is given by Mecklenburg *et al.* (2011). See text for further information.

subspecies, populations of a species and gene pools, are discussed briefly where appropriate (Sections 6.3.4.3 and 6.3.7.3). The study of fish taxonomy and classification is a continuing, diligent and dynamic activity, and two acknowledged and authoritative sources are consulted: the *Catalog of Fishes*, which is the most comprehensive and thorough account on the Internet (Eschmeyer online) and the printed classic monograph *Fishes of the World* by Joseph S. Nelson (2006) in its 4th edition. Other useful online sites include: FishBase, GBIF, ICZN, ITIS, OBIS, WoRMS and ZooBank (cf. References for acronyms and web-addresses).

In Appendix 6.2, fish families are numbered and listed in phylogenetic order according to Nelson (2006). The scientific names of genera and species are listed alphabetically and authorships (following Eschmeyer online), and zoogeographic affiliations (Section 6.3.1) are shown. Vernacular names are given for families according to Nelson (2006) and Mecklenburg *et al.* (2011). For reasons given in Section 6.3.2, we outline primarily the actual numbers of species (species richness), genera and families for given AOAS regions and do not attempt to employ sophisticated measures of biodiversity (Magurran 2004, Tuomisto 2010). In this sub-chapter, being a grand overview of the marine fishes in the AOAS, single species will not be accounted for. However, taxa that deserve particular attention, such as keystone species that are important for ecosystem structuring and processes and species with a complex and controversial taxonomy, are highlighted in Section 6.3.5.

Several marine fish species that inhabit the main entrances ('gateways') to the Arctic seas, i.e. the Norwegian Sea and the Barents Sea in the NE Atlantic and the Bering Sea in the N Pacific, are of high socioeconomic importance and support some of the largest industrial fisheries worldwide. Targeted species are indicated in the fish checklist (Appendix 6.2), and their status and trends are briefly discussed in Section 6.3.7.3.

### 6.3.1. Distribution and zoogeography

The term 'distribution' is ambiguous, and we distinguish zoogeographic patterns from phylogeographic processes of fish distribution. Whereas zoogeography simply provides the total geographic range for a given taxon (the pattern), phylogeography reflects the origin, evolutionary history and the putative dispersal routes of taxa through space and time (the underlying processes). Obviously, the study of phylogeography is much more multifaceted and requires ample information both on genetic lineages among fish taxa and populations and on temporal dynamics in environmental barriers that give rise to certain zoogeographic patterns (cf. Sections 6.3.2.3 and 6.3.4.3; Briggs 1974, Chen & Mayden 2010, Hardy *et al.* 2011). In the following, we use 'distribution' in the zoogeographic context unless stated otherwise.

The study of distribution patterns for marine fishes in the AOAS is of utmost importance due to ocean warming and observed northward shifts in latitudinal range for a number of boreal species in recent years (Perry *et al.* 2005, Rose 2005, Rijnsdorp *et al.* 2009, Chen *et al.* 2011, Wienerroither *et al.* 2011a, Hollowed *et al.* 2013). Our definition of zoogeographic affiliations largely follows Andriashev & Chernova (1994), Karamushko (2008) and Mecklenburg *et al.* (2011). All marine fish species encountered in the AOAS are classified in this overview into one of four indicative categories determined mainly by the nature of ambient water masses and the thermal habitat of reproduction:

- Arctic (A): species that are distributed in Arctic waters and which spawn solely at sub-zero temperatures and are only infrequently found in boreal waters.
- Arctic-boreal (AB): species that are distributed in Arctic and boreal waters and which may spawn at both sub-zero and positive temperatures.
- Boreal (B): species that are distributed in boreal waters and which spawn solely at positive temperatures. Boreal fishes are only occasionally found in the border regions of Arctic waters.
- Widely distributed (WD): species that are common in boreal and subtropical waters and also in or below the warm waters of at least two oceans (or are known from the southern hemisphere). They occur only rarely in the Arctic. Many deep-sea and migratory fishes belong to this category.

A credible account of the actual number and distribution of Arctic marine fish taxa must be founded on a common understanding and definition of the spatial delineation of the Arctic region past and present to include or exclude fish taxa of concern. From an ecological point of view, the southern border of the marine Arctic is far from static, and transitional zones (*sensu* Chernova 2011) between Arctic and boreal waters may vary in conjunction with seasonal and long-term fluctuations in climate. Several definitions of the marine Arctic have been proposed. For example, based on major shifts in the Arctic and boreal faunas, Ekman (1953) placed the Arctic marine eco-region within the summer isotherm of maximum 5-7 °C at 25-75 m depth. Glacial ice and sea ice are dynamic and essential environmental structures of the Arctic seas, and our account mainly comprises those species which are associated with ice-laden waters either seasonally or perennially. The geographic delineations for the 16 AOAS regions employed here are shown in Fig. 6.4 and further descriptions are given in Section 6.3.3.

## 6.3.2. Status of knowledge

### 6.3.2.1. The roots of Arctic ichthyology

The roots of Arctic ichthyology can be ascribed to the eminent Danish priest (by trade) and polyhistor Otto Fabricius (Othonis Fabricii, 1744-1822). Equipped with his volume of *Systema Naturae* (10th edition, Linnaeus 1758), Fabricius initiated the study of the Arctic fauna, and was the first to develop a scientific and annotated account of the Arctic fishes in his treatise *Fauna Groenlandica* (Fabricius 1780). In this work, he described no less than 473 invertebrate and vertebrate species of which he categorized 36 as fishes (Pisces) and nine species of cartilaginous fishes (Chondrichthyes) and lumpsuckers (*Cyclopterus*) as Amphibia [sic]. Altogether, *Fauna Groenlandica* contains comprehensive descriptions of 45 fish species. Several of Fabricius's descriptions of the approximately 130 species new to science, however, were published a few years earlier in *Zoologiae Danicae Prodomus* (1776) by his contemporary countryman, the renowned zoologist Otto F. Müller (1730-1784). Fabricius is unquestionably a pioneer of Arctic zoology, and many of his scientific contributions are still valid (Kapel 2005). Moreover, Fabricius broke new ground during his stay in W Greenland (Paamiut district 1768-1773), since he fully appreciated the value of and extensively employed traditional ecological knowledge (TEK) in his scientific work (Jensen 1923). Prominent zoologists and ichthyologists of the 19th century and the first half of the 20th century, mainly from Denmark – J.C.H. Reinhardt (1776-1845), C.F. Lütken (1827-1901) and A.S. Jensen (1866-1953) – and Russia and the Soviet Union – L.S. Berg (1876-1950), G.U. Lindberg (1894-1976), A.N. Svetovidov (1903-1985) and A.P. Andriashev (1910-2009) – invigorated Fabricius's work and developed the classification and zoogeographic knowledge of Arctic fishes even further.

### 6.3.2.2. Uses and abuses of fish data from the AOAS

The ice-covered Arctic seas are little studied, and despite the efforts of outstanding ichthyologists, knowledge of the Arctic fishes *sensu stricto* remains scarce compared with other areas, such as the fish fauna in the Southern Ocean (Kock 1992, Eastman 1993, Piepenburg 2008). Besides logistical constraints, the most serious hindrance to a comprehensive understanding of species richness and species distributions in the AOAS lies in the fact that our information, by and large, is based on opportunistic and fragmentary observations accumulated over periods of time and reveals no coherent time series.

Marine fish species have been described scientifically in the AOAS since the publication of Carl von Linné's (Linnaeus, 1707-1778) *Systema Naturae* in 1758 (Fig. 6.5, Appendix 6.2). The growth in the cumulative number of described non-Arctic species (cf. Section 6.3.1) from 1758 until the present day follows a fairly typical *S*-shaped function (May 1990, Gaston & Spicer 2004). That is, the rate of describing new non-Arctic species (n = 570) was rapid at first and then slowed down, and 75% of these species were known to science as early as 1912. By contrast, Arctic species (n = 63) have been described at a consistently slower pace, and 75% were known as recently as 1976. The periods 1780-1824 and 1944-1975 completely lack descriptions of new Arctic species. Three periods, however, are particularly conspicuous with several new descriptions: 1874-1881 and 1902-1914, following the great Arctic marine research

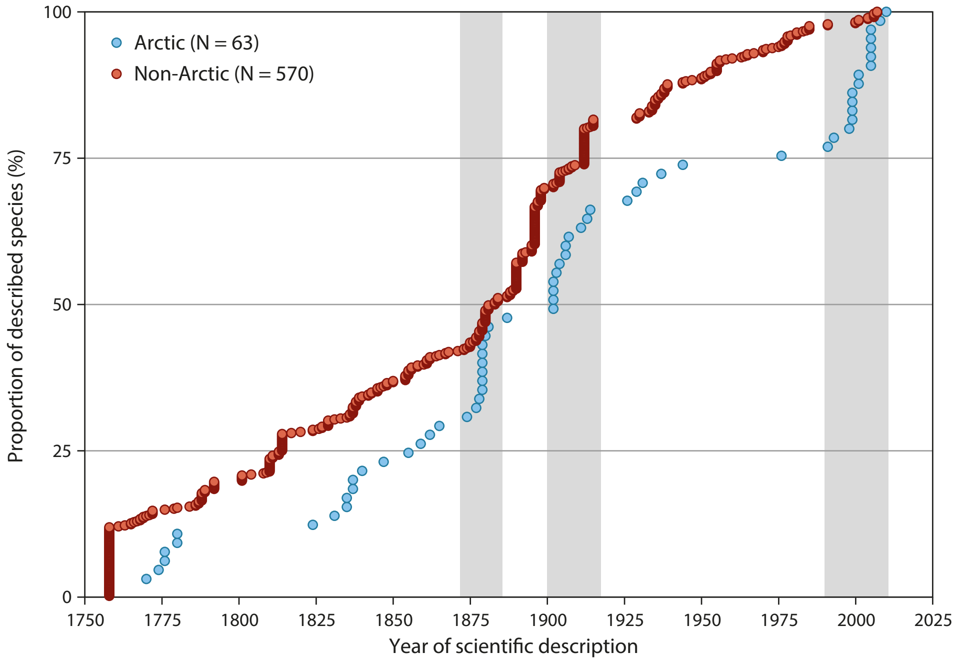

**Figure 6.5.** Cumulative numbers of marine fish diversity (n = 633, Appendix 6.2) in the Arctic Ocean and adjacent seas (AOAS) from 1758 to the present. Species are broadly grouped according to zoogeographic pattern (cf. Section 6.3.1): Arctic (A, blue symbols) and non-Arctic (Σ AB, B, WD, red symbols). Grey bars denote periods with many descriptions of new Arctic species. Note that 75% of the non-Arctic species known to science were described by 1912, whereas the same proportion for Arctic species was only reached in 1976. See text for further information.

expeditions (Sandbeck 2007, Møller *et al.* 2010) and the first International Polar Year (IPY 1881-1884) and the present-day 1991-2010 in light of the fourth IPY (Fig. 6.5). It should be noted that there can be a considerable time lag between the actual year of sampling and the year of scientific description. For example, the gadoid fish, *Theragra finnmarchica* Koefoed, 1956 (now classified *Gadus chalcogrammus* Pallas, 1814), was discovered in 1932 but was scientifically described almost 25 years later (cf. Section 6.3.4.3; Christiansen *et al.* 2005). Therefore, type specimens in museum research collections should be consulted to establish the exact date of first occurrence of a species.

The effort of investigations and the efficiency of gear deployed in fish sampling vary considerably both among regions and in time. For example, knowledge of the fish faunas near shore (< 20 m) and in deep waters (> 1,500 m) is limited compared with the Arctic shelves. The Arctic seas of central Russia and the Arctic Central Basin have barely received any scientific attention (Andriashev 1954, Karamushko 2012). In recent years, investigations of regional Arctic marine fish faunas have been conducted in the Chukchi Sea through the 'Russian-American Long-term Census of the Arctic' research initiative (RUSALCA, Mecklenburg *et al.* 2007, Bluhm *et al.* 2010), on the shelf of the Beaufort Sea (Rand & Logerwell 2011) and in the fjords and on the shelves of NE Greenland through the TUNU-Programme (Christiansen 2012). The fish fauna of the nearly landlocked White Sea, NW Russia, has been extensively studied and supports a regional fishery (Lajus *et al.* 2007, Zhitniy 2007). The fish faunas of the adjacent Norwegian, Barents and Bering Seas are obviously well described due to their socioeconomic importance for centuries (e.g. Wienerroither *et al.* 2011b). It is critical, therefore, to distinguish 'true' and 'apparent' numbers of fish species in comparisons of species richness across the AOAS regions (cf. Section 6.3.4.2).

The actual count of species within a particular geographic area, i.e. species richness, is often referred to as alpha (α) diversity. However, biodiversity *sensu stricto* and its numerous derived indices require quantitative information (biomass or number of individuals) for single species (Hurlbert 1971, Henderson & Magurran 2010, Tuomisto 2010, Green & Chapman 2011, Magurran *et al.* 2011; see also Oecologia 167: 885-911, 2011 for further discussion). With the exception of the relatively well-studied fishes that are targeted by industrial fisheries (cf. Section 6.3.7.3), AOAS fish species are known largely by presence-absence data, and a lack of abundance estimates precludes the use of demographic analyses and most measures of biodiversity except species richness (Beck & Schwanghart 2010, Tuomisto 2010). It is striking that nearly 95% of the 63 marine fish species designated Arctic (cf. Section 6.3.4.4) have not been assessed by the IUCN (IUCN online) or any other scientific body.

Moreover, the species concept *per se* is far from trivial (Marris 2007, Ereshefsky 2011), and taxonomic controversies can be ascribed to the level of taxonomic resolution employed (Kullander 1999) and traditions and preferences for specific taxa among taxonomists (Gaston & May 1992, Clark & May 2002; see also Section 6.2). The implementation of molecular techniques (e.g. barcoding; Ward *et al.* 2009) has altered the perception of valid fish species to an ever-increasing degree (Nellen & Dulčič 2008, Hausdorf 2011), and species may be synonymized faster than new ones are described (Nelson 2006, Byrkjedal *et al.* 2007, Scheffers *et al.* 2012). Obviously, given the temporal hiatus in observations and the lack of abundance data, species turnover cannot be deduced, trends and changes in the AOAS fish communities cannot be revealed, and importantly, correlations cannot be made between past snapshots of species occurrences and present environmental changes. Muddling of historical and modern observations of species occurrences are clearly fallacious, although recent developments in statistics and modelling attempt to bridge the empirical gaps (Tingley & Beissinger 2009). Consequently, we report accumulated and conservative estimates of numbers and patterns of distribution for marine fish species in the AOAS rather than the dynamic processes underpinning those patterns.

### 6.3.2.3. Arctic-Antarctic comparisons

There is a general consensus that the Arctic marine fish fauna was established relatively recently (2-3 million years ago) compared with its counterpart in the Southern Ocean, Antarctica, which may have evolved under cold environmental conditions over the past 10-17 million years ago (Clarke & Johnston 1996, DeVries & Steffensen 2005, Patarnello *et al*. 2011). A recent study on ocean floor sediments disputes this view and suggests that the modern circulation in the Arctic Ocean actually dates back about 17 million years ago, and that a perennial sea ice cover was formed about 13-14 million years ago (Krylov *et al*. 2008, Polyak *et al*. 2010). Given this perspective, Arctic and Antarctic regions underwent a coeval freeze, and their polar marine faunas should be viewed on the same geological time scale. This may not affect our current perception of polar fish evolution, however, in view of the fact that the Arctic and Antarctic regions differ significantly in invasion history, biogeographic isolation and climate stability (Turner & Overland 2009; see also Box 1.3 in Meltofte *et al.*, Chapter 1). Bipolar comparisons, therefore, are particularly valuable for grasping the evolutionary history and prospects of polar marine fishes at large, cf. the international research programme Evolution and Biodiversity in the Antarctic–The Response of Life to Change (EBA; www.scar.org).

The Norwegian and Barents Seas in the Atlantic sector and the Bering and Chukchi Seas in the Pacific sector are the two main marine entrances to the Arctic Ocean (cf. Section 6.3.3), but their relative importance in the interchange of fishes between Arctic and lower latitude regions differs on a geological time scale. The Norwegian and Barents Seas constitute an open gateway in the NE Atlantic (Fig. 6.4). The area between the Bering Sea and the Chukchi Sea, on the other hand, may in turn have acted as a natural passage (Bering Strait) or a natural barrier (Bering Land Bridge; O'Neill 2004) for marine organisms as a result of Neogene and Quaternary fluctuations in sea level and glaciation (Vermeij & Roopnarine 2008, Hardy *et al*. 2011, Fraser *et al*. 2012). Episodic interchanges of marine fishes via the Bering Strait are well illustrated by the fact that several genera and species show remarkable disjunctive distributions

**Table 6.4.** ID codes and physical properties for the Arctic Ocean and adjacent seas (AOAS). Estimated sea-surface area (1,000 km$^2$), mean depth (m) and other bathymetric features are from Jakobsson (2002). Major rivers and freshwater sources are from Gordeev (2006) and McClelland *et al*. (2012).

| ID codes | AOAS regions | Area | Mean depth | Rivers and other freshwater sources | Comments |
|---|---|---|---|---|---|
| **Arctic seas** | | | | | |
| ACB | Arctic Central Basin | 4,737 | 2,418 | | Deep basins, Chukchi borderlands |
| WHI | White Sea | 85 | 56 | Severnaya Dvina | Shelf |
| KAR | Kara Sea | 873 | 114 | Ob, Yenisey | Shelf |
| LAP | Laptev Sea | 654 | 552 | Lena | Shelf |
| SIB | East Siberian Sea | 895 | 52 | Indigirka, Kolyma | Shelf |
| BEA | Beaufort Sea | 447 | 1,420 | Colville, Mackenzie | Shelf & deep |
| CAN | Canadian Arctic Archipelago | na | 177 | | Shelf, Northwest Passages |
| HUD | Hudson Bay complex (HB) | 1,035 | 103 | HB Watershed | Shelf, incl. Hudson Strait & Labrador coast |
| BAF | Baffin Bay | 516 | 845 | | Deep basin |
| CWG | Coastal W Greenland | na | < 50 | River runoff, glacial and sea ice | Shelf & fjords, S of Arctic Circle |
| CEG | Coastal E Greenland | na | < 50 | River runoff, glacial and sea ice | Shelf & fjords, S of Arctic Circle |
| GRS | Greenland Sea | 898 | 1,580 | Glacial and sea ice | Shelf & deep |
| **Atlantic Arctic gateway** | | | | | |
| NOR | Norwegian Sea | 1,301 | 1,816 | Alta, Namsen | Shelf & deep, Atlantic & Arctic waters |
| BAR | Barents Sea | 1,399 | 198 | Kola-Tuloma, Pechora, Tana | Shelf, Arctic & Atlantic waters |
| **Pacific Arctic gateway** | | | | | |
| BER | Bering Sea | 2,292 | 1,547 | Anadyr, Kuskokwim, Yukon | Shelf & deep, Pacific & Arctic waters |
| CHU | Chukchi Sea | 347 | 41 | Kobuk, Noatak | Shelf |

na = not applicable or imprecise estimates.

and occur both in the Pacific and Atlantic sector of the AOAS, but with a huge geographic gap in between (cf. Section 6.3.4.3).

The marine Arctic is strongly influenced by the large rivers of the Palearctic and Nearctic continents (Tab. 6.4; McClelland *et al.* 2012) and the seasonal melt of sea ice (marginal ice zone). Arctic marine fishes are, thus, exposed to all aquatic environments ranging from the pure freshwaters of river mouths to brackish and strictly marine waters and even brine from sea ice. The fishes of the Southern Ocean, on the other hand, are environmentally isolated by the stable Antarctic Polar Front (Fraser *et al.* 2012), although eddy fields in the Drake Passage may break this oceanographic barrier (Clarke *et al.* 2005). The freshwater runoff from the Antarctic continent is negligible, and consequently the Antarctic biogeographic realm is devoid of freshwater and diadromous fishes (Lévêque *et al.* 2008).

The Arctic seas *sensu stricto* are inhabited by nearly 250 fish species (Mecklenburg *et al.* 2011). In the Antarctic, new species in the families Liparidae (snailfishes), Zoarcidae (eelpouts), Harpagiferidae (plunderfishes) and Nototheniidae (Antarctic 'cods') have been described resulting in a total of about 275 Antarctic species (Eastman 2005). The number of undescribed Antarctic species is estimated to be 30-60, presumably in the family of snailfishes (Liparidae) and other deep-sea fish families, and the level of Antarctic endemism is extreme (> 80%) compared with the fish faunas in other isolated marine habitats (Eastman 2005). The numbers of polar fish species are thus conservative, and new polar species are yet to be discovered, but *pro tem* the overall number of Arctic and Antarctic fish species appears relatively similar.

Based on the zoogeographic borders and the annotated fish checklist by Møller *et al.* (2005), polar fishes *sensu stricto* are represented by 33 Arctic and 28 Antarctic families. In addition, 10 families are encountered in both the Arctic and Antarctic regions, i.e. the bipolar fish families. Given 515 fish families globally (Nelson 2006), polar fishes thus represent nearly 14% of the known fish families. There is a striking difference between polar hemispheres in the number of families represented by only a single species, i.e. the monotypic families (Fig. 6.6). The Antarctic fish fauna has 17 monotypic families, which correspond to about 45% of all the Antarctic families. By contrast, the Arctic monotypic families constitute nine or about 21% of all the Arctic families. The numerical dominance of Antarctic monotypic families suggests a phylogenetically more diverse fish fauna. If one employs a higher taxonomic rank, however, about 75% of the Antarctic fish species have probably evolved as a result of adaptive radiation ('species flock'; Rutschmann *et al.* 2011) within one suborder, the Notothenioidei (Eastman 2005, Patarnello *et al.* 2011). Some families, on the other hand, are species-rich with 33 species of Antarctic notothens (Nototheniidae) and 40 species of Arctic sculpins (Eastman 2005). None of the bipolar families are monotypic, and they are among the most species-rich with eelpouts (Zoarcidae) and snailfishes (Liparidae) being represented by 64 and 86 species, respectively (Fig. 6.6; Section 6.3.5.1). But see Stein (2012) for an update on the Antarctic snailfishes since Eastman (2005).

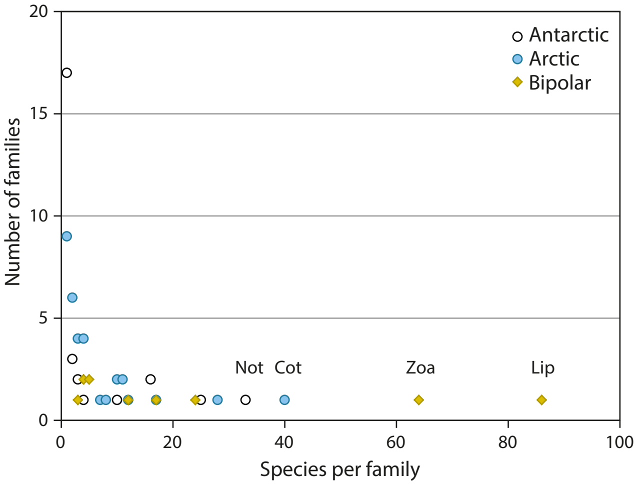

**Figure 6.6.** Relationship between number of Antarctic, Arctic and bipolar fish families and number of species within given families. Monotypic families include only one species. Not = Nototheniidae, Cot = Cottidae, Zoa = Zoarcidae and Lip = Liparidae. Data from Møller *et al.* (2005).

### 6.3.3. Regional considerations

Topographic and oceanographic peculiarities across the AOAS structure species richness and distribution. Our definition of the AOAS largely follows the geographic limits proposed by the International Hydrographic Organization (IHO online), Large Marine Ecosystems (LME online) and Jakobsson (2002). Our delineations of the southern border of the AOAS and its 16 regions are shown in Fig. 6.4. The key physical properties for each region are given in Tab. 6.4. Note that the entire southern AOAS border can be regarded as a transitional zone between boreal and Arctic waters where the interchange of marine fishes may occur (Chernova 2011). For operational reasons we depict the AOAS by two major subdivisions: the Arctic gateways and the Arctic seas. We refer also to the overview of Arctic marine ecosystems at large by Michel (Chapter 14).

The oceanographic significance of the two Arctic gateways differs markedly. About 90% of the total inflow of temperate waters into the Arctic Ocean takes place via the Atlantic Arctic gateway (Blindheim 2004), whereas just about 10% enter the Bering Strait which separates the southern and northern parts of the Pacific Arctic gateway (Roach *et al.* 1995).

The Arctic Ocean proper embraces the marginal seas of the Palearctic and Nearctic continents and the Arctic Central Basin (Fig. 6.4). The Arctic seas are mainly confined to the shallow shelves surrounding the abyssal plains and ridges of the Arctic Central Basin. The Arctic

Central Basin is largely covered with sea ice throughout the year, and it is the largest region of the Arctic Ocean with an estimated surface area of about 4.7 million km$^2$ and depths > 5,000 m.

Moreover, some of the biggest rivers in the world enter the Arctic Seas resulting in large regional deposits of fluvial sediments and low salinity waters (Tab. 6.4; Gordeev 2006, McClelland *et al.* 2012). In light of climate change, it might be tempting to examine the consequence of river discharges on regional gradients in species richness, but fragmentary and opportunistic species data (cf. Section 6.3.2.2) clearly impede credible correlations with modern increases in river runoff (Peterson *et al*. 2002).

The adjacent and nearly landlocked Baltic Sea in NE Europe and the Sea of Okhotsk in the Far East (Fig. 6.4) are seasonally covered with sea ice and may be considered sub-Arctic. They are both excluded from this overview due to their complex and in many ways atypical natural history. We refer to previous accounts of the fish faunas for the Baltic Sea (Urho & Lehtonen 2008) and the Sea of Okhotsk through the classic works by G.U. Lindberg (Ivankov 2000).

## 6.3.4. Species richness and zoogeographic patterns

### 6.3.4.1. Species richness

In their recent synthesis, Mecklenburg *et al*. (2011) reported nearly 250 fish species in the marine Arctic *sensu stricto* (see Fig. 6.4). We employ a broader geographic definition, including entire seas and, obviously, count more species than did Mecklenburg *et al.* (2011).

The 633 marine fish species in 312 genera, 106 families, 31 orders and three classes encountered in the AOAS are shown in the fish checklist (Appendix 6.2). Given a grand total of about 28,400 extant fish species in 515 families worldwide (Nelson 2006), the marine fishes in the AOAS make up 2.2% of the species and about 20% of the families worldwide. The 633 AOAS species and the corresponding number of marine fish species worldwide are shown in Tab. 6.5. In the AOAS, the hagfishes embody only a single species, *Myxine glutinosa*, whereas the cartilaginous fishes (Class Chondrichthyes) constitute 49 species or 7.7% of the total species. Bony fishes (Class Actinopterygii) are by far the principal taxon with 583 or 92.1% of the AOAS species.

The proportion of hagfishes in the AOAS appears much lower than worldwide (Knapp *et al*. 2011). However, the biological significance is doubtful since the overall number of hagfish species is low. The proportions of cartilaginous and bony fishes in the AOAS and those worldwide, on the other hand, are quite similar (Tab. 6.5). This suggests that these fish classes are equally successful at colonizing cold marine waters. The mere number of species, however, does not necessarily signify their ecological importance and, although they are few in numbers, several of the cartilaginous fishes are top predators and trophic key regulators (Baum & Worm 2009). Cartilaginous fishes are well represented in most of the AOAS regions, and this is consistent with the predominance of ecological top-down control in northern shelf ecosystems (cf. Section 6.3.5.3; Frank *et al*. 2007).

The numbers of AOAS fish species, genera and families in the 16 regions are shown in Tab. 6.6. There are huge regional differences, and the Arctic gateways are among the largest regions and, unquestionably, also the most species-rich with 75-385 species in 19-75 families. By contrast, species richness for the Arctic seas is markedly lower with only 13-87 species in 4-26 families.

**Table 6.5.** Numbers (N) and proportions (%) of marine fish species in the Arctic Ocean and adjacent seas (AOAS, this study) and those worldwide (Nelson 2006). All AOAS taxa are listed in Appendix 6.2.

| **Class** | **AOAS** | | **Worldwide** | |
|---|---|---|---|---|
| | N | % | N | % |
| Hagfishes | 1 | 0.2 | 70 | 0.4 |
| Cartilaginous fishes | 49 | 7.7 | 945 | 5.9 |
| Bony fishes | 583 | 92.1 | 15,000 | 93.7 |
| **Total** | **633** | **100** | **16,015** | **100** |

**Table 6.6.** Estimated numbers of marine fish taxa for the 16 regions in the Arctic Ocean and adjacent seas (AOAS). Note: the same species may occur in more than one region.

| **Code** | **AOAS regions** | **Species** | **Genera** | **Families** |
|---|---|---|---|---|
| **Arctic seas** | | | | |
| ACB | Arctic Central Basin | 13 | 7 | 4 |
| WHI | White Sea | 49 | 40 | 23 |
| KAR | Kara Sea | 60 | 39 | 18 |
| LAP | Laptev Sea | 50 | 30 | 15 |
| SIB | East Siberian Sea | 32 | 24 | 12 |
| BEA | Beaufort Sea | 66 | 41 | 17 |
| CAN | Canadian Arctic Archipelago | 57 | 35 | 16 |
| HUD | Hudson Bay complex | 87 | 55 | 26 |
| BAF | Baffin Bay | 81 | 49 | 24 |
| CWG | Coastal W Greenland | 59 | 42 | 24 |
| CEG | Coastal E Greenland | 40 | 33 | 19 |
| GRS | Greenland Sea | 57 | 36 | 20 |
| **Atlantic Arctic gateway** | | | | |
| NOR | Norwegian Sea | 204 | 157 | 75 |
| BAR | Barents Sea | 153 | 110 | 52 |
| **Pacific Arctic gateway** | | | | |
| BER | Bering Sea | 385 | 194 | 58 |
| CHU | Chukchi Sea | 75 | 52 | 19 |
| **Entire AOAS** | | **633** | **313** | **106** |

Notably, the number of species differs markedly within and between the Atlantic and Pacific Arctic gateways. The species richness of the Barents Sea (n = 153) is 75% that of the Norwegian Sea (n = 204) and reflects well the open nature of the Atlantic Arctic gateway. Within the Pacific Arctic gateway, on the other hand, the number of species in the Chukchi Sea (n = 75) plummets to less than 20% of the number in the Bering Sea (n = 385). The flooded Bering Land Bridge may act as a biogeographic filter for the overall interchange of fishes between the North Pacific and the Arctic seas (Tab. 6.6; Sections 6.3.2.3 and 6.3.4.3).

### 6.3.4.2. Species-area relationships

Intuitively one would expect the number of species to increase with the size of the area investigated. Indeed, strong and positive species-area relationships (SARs) have been demonstrated for a number of taxa ranging from plants to vertebrates across ecosystems (Gaston & Spicer 2004, Drakare *et al.* 2006). Water volume, and not surface area, may seem a more appropriate variable when examining species richness in 3D aquatic environments. However, most of the AOAS fishes are associated with the seabed rather than the water column (Karamushko 2012), and a study from NE Greenland suggests that ~ 95% of the species are found at or near the bottom (see Fig. 6.12; Christiansen 2012). The relationship between the number of marine fish species and surface area for 13 AOAS regions (excl. CAN, CWG & CEG) is shown in Fig. 6.7A (data from Tabs. 6.4 and 6.6).

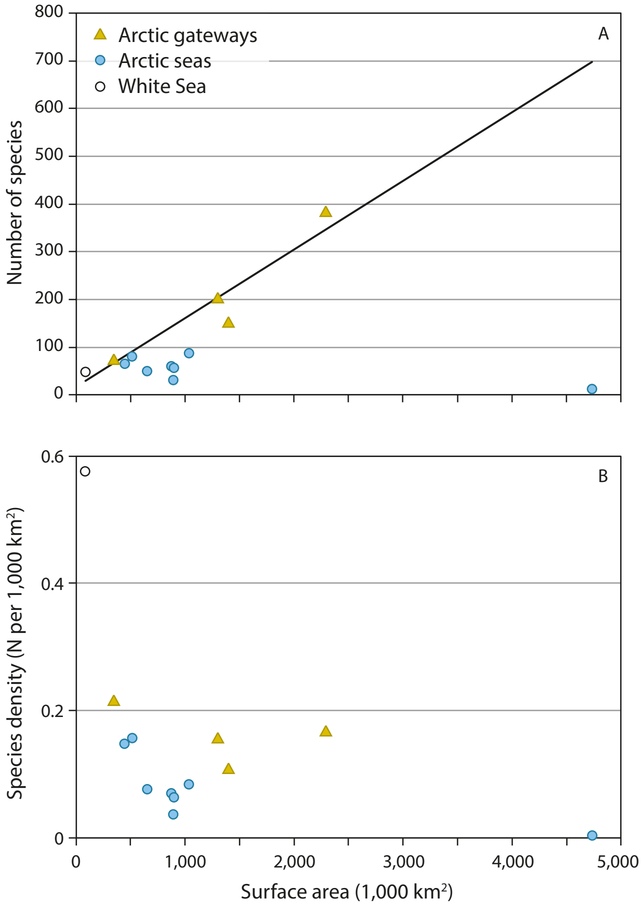

**Figure 6.7.** Panel A: number of marine fish species (*S*) vs. surface area (*A*) for 13 regions in the Arctic Ocean and adjacent Seas (AOAS) (Tabs. 6.4 and 6.6). The regression line denotes a strong relationship for the well-studied Arctic gateways and the White Sea: $S = 0.151A$, $R^2 = 0.906$ ($\alpha = 0$). Panel B: density of marine fish species (number of species per 1,000 km²) vs. surface area for the same regions. Arctic gateways = yellow triangles, Arctic seas = blue circles, White Sea = open circle. Note that the same species may occur in more than one region. See text for further information.

We presume that the numbers of marine fish species are reliable and 'true' for the relatively well-studied Arctic gateways and the White Sea compared with the other AOAS regions (cf. Section 6.3.2.2). Hence, these five seas closely fit an anticipated species (*S*, number)-area (*A*, 1,000 km²) relationship as shown in Fig. 6.7A. By contrast, the numbers of species inhabiting the Arctic seas are completely decoupled from surface area and the largest and least studied region, the Arctic Central Basin, has a disproportionately low taxa richness compared with all the other AOAS regions with only 13 species in four families (Tab. 6.6, Fig. 6.7A).

Fig. 6.7A illustrates well the innate problem of lumping 'true' and 'apparent' numbers of fish species from well-studied and little known regions. The lack of SARs for most of the Arctic seas would suggest that the numbers of species either are underestimated (i.e. 'apparent') due to poor sampling, low abundances and unresolved taxonomy or a biological reality of unknown causes (cf. the idea of 'dark diversity' by Pärtel *et al.* (2011); Section 6.3.5.3). This clearly calls for further scientific attention.

Spatial scaling, that is regional differences in surface area (Tab. 6.4), is eliminated in Fig. 6.7B and the use of species density (i.e. concentration) changes the pattern of Fig. 6.7A radically. Apart from the White Sea, the number of species per 1,000 km² lies between 0.003 (Arctic Central Basin) and 0.216 (Chukchi Sea), with a mean value of 0.107 species, and reveals no clear relationship with surface area. The White Sea, on the other hand, displays a species density fivefold that of the other seas, with 0.576 species per 1,000 km². The concept of 'biodiversity hotspots' is usually confined to terrestrial ecosystems that are characterized by high levels of endemic species (Myers *et al.* 2000). Marine biodiversity hotspots are much less investigated and are identified almost solely from tropical waters (Roberts *et al.* 2002). If we employ a simplified definition and take into account only numbers of registered species in the specific AOAS regions, the Bering Sea is indeed a marine 'hotspot' in terms of mere species richness (Fig. 6.7A), whereas the White Sea is undeniably a true Arctic marine 'hotspot' in terms of species density (Fig. 6.7B; Section 6.3.4.4).

### 6.3.4.3. Rare and disjunctive taxa

Fifteen marine fish species are considered extremely rare (i.e. rarely encountered) and endemic to the AOAS (Tab. 6.7). Holotypic species are known only from singletons

**Table 6.7.** Extremely rare marine fish species known only from holotypes (singletons) or less than five specimens. All listed species are endemic to the Arctic Ocean and adjacent seas (AOAS).

| Taxon and authority | Comments |
|---|---|
| Family Cottidae (sculpins) | |
| *Archistes plumarius*<br>(plumed sculpin)<br>Jordan & Gilbert, 1898 | BER |
| *Porocottus quadrifilis*<br>Gill, 1859 | Bering Strait – holotype in poor condition, controversial |
| Family Liparidae (snailfishes) | |
| *Careproctus attenuatus*<br>Gilbert & Burke, 1912 | BER – holotype |
| *Careproctus opisthotremus*<br>Gilbert & Burke, 1912 | BER – holotype |
| *Careproctus solidus*<br>(thickset tadpole)<br>Chernova, 1999 | LAP – holotype |
| *Crystallichthys cameliae*<br>Nalbant, 1965 | BER – holotype, controversial |
| *Gyrinichthys minytremus*<br>Gilbert, 1896 | BER |
| *Liparis grebnitzkii*<br>Schmidt, 1904 | BER – holotype, controversial |
| *Liparis mednius*<br>Soldatov, 1930 | BER – holotype, controversial |
| *Lopholiparis flerxi*<br>(hardhead snailfish)<br>Orr, 2004 | BER – 4 specimens,<br>Aleutian Islands |
| *Paraliparis violaceus*<br>Chernova, 1991 | ACB – holotype |
| Family Zoarcidae (eelpouts) | |
| *Gymnelus taeniatus*<br>Chernova, 1999 | BAR – holotype, controversial |
| *Lycenchelys alta*<br>Toyoshima, 1985 | BER – holotype, controversial |
| *Lycenchelys rosea*<br>Toyoshima, 1985 | BER |
| *Lycenchelys volki*<br>Andriashev, 1955 | BER – holotype |

kept in museum research collections and, interestingly, they are all bony fishes. Of these, eight species were described after 1955, twelve are encountered in the Bering Sea, and all belong to the three most species-rich families in the AOAS, namely snailfishes (Liparidae), eelpouts (Zoarcidae) and sculpins (Cottidae) (cf. Section 6.3.5.1). The taxonomy is still unresolved for several of these rare species.

One group of AOAS fish taxa attracts particular scientific attention due to their peculiar disjunctive geographic distribution, i.e. the amphi-boreal taxa *sensu* Berg (1934) (Tab. 6.8). Disjunctive taxa result from phylogeographic events and reveal the historical biogeography and trans-Arctic dispersal of genetically related taxa (cf. Section 6.3.1; Hardy *et al*. 2011). The genuine disjunctive taxa comprise those genera and species which occur both in the Atlantic and the Pacific sector but are absent from the seas in between. Acknowledging the poor data on species occurrences (Section 6.3.2.2), two scenarios may be envisaged for the disjunctive species: either they have performed a trans-Arctic passage and finally relocated in the Arctic gateways (dispersal events), or they represent the marginal remnants of a distribution continuum which eventually broke up and disappeared from the intervening seas as the Arctic cooled (vicariance events; see Mecklenburg *et al*. 2011 and references therein).

Several genera of cartilaginous and bony fishes – e.g. sleeper sharks (*Somniosus*), dogfish sharks (*Squalus*), herrings (*Clupea*), cods (*Eleginus*, *Gadus*), wolffishes (*Anarhichas*), sand lances (*Ammodytes*) and righteye flounders (*Limanda*) – are each represented by sister species in the Atlantic and Pacific sectors of the AOAS (Tab. 6.8). Three species occur in both sectors and may, thus, be regarded as populations: Pacific herring *Clupea pallasii*, Alaska pollock (or walleye pollock in North America) *Gadus chalcogrammus* and alligatorfish *Aspidophoroides monopterygius*. Note that for some species, subspecies are listed (Tab. 6.8), although genetic support for maintaining this taxonomic rank is as yet inconclusive. The use of the subspecies rank for marine fishes has decreased markedly in modern ichthyology (see Eschmeyer *et al*. 2010 for further discussion).

The number of taxa exhibiting amphi-boreal distribution patterns was believed to be much higher (e.g. Andriashev 1954) than is shown on the current list (Tab. 6.8), but recent studies have revealed that most of them have populations and continuous or nearly continuous distributions in the AOAS, e.g. Atlantic poacher *Leptagonus decagonus*, daubed shanny *Leptoclinus maculatus* and Greenland halibut *Reinhardtius hippoglossoides* (Mecklenburg *et al*. 2011).

A few species display exceptional distribution patterns. The Pacific population of Alaska pollock supports one of the largest whitefish fisheries in the world, whereas a minuscule Atlantic population along the northern coast of Norway is known to science from less than 70 specimens since its discovery in 1932 (Christiansen *et al*. 2005, Byrkjedal *et al*. 2008). Most interestingly, genetic lineages of the Pacific herring also occur in the Barents Sea, the White Sea (*Clupea pallasii marisalbi*) and in a small population from the secluded Balsfjord in northern Norway (Jørstad *et al*. 1994, Jørstad 2004, Laakkonen *et al.* 2013). The White Sea eelpout *Lycodes marisalbi* also displays a remarkable disjunctive distribution with occurrences in the White Sea and the Beaufort Sea (Møller 2000). However, this species may be considered amphi-Arctic since it is not known south of Bering Strait. Atlantic cod reveals another example of peculiar distribution patterns among Arctic marine fishes. Isolated Atlantic cod populations occur in coastal meromictic lakes which are highly stratified with freshwater at the surface and a deep saline layer. Thus far, eight lacustrine Atlantic cod populations have been recorded across the Arctic (Hardie *et al*. 2008; see also

**Table 6.8.** Disjunctive marine fish genera and species occurring in both the Atlantic and Pacific sectors of the Arctic Ocean, but not in the intervening Arctic seas (cf. Section 6.3.4.3). Disjunctive populations of the same species are highlighted. See text for further information.

| Atlantic sector | Pacific sector |
|---|---|
| Family Lamnidae (mackerel sharks) | |
| *Lamna nasus*<br>(porbeagle) | *L. ditropis*<br>(salmon shark) |
| Family Squalidae (dogfish sharks) | |
| *Squalus acanthias*<br>(spiny dogfish) | *S. suckleyi*<br>(spotted spiny dogfish) |
| Family Somniosidae (sleeper sharks) | |
| *Somniosus microcephalus*<br>(Greenland shark) | *S. pacificus*<br>(Pacific sleeper shark) |
| Family Clupeidae (herrings) | |
| *Clupea harengus*<br>(Atlantic herring) | *C. pallasii*<br>(Pacific herring) |
| *C. pallasii marisalbi*<br>(White Sea herring)<br>*C. p. suworowi*<br>(chosa herring) | *C. pallasii*<br>(Pacific herring) |
| Family Gadidae (cods) | |
| *Eleginus nawaga*<br>(navaga) | *E. gracilis*<br>(saffron cod) |
| *Gadus chalcogrammus*<br>(Berlevågfisk) | *G. chalcogrammus*<br>(Alaska pollock, walleye pollock) |
| *Gadus morhua*<br>(Atlantic cod) | *G. macrocephalus*<br>(Pacific cod, ogac) |
| Family Agonidae (poachers) | |
| *Aspidophoroides monopterygius*<br>(alligatorfish) | *A. monopterygius*<br>(alligatorfish) |
| Family Cyclopteridae (lumpsuckers) | |
| *Eumicrotremus spinosus*<br>(Atlantic spiny lumpsucker) | *E. andriashevi*<br>(pimpled lumpsucker)<br>*E. orbis*<br>(Pacific spiny lumpsucker) |
| Family Zoarcidae (eelpouts) | |
| *Lycodes lavalaei*<br>(Newfoundland eelpout) | *L. raridens*<br>(marbled eelpout) |
| *Lycodes marisalbi*<br>(White Sea eelpout) | *L. marisalbi*<br>(White Sea eelpout) |
| Family Stichaeidae (pricklebacks) | |
| *Chirolophis ascanii*<br>(Atlantic warbonnet) | *C. decoratus*<br>(decorated warbonnet)<br>*C. nugator*<br>(mosshead warbonnet) |
| *Lumpenus lampretaeformis*<br>(snakeblenny) | *L. sagitta*<br>(snake prickleback) |
| Family Anarhichadidae (wolffishes) | |
| *Anarhichas denticulatus*<br>(northern wolffish)<br>*A. lupus*<br>(Atlantic wolffish)<br>*A. l. marisalbi*<br>(Atlantic wolffish) | *A. orientalis*<br>(Bering wolffish) |
| Family Ammodytidae (sand lances) | |
| *Ammodytes marinus*<br>(lesser sand-eel) | *A. hexapterus*<br>(Pacific sand lance,<br>stout sand lance) |
| Family Pleuronectidae (righteye flounders) | |
| *Hippoglossoides platessoides*<br>(American plaice) | *H. elassodon*<br>(flathead sole)<br>*H. robustus*<br>(Bering flounder) |
| *Hippoglossus hippoglossus*<br>(Atlantic halibut) | *H. stenolepis*<br>(Pacific halibut) |
| *Limanda ferruginea*<br>(yellowtail flounder) | *L. proboscidea*<br>(longhead dab) |
| *Microstomus kitt*<br>(lemon sole) | *M. pacificus*<br>(Dover sole) |
| *Platichthys flesus*<br>(flounder, European flounder) | *P. stellatus*<br>(starry flounder) |
| *Pleuronectes platessa*<br>(plaice) | *P. quadrituberculatus*<br>(Alaska plaice) |

Section 6.2.2.1). From points of colonization history and dispersal processes of fishes, it is interesting to note that some of these populations apparently persist outside the extant range of ocean-dwelling Atlantic cod (Hardie *et al.* 2008). Recently, however, Atlantic cod in the Barents Sea has become abundant north and east of the Svalbard archipelago (IMR online). Finally, the extraordinary occurrence of a single specimen of Patagonian toothfish *Dissostichtus eleginoides* off Greenland may represent the first evidence of trans-equatorial migration from the Southern Ocean (Møller *et al.* 2003).

### 6.3.4.4. Zoogeographic patterns

A grand overview of the three marine fish classes in the AOAS and their zoogeographic affiliations are shown in Tab. 6.9. Given our delineation of the AOAS and definitions of zoogeographic categories (cf. Section 6.3.1), about 72% of the 633 marine fish species are considered boreal (B, 457 species) and only 10% Arctic (A, 63 species). There are, however, some notable zoogeographic traits among the AOAS fish classes. Nearly 11% of the 583 bony fish species are Arctic, whereas only a single cartilaginous species (2%), the Arctic skate *Amblyraja hyperborea*, belongs to this zoogeographic category. Cartilaginous fishes, on the other hand, dominate among the widely distributed (WD) species with a twofold higher proportion (24.5%) compared with bony fishes (11.9%). This is unsurprising since most sharks are large-bodied species capable of long-distance migrations across seas. The actual numbers and proportions of species and the corresponding zoogeographic category across the AOAS regions are shown in Tab. 6.10 and Fig. 6.8, respectively.

In Fig. 6.8, the AOAS regions are ranked according to the proportion of marine fish species with an Arctic zoogeographic pattern. There are huge regional differences, and zoogeographic gradients are evident across the entire AOAS from genuinely Arctic (A), via Arctic-boreal (AB) to the pure boreal (B) species. The proportion of

**Table 6.9.** Proportions (%) of marine fish classes in the Arctic Ocean and adjacent seas (AOAS) associated with zoogeographic patterns: A = Arctic, AB = Arctic-boreal, B = boreal, WD = widely distributed (cf. Section 6.3.1). The number of species in each class is shown in brackets and in Tab. 6.5.

| **Class** | **Zoogeographic pattern (%)** | | | |
|---|---|---|---|---|
| | A | AB | B | WD |
| Hagfishes (1) | 0 | 0 | 100 | 0 |
| Cartilaginous fishes (49) | 2.0 | 2.0 | 71.5 | 24.5 |
| Bony fishes (583) | 10.6 | 5.3 | 72.2 | 11.9 |
| All classes (633) | 10.0 | 5.1 | 72.2 | 12.7 |

**Table 6.10.** Estimated number of marine fish species in the Arctic Ocean and adjacent seas (AOAS, Tab. 6.6) associated with zoogeographic patterns: A = Arctic, AB = Arctic-boreal, B = boreal and WD = widely distributed (cf. Section 6.3.1). Note that the same species may occur in more than one region.

| **Code** | **AOAS regions** | **Zoogeographic pattern (N)** | | | | |
|---|---|---|---|---|---|---|
| | | A | AB | B | WD | Total |
| **Arctic seas** | | | | | | |
| ACB | Arctic Central Basin | 12 | 0 | 1 | 0 | 13 |
| WHI | White Sea | 15 | 1 | 28 | 5 | 49 |
| KAR | Kara Sea | 35 | 3 | 21 | 1 | 60 |
| LAP | Laptev Sea | 37 | 4 | 8 | 1 | 50 |
| SIB | East Siberian Sea | 20 | 7 | 5 | 0 | 32 |
| BEA | Beaufort Sea | 31 | 22 | 13 | 0 | 66 |
| CAN | Canadian Arctic Archipelago | 29 | 21 | 7 | 0 | 57 |
| HUD | Hudson Bay Complex | 24 | 24 | 36 | 4 | 88 |
| BAF | Baffin Bay | 33 | 22 | 21 | 5 | 81 |
| CWG | Coastal W Greenland | 16 | 16 | 24 | 3 | 59 |
| CEG | Coastal E Greenland | 12 | 10 | 15 | 3 | 40 |
| GRS | Greenland Sea | 31 | 13 | 10 | 3 | 57 |
| **Atlantic Arctic gateway** | | | | | | |
| NOR | Norwegian Sea | 21 | 16 | 126 | 41 | 204 |
| BAR | Barents Sea | 41 | 3 | 89 | 20 | 153 |
| **Pacific Arctic gateway** | | | | | | |
| BER | Bering Sea | 16 | 21 | 313 | 35 | 385 |
| CHU | Chukchi Sea | 20 | 22 | 33 | 0 | 75 |
| **Entire AOAS** | | **63** | **32** | **457** | **81** | **633** |

Arctic species within the Arctic seas (cf. Section 6.3.3) ranges from 92.3% in the Arctic Central Basin (ACB) to about 27% along the Greenland west coast (CWG) and exceeds 50% for all the central Russian seas (KAR, LAP, SIB), the Greenland Sea (GRS) and the Canadian Arctic Archipelago (CAN). The Arctic seas that border the Arctic gateways (cf. Section 6.3.3) and the temperate waters of the Atlantic Ocean proper (Fig. 6.4) reveal relatively high proportions of Arctic-boreal and boreal species. For example, the secluded White Sea acts as a biological backwater and trap for boreal species with a proportion similar to that of the Barents Sea (57-58%; Fig. 6.8).

Unsurprisingly, the Arctic gateways *per se* are completely dominated by boreal species with the Bering Sea having 81.3% boreal and only 4.2% Arctic marine fish species. Moreover, the Atlantic Arctic gateway (NOR & BAR) has the highest proportion of widely distributed (WD) marine fish species (~ 13-20%) which is consistent with

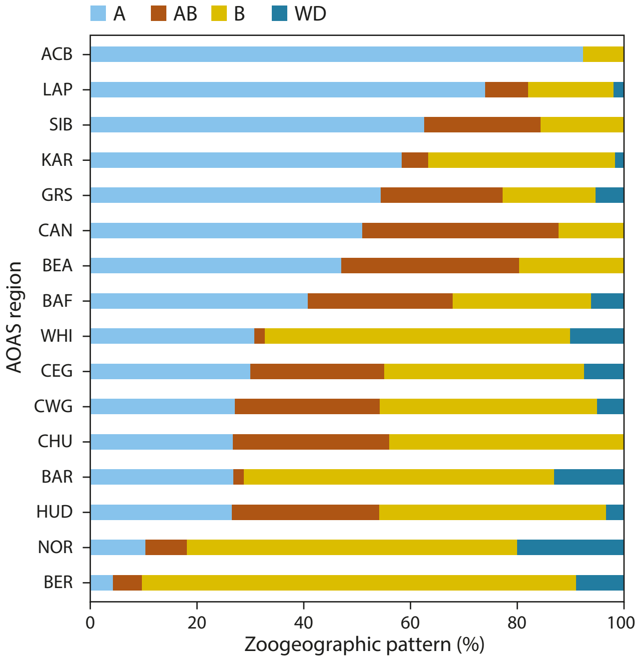

**Figure 6.8.** Proportions of marine fish species in the Arctic Ocean and adjacent seas (AOAS) associated with certain zoogeographic patterns: A = Arctic, AB = Arctic-boreal, B = boreal and WD = widely distributed (cf. Section 6.3.1, Tab. 6.10). Regional codes are given in Fig. 6.4. Note that the same species may occur in more than one region.

the relatively high numbers of migratory cartilaginous fishes in these seas (Fig. 6.8; Section 6.3.5.3).

## 6.3.5. Prominent fish taxa

This section addresses the most speciose fish families, *sensu* Hart (2008), cartilaginous fishes and other key-stone species that deserve particular attention. Comprehensive descriptions of single species and taxa are beyond the scope of this overview, and we suggest Mecklenburg *et al.* (2011) and references therein for further information.

### 6.3.5.1. Top 10 species-rich families

Nearly 60% (n = 360) of the 633 marine fish species in the AOAS are found in only 10 of the 106 families (Fig. 6.9; Appendix 6.2). Nine of the top 10 families are bony fishes, and only skates (family Rajidae) represent the cartilaginous fishes, with 27 species (cf. Section 6.3.5.3). Three families are disproportionally species-rich: the snailfishes (Liparidae, 77 species), the eelpouts (Zoarcidae, 72 species) and the sculpins (71 species). Two families also include the most species-rich genera: *Careproctus* (32 species) and *Liparis* (20 species) in family Liparidae (snailfishes) and *Lycodes* (31 species) in family Zoarcidae (eelpouts). It is noteworthy that these genera are also considered to be the most complex and controversial from a taxonomic point of view (e.g. Kai *et al.* 2011). Most species within the top 10 families are classified boreal (Section 6.3.1).

### 6.3.5.2. Arctic cods

Two gadoids (family Gadidae) are endemic to the AOAS with each genus being represented by just a single species: ice cod *Arctogadus glacialis* (Jordan *et al.* 2003) and polar cod *Boreogadus saida* (Fig. 6.10). These species are the only cryopelagic fishes, *sensu* Andriashev (1970), in the northern hemisphere as they utilise sea ice as habitat and spawning substrate. The polar cod is beyond doubt a keystone species in the marine Arctic, both in terms of mere abundance and its role as a trophic ‘wasp-waist’ species, *sensu* Bakun (2006). It is the only marine fish species that is widespread throughout the entire AOAS, including the Arctic Central Basin (Christiansen & Fevolden 2000). The elusive ice cod, on the other hand, is much less abundant and is primarily associated with fjords and Arctic shelves (Aschan *et al.* 2009, Christiansen *et al.* 2012). The two species are readily distinguished using simple morphological features for juveniles and adults and genetic markers for the larval stages (Madsen *et al.* 2009).

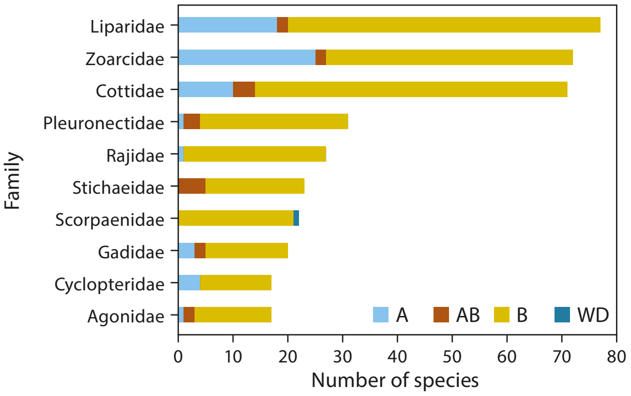

**Figure 6.9.** Numbers of marine fish species in the 10 most species-rich families in the Arctic Ocean and adjacent seas (AOAS, n = 370). Families are ranked according to number of species and zoogeographic patterns are indicated as: A = Arctic, AB = Arctic-boreal, B = boreal and WD = widely distributed (cf. Section 6.3.1, Appendix 6.2).

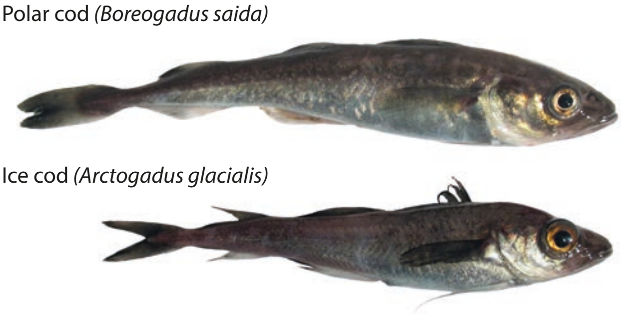

**Figure 6.10.** Endemic gadoids of the Arctic Ocean and adjacent seas (AOAS) (Christiansen 2012). The specimens are adults with a body size of 20-25 cm.

Use of vernacular names in scientific communication has led to taxonomic confusion. There are several unfortunate examples from the scientific literature where the identification of these Arctic cods has been mixed up due to lack of consistency in the use of local common names. Hence, *Boreogadus saida* is known both as ‘polar cod’ and ‘Arctic cod’ and *vice versa* for *Arctogadus glacialis*. To add further confusion, the migratory population of Atlantic cod (Norwegian: skrei, from Old Norse ‘skríða’ = to wander) is known also as ‘North East Arctic cod’, and it has been mistaken for *Boreogadus saida*.

The scientific name is conclusive and should follow the vernacular name at first mention for these species. Whenever vernacular names are used, we suggest ‘ice cod’ for *Arctogadus glacialis* (Latin: glacialis = ice; Russian: ледовая треска) and ‘polar cod’ for *Boreogadus saida*. Fish names lists representing the official stand of national and international organizations such as the American Fisheries Society and American Society of Ichthyologists and Herpetologists (Nelson *et al.* 2004) and the Fisheries Society of the British Isles (Wheeler 1992) differ and, thus, preclude establishment of universal common names. Fortunately, use of scientific names at first mention allows preferential use of vernacular names.

### 6.3.5.3. Cartilaginous fishes

The cartilaginous fishes in the AOAS comprise 49 species *in toto* with 21 shark species in 13 families, 27 skate species in family Rajidae and a single species of rabbit fish *Chimaera monstrosa* in family Chimaeridae (Lynghammar *et al.* 2013). The taxonomic subdivision Batoidea comprises skates and rays (Nelson 2006). Rays are associated with tropical and subtropical waters, whereas skates are highly successful cold-water fishes. The extant Antarctic cartilaginous fish fauna is represented solely by skates, as fossil records suggest that sharks and rays became extinct there during the Paleogene 23-65 million years ago (Long 1994).

Cartilaginous fish species are well represented in the AOAS (Tab. 6.5, Fig. 6.11). However, there are marked regional differences with the Atlantic Arctic gateway (Section 6.3.3) being the most species-rich (12-14%). Note that the disproportionately high proportion of cartilaginous fishes in the Arctic Central Basin (ACB, 15.4%) is strongly biased by the overall small number of recorded species in this area. The proportions of cartilaginous fishes in the Arctic seas of central Russia (KAR, LAP & SIB) and North America (BEA & CAN), on the other hand, are all well below the AOAS mean of 7.7% (Tab. 6.5, Fig. 6.11).

The Chukchi Sea is practically devoid of cartilaginous fishes with only a single record of a live specimen of the shark species, the spotted spiny dogfish *Squalus suckleyi*. This is intriguing as two skate species, Arctic skate *Amblyraja hyperborea* and thorny skate *Amblyraja radiata*, are present in the adjoining Arctic seas: LAP, SIB, BEA, CAN and ACB (Fig. 6.4). One would expect, therefore, skates to occur also in the intervening Chukchi Sea. This peculiar lack of cartilaginous fishes may represent a genuine example of 'dark diversity' as coined by Pärtel *et al.* (2011). Furthermore, it demonstrates that the now submerged Bering Land Bridge within the Pacific Arctic gateway is an effective barrier against the dispersal of cartilaginous fishes into the Arctic Ocean.

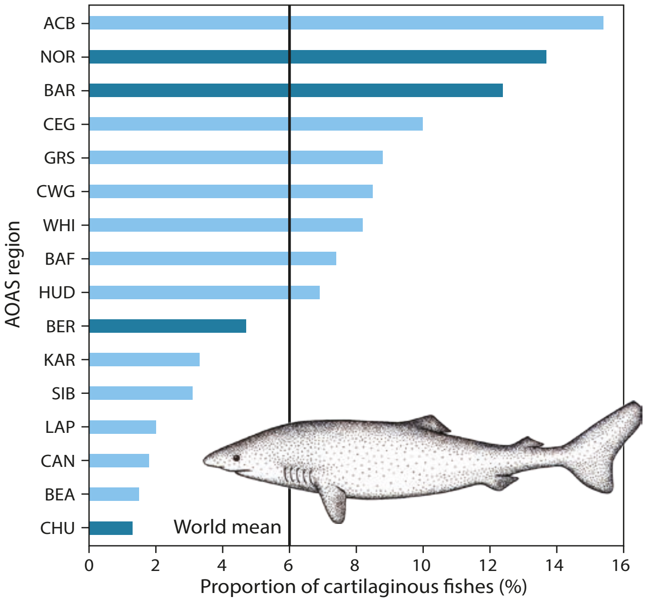

**Figure 6.11.** Proportions of cartilaginous fish species (n = 49) in the Arctic Ocean and adjacent seas (AOAS). Bars show the Arctic gateways (dark blue) and Arctic seas (light blue). Regional codes are given in Fig. 6.4. Cartilaginous fishes in the Chukchi Sea are known only from a single live specimen of spotted spiny dogfish *Squalus suckleyi*. The vertical line denotes the world mean (cf. Tab. 6.5). The inserted artwork shows Greenland shark *Somniosus microcephalus* (courtesy of Campagno 1984). Note that the same species may occur in more than one region.

About 57% of the sharks and 33% of the skates are classified *Near Threatened* (category NT), *Vulnerable* (category VU) or *Critically Endangered* (category CR) according to the IUCN Red List criteria (IUCN online). This is clearly a cause for concern (Caro & Sherman 2011). Ironically, even the common skate *Dipturus batis* species complex has become critically endangered (Dulvy & Reynolds 2009, Griffiths *et al.* 2010). We refer to Lynghammar *et al.* (2013) for a detailed account on the AOAS cartilaginous fishes.

### 6.3.6. Status and trends

For reasons given in Section 6.3.2.2, accounts on status and trends for most fishes in the AOAS are as yet speculative. Even simple measures of biodiversity are tentative, and data on population sizes are virtually non-existent except for those few species that are targeted by commercial fisheries (Section 6.3.7.3). Species richness and zoogeographic patterns for marine fishes in the AOAS are outlined in Section 6.3.4. Trend analyses, on the other hand, are futile for most marine fish species native to Arctic waters due to a lack of basic biological knowledge and fragmentary time series for specific Arctic regions. In other words, studies of the biodiversity of Arctic marine fishes are still exploratory, and unresolved taxonomic issues, lack of standardized sampling methods and inconsistent use of indices (Tuomisto 2010, Scheffers *et al.* 2012) clearly hamper comparisons across spatial and temporal scales (Merilä 2012; Section 6.3.2.2).

Currently, less than 10% of the marine fish species in the AOAS are harvested. These species are monitored and assessed by national and international research bodies, which also provide relevant and credible advice for management and policy makers (Section 6.3.7.3). By contrast, there is a dearth of biological knowledge for the remaining 90% of the AOAS fish species, and legitimate risk assessments that address vulnerability and responses to climate change and human intervention are clearly timely and imperative for this group of fishes.

As mentioned, the taxonomy of many Arctic marine fishes is unsettled and controversial, and in light of the molecular revolution, putative species-rich families are ripe for major revisions include the sculpins (Cottidae and Psychrolutidae), snailfishes (Liparidae) and eelpouts (Zoarcidae) (Section 6.3.5.1). Genomic barcoding has become a major analytical tool in fish species identification (Ward *et al.* 2009, Hanner *et al.* 2011), but molecular techniques are no substitute for conventional morphological studies. For example, strong intra-specific phenotypic variations exist among Arctic fishes (Rees & Byrkjedal 2013), and in at least one instance, barcoding has revealed that two supposedly distinct species are actually males and females of one and the same species (Byrkjedal *et al.* 2007). The combination of classic taxonomy (the phenotype) and a molecular approach (the underlying genotype) will provide not only information but also knowledge about the phylogeny of Arctic marine fishes and their environments (Naish & Hard 2008, Deans *et al.* 2012).

Polar seas are usually considered species-poor compared with lower latitudes. Recent investigations of marine invertebrates in the Southern Ocean, however, reveal a much higher biodiversity than was previously thought (Brandt *et al.* 2007, Rogers *et al.* 2012). This illustrates well that the paradigm of declines in species richness towards higher latitudes is probably overly simplistic for marine ecosystems (Clarke 1992; see also Josefson & Mokievsky, Chapter 8 and Michel, Chapter 14). The exercise of uncovering patterns in biodiversity is often regarded as unfashionable and even nonscience compared with strict hypothesis-driven studies and sophisticated modelling (Crisp *et al.* 2011; but see Boero 2009). Given this somewhat presumptuous view, it might be worth noting that the very root of 'evolution' is an inductive and meticulous recognition of patterns. The premises for deductive reasoning are largely absent for the Arctic marine fish fauna, as real-world data and knowledge are still at a level that hardly justifies making sensible hypotheses. Once credible patterns and trends start to emerge, rational questions may be asked and hypotheses tested, for example: phenotypic plasticity vs. genetic makeup, the apparent lack of SARs for the Arctic seas and the 'missing' cartilaginous fishes in the Chukchi Sea (cf. Sections 6.3.4.2. and 6.3.5.3). Key questions comprise:

- Do the observed phenotypes within taxonomically complex fish families represent few valid species or do they include cryptic species and species flocks, each with explicit requirements for conservation actions?
- Is species richness of the Arctic seas simply underestimated due to poor and incomplete sampling or a biological phenomenon of yet unknown causes?

## 6.3.7. Drivers and prospects

The ongoing loss of summer sea ice (Walsh 2008, Polyak *et al.* 2010, Cressey 2011; see Fig. 1.5 in Meltofte *et al.*, Chapter 1) has brought attention to the marine Arctic. Currently, geopolitics and economics are boosting the transition from fragmentary scientific knowledge into full-scale commercial exploitation of minerals and living resources in hitherto pristine parts of the Arctic seas: petroleum exploitation has begun, new commercial fisheries are imminent, aquaculture is pushing its limits northward, and shipping routes across the Arctic Ocean are in operation with novel pollutants such as antifouling, ballast water and noise in their wake. Recently, elevated atmospheric carbon dioxide ($CO_2$) levels and the putative effects and consequences of ocean acidification on marine biota have attracted particular attention (Quesne & Pinnegar 2011, Schmidt & Ridgwell 2011, Anderson & Mackenzie 2012, Briffa *et al.* 2012, AMAP 2013; see also Josefson & Mokievsky, Chapter 8 and Michel, Chapter 14). Legitimate grounds for concern can be ascribed to marine bioprospecting enterprises, which eagerly extract commercially valuable compounds and patent genomes from otherwise little-known Arctic organisms (Leary 2008).

It is an intricate task to disentangle the consequences of large-scale climate drivers from those of direct human interventions. Regardless of the contribution of the respective stressors, the combination of the two will inevitably affect the Arctic ecosystem profoundly, although the magnitude of impact is as yet speculative. Given the warming of the AOAS (Cressey 2011, Reid & Beaugrand 2012), forthcoming Arctic fisheries will broadly affect two groups of fishes: species that are already commercially harvested and of boreal origin, and fishes that are native to Arctic waters. Three topics deserve further attention: functional biodiversity, climate change and the effects of human interventions, such as modern fisheries and petroleum exploitation.

### 6.3.7.1. Functional biodiversity

Biodiversity should not be limited to a mere inventory of species richness but also needs to address the functional role, e.g. trophic positions and interactions, of species in Arctic fish communities (Boero & Bonsdorff 2007). Diadromous fishes often constitute a significant part of coastal fish faunas, particularly in regions where large rivers enter the Arctic seas (Tab. 6.4; McClelland *et al.* 2012). Therefore, it is important to recognise and integrate this group of fishes in future assessments of AOAS fish communities at large (Karamushko 2012).

Due to a harsh environment and seasonal food shortage, Arctic marine fishes are thought to grow and reproduce slowly, but even fundamental data on demographic structuring (e.g. von Bertalanffy growth functions), body size spectra, longevity and life history traits are lacking. Some Arctic fish species, such as Greenland shark *Somniosus microcephalus*, may be extremely long-lived (J.F. Steffensen pers. comm.), and single specimens may display a life span that corresponds to about 100 generations (~ 300 years) of capelin *Mallotus villosus*. Given ages of 'Methuselah', it is not the species *per se*, but the *personality traits of the individual animal* (Tinbergen 1963, Budaev & Brown 2011, Wolf & Weissing 2012) that play an exceptional and dominating role in shaping the ecosystem. Longevity and age structuring are neglected key demographic factors that can underpin the functioning and stability of Arctic marine ecosystems.

Vertical fluxes of bio-energy driven by pelagic-benthic couplings low in the food chain are moderately well studied in Arctic waters (Wassmann 2011). Most Arctic marine fish species are thought to be bottom dwelling and substrate spawning (Fig. 6.12; Christiansen *et al.* 1998, Christiansen 2012, Karamushko 2012). The abundant polar cod, on the other hand, constitutes a cryopelagic wasp-waist species between zooplankton and a range of top predators (Section 6.3.5.2). It is important to realise therefore that polar cod is presently the only true Arctic fish species that undertakes long-distance migrations (Ponomarenko 1968) and thus

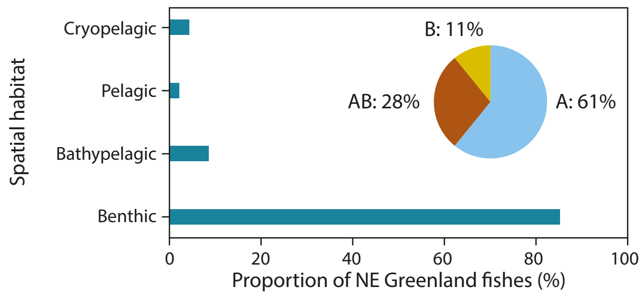

**Figure 6.12.** Spatial habitat and zoogeographic affiliation (pie chart) as exemplified by fish species (n = 47) from the Greenland Sea (Christiansen 2012). Cryopelagic fishes use sea ice as habitat (cf. Section 6.3.5.2). A = Arctic, AB = Arctic-boreal, B = boreal.

drives horizontal energy fluxes across distinct Arctic marine ecosystems, e.g. from fjords to shelves and *vice versa*. Moreover, it uses the sea ice as habitat for feeding, protection from predators and as a spawning substrate for pelagic eggs. The diminishing sea ice cover will most likely have severe adverse effects on the survival of this important species and will probably initiate a regime shift, *sensu* Lees *et al.* (2006), in the marine Arctic (Wassmann *et al.* 2011).

Patterns of biodiversity are transitional and dynamic, and turnover in species numbers and abundances is a continuous process and a natural part of evolution (Boero & Bonsdorff 2007). Crises in marine ecosystems are associated with abrupt losses of species, and the focus for conservation actions are directed accordingly (Worm *et al.* 2006). This is a debated view, however (cf. Kavanagh 2007). High species richness *per se* is not necessarily a positive attribute for the stability and well-being of an ecosystem (Węsławski *et al.* 2008, Rooney & McCann 2012). In contrast, the removal of dominant species through overharvesting (Karamushko 2012) and invasions of boreal fishes and other marine organisms may temporarily increase species richness in the AOAS. This will likely perturb ecosystem functioning as extant trophic links are disrupted and novel links formed (cf. Section 6.3.7.3). Key questions are:

- Are native Arctic marine fishes specialized or opportunistic feeders, and how does that reflect their demographic structuring? In other words, what are the trophic positions and species interactions through ontogenesis, and which are the key-stone species that depict the strength of interactions?
- How will boreal newcomers interact with polar cod and other fishes that are native to Arctic waters, and, ultimately, how will they affect pelagic-benthic couplings and the flow of bio-energy and matter in Arctic marine ecosystems at large?

### 6.3.7.2. Climate change

The indisputable warming of the northern seas during the past two decades (Reid & Beaugrand 2012) has resulted in significant ecological regime shifts in the sub-Arctic Barents (Johannesen *et al.* 2012) and Bering Seas (Grebmeier *et al.* 2006). Rapid evolutionary adaptations may to a certain extent counteract or delay putative adverse effects of environmental stressors (Hendry *et al.* 2000, Hoffmann & Sgrò 2011). Polar bony fishes (Arctic and Antarctic) have evolved an array of exceptional physiological and biochemical adaptations, e.g. biological antifreezes, to tackle environmental constraints (DeVries & Cheng 2005). These life supporting adaptations, however, may also truncate genetic variability (Patarnello *et al.* 2011) and so compromise their flexibility to overcome novel stressors, such as ocean warming and pollutants (Christiansen *et al.* 2010 and references therein).

The thermal zone of Arctic waters is narrow with ambient temperatures spanning from the freezing point of sea water (-1.9 °C) to just a few degrees above zero. Still, the thermal habitat among Arctic marine fishes is strongly structured. That is, some species occur only close to the freezing point of sea water, others only between -1 °C and zero, whereas a few species such as polar cod thrive across the entire thermal zone (Schurmann & Christiansen 1994, Christiansen *et al.* 1997). Two focal points should be noted: (1) fishes are extremely susceptible to changes in ambient temperature, and their spatial distribution will shift accordingly, and (2) fishes (species and life stages) respond differently to ocean warming, precluding uncritical extrapolation from one species and life stage to another (Christiansen *et al.* 1997, Perry *et al.* 2005).

In addition to compressing the thermal habitat of stenothermal AOAS fishes, a warmer ocean will inevitably raise standard metabolism and so reduce aerobic scope and physiological performance (Pörtner & Knust 2007, Pörtner & Farrell 2008, Dillon *et al.* 2010). Other key physiological properties may decline exponentially by a change from sub-zero to positive ambient temperatures (Christiansen *et al.* 1995). For this reason, even a slight rise in sea temperature may have disproportionately large consequences for the overall fitness of Arctic marine fishes compared with lower latitude counterparts.

The biological impacts of ocean acidification are believed to be particularly pertinent in the AOAS due to the increased solubility of atmospheric $CO_2$ in frigid waters (Fabry *et al.* 2009). Experimental studies on inland silverside *Menidia beryllina*, a boreal fish, show that embryonic tissue damages and high egg mortality are directly linked to $CO_2$ concentrations from the modern-day ~ 400 ppm to the projected level of ~ 1000 ppm by the late 21st century (Baumann *et al.* 2011). Similar investigations on fishes native to Arctic waters are lacking. Key questions are:

- What are the realized thermal habitats (niches), and what are the putative long-term effects of ocean warming on species richness, species composition and the stability of native Arctic fish communities?
- Arctic surface waters appear particularly prone to ocean acidification (Fabry *et al.* 2009). Polar cod

deposits its pelagic eggs in surface waters beneath the sea ice (cf. Section 6.3.5.2). Therefore, is this keystone species likely to be a principal target of ocean acidification?

#### 6.3.7.3. Human intervention

History has repeatedly shown that large-scale commercial exploitation of our seas moves faster than scientific insights and often with unforeseen and infamous consequences (Jackson *et al.* 2001, Palkovacs 2011). The expanding fisheries and petroleum industries are becoming the major human stressors in Arctic waters and, consequently, a strict precautionary approach towards the native Arctic fauna should be employed. For this reason, an Open Letter signed by more than 2,000 scientists, and broadcast at the International Polar Year Conference (IPY) in Montréal 22 April 2012, expresses justified alarm and strongly advocates for a fisheries moratorium in unregulated Arctic waters (PEG 2012).

Fisheries broadly comprise the small-scale artisanal and recreational catches of local importance and the high-tech commercial fishing fleets that support fishing industries worldwide. The latter activity has a long history of overexploitation and depleted fish stocks (Worm *et al.* 2009), although the state and future of modern fisheries and the recovery potential of exploited marine animals may seem less bleak than was previously anticipated (Daan *et al.* 2011, Lotze *et al.* 2011, Worm & Branch 2012). The terms 'stock' and 'population' are often used synonymously for groups of fish species, though the former refers to a harvestable management unit based upon legitimate and socioeconomic issues and the latter to a strict biological entity demarcated by population genetics and other biological features (Reiss *et al.* 2009). Politics and fisheries sciences are clearly intertwined (Froese 2011), and there may be marked discrepancies in total allowable catches (TACs) between scientific recommendations and those finally set by political decisions. Hence, a study of 11 European fish stocks showed that TAC advisories from science were typically raised by 33% following political adjustments (O'Leary *et al.* 2011).

This brief account is limited to fish species directly targeted by large-scale industrialized fisheries in the AOAS. Targeted species of southern origin that occur only occasionally or in low abundances in the AOAS are excluded. Moreover, some species are harvested in certain AOAS regions and not in others. For example, the polar cod is abundant throughout the AOAS but harvested only by Russia in the Barents Sea (Sunnanå & Christiansen 1997, IMR online).

In light of ocean warming, invasions of fish species are projected to be most intensive for the Arctic Ocean (Cheung *et al.* 2009), and the AOAS fisheries are expected to adjust accordingly (Dalpadado *et al.* 2012, Johannesen *et al.* 2012). Boreal seas house large stocks of fishes, and many of these are now moving into yet unexploited AOAS regions (Rose 2005, Wienerroither *et al.* 2011a, Renaud *et al.* 2012, Hollowed *et al.* 2013). Huge biomasses of targeted species dominate the Atlantic Arctic gateway, and their abundances in Arctic waters are likely to increase

**Table 6.11.** Selected commercial fisheries in the Arctic Ocean and adjacent seas (AOAS). Species are shown in phylogenetic order (Nelson 2006). Note: data are regularly updated by national and international advisory bodies (see text). Biomass is spawning stock including both sexes (sex ratio ~ 1:1) unless stated otherwise. Current trends in biomass for the specific stocks are depicted as positive (↑), negative (↓) or highly variable (↑↓). P = pelagic, D = demersal (cf. Section 6.3.7.3 for further information).

| Taxa | Stock | AOAS region | Habitat | Biomass (× 1,000 tonnes) | Trend |
|---|---|---|---|---|---|
| Family Lamnidae (mackerel sharks) | | | | | |
| *Clupea harengus* | Atlantic herring | NOR & BAR | P | 7,900 | ↓ |
| Family Osmeridae (smelts) | | | | | |
| *Mallotus villosus* | Barents Sea capelin | BAR | P | 2,100 | ↑↓ |
| Family Gadidae (cods) | | | | | |
| *Boreogadus saida* | Polar cod | BAR | P & D | ~1,000; uncertain | ↑↓ |
| *Gadus chalcogrammus* | Alaska pollock | BER | D & P | 8,400 | ↑ (↓)[a] |
| *Gadus macrocephalus* | Pacific cod | BER | D | 345 | ↑ |
| *Gadus morhua* | Northeast Arctic cod | BAR | D | 2,100; historical high | ↑ |
| *Melanogrammus aeglefinus* | Haddock | BAR | D | 350 | ↓ |
| *Micromesistius poutassou* | Blue whiting | NOR | P | 3,000 | ↓ (↑)[b] |
| *Pollachius virens* | Saithe | NOR & BAR | P | 375 | ↓ |
| Family Scombridae (mackerels and tunas) | | | | | |
| *Scomber scombrus* | Atlantic mackerel | NOR | P | 3,000 | ↑ |
| Family Pleuronectidae (righteye flounders) | | | | | |
| *Reinhardtius hippoglossoides* | Greenland halibut | BAR | deep P | 40-90 (females only); uncertain | ↑ |

a) See Morell 2009.

b) Surveys in autumn 2012 indicate new strong year classes for this species (IMR online; but see Payne *et al.* 2012).

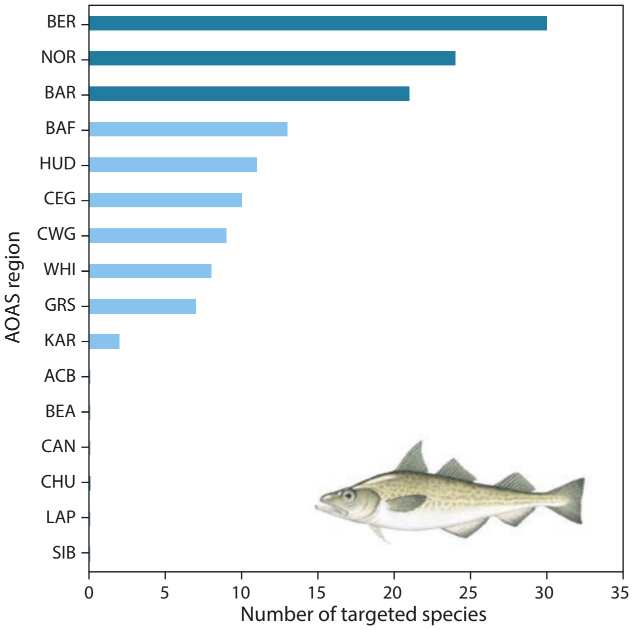

**Figure 6.13.** Number and distribution of commercially targeted fish species (n = 59) in the Arctic Ocean and adjacent seas (AOAS). Regional codes are given in Fig. 6.4. Arctic gateways are shown in dark blue and Arctic seas in light blue. The inserted illustration shows the Alaska pollock *Gadus chalcogrammus* – one of the most important fisheries resources in the Bering Sea and the world.

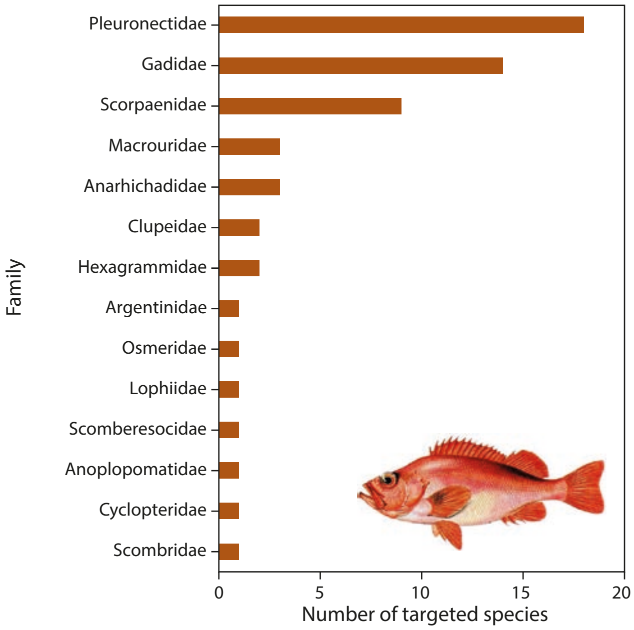

**Figure 6.14.** Number of commercially targeted fish species (n = 59) by family in the Arctic Ocean and adjacent seas (AOAS). The inserted illustration shows the red-listed golden redfish *Sebastes norvegicus* (family Scorpaenidae) – one of the most vulnerable fisheries resources in the NE Atlantic.

considerably in coming years: Atlantic cod, Atlantic herring *Clupea harengus*, blue whiting *Micromesistius poutassou*, mackerel *Scomber scombrus* and capelin (Tab. 6.11).

The AOAS stocks are regularly surveyed and monitored by several national and intergovernmental bodies as well as a range of non-governmental organizations (NGOs). We refer to the websites of FAO and WWF (worldwide), ICES and NAFO (North Atlantic sector), PICES (North Pacific sector), NOAA and VNIRO (North Atlantic and North Pacific sectors), GINR (Greenland), IMR (Atlantic Arctic gateway) and MRI (Iceland) for detailed online accounts of status, statistics and advisory procedures for these stocks (cf. References for acronyms and web-addresses). Currently, the targeted AOAS fishes count 59 species (~ 9%) in 14 families (~ 13%) (Appendix 6.2). They all belong to the bony fishes, although cartilaginous fishes, e.g. the sleeper sharks *Somniosus* spp., constitute a significant but largely unreported bycatch (Rusyaev & Orlov 2013). There are huge regional differences in the AOAS. By far the largest fisheries are found in the Bering Sea (n = 30 stocks) and the Atlantic Arctic gateway (n = 21-24 stocks; Fig. 6.13). Significant fisheries also take place along the west coast of Greenland, in Baffin Bay and around Iceland, whereas the remaining AOAS regions are characterized by small-scale subsistence fisheries among indigenous peoples mainly for freshwater and diadromous fishes (Zeller *et al*. 2011).

The most important AOAS fish families in terms of number of targeted species are the righteye flounders (Pleuronectidae, n = 18), the cods (n = 14) and the rockfishes (Scorpaenidae, n = 9) (Fig. 6.14). Some families, on the other hand, comprise only a single targeted species. For example, the Barents Sea capelin (family Osmeridae) is the largest capelin stock in the world and may reach almost eight million tonnes in top years (Tab. 6.11; Gjøsæter 1998).

The cods are without doubt the most highly prized species for human consumption in the AOAS. The Alaska pollock (Fig. 6.13) in the eastern Bering Sea supports the world's largest whitefish fishery with annual landings of about 1.3 million tonnes. Its sister species, the Atlantic cod, in the Barents Sea is presently at a historical high with a spawning stock of 2.1 million tonnes (Tab. 6.11). The cod quota shared between Norway and Russia also makes history and was recently set to 1 million tonnes for 2013 (IMR online). The large fisheries for Atlantic cod along the west coast of Greenland collapsed in the early 1970s, but a positive trend in recruitment has been observed in inshore waters since 2005 (Fig. 6.15; GINR online).

The infamous collapse of the Atlantic herring stock in the Norwegian Sea in the late 1960s (Toresen & Østvedt 2000) and that of the NW Atlantic cod stock off Newfoundland in the early 1990s (Frank *et al*. 2011) had severe and lasting socioeconomic consequences. Both Atlantic herring and Atlantic cod are long-lived species, and depleted stocks recover only slowly. Despite strict regulations, the herring stock remained depleted for almost 20 years, and just recently the NW Atlantic cod has shown signs of recovery (Frank *et al*. 2011).

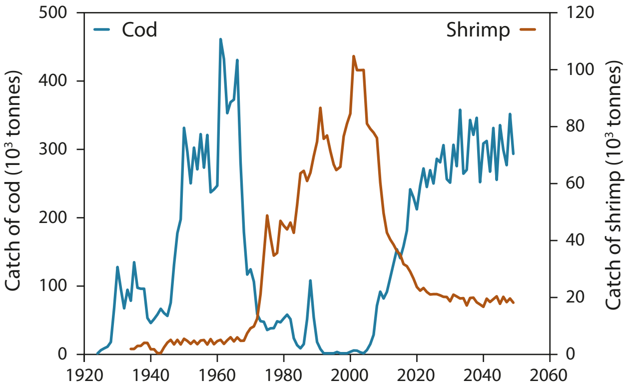

**Figure 6.15.** A socioeconomic transition from hunting to industrial fisheries took place in W Greenland around 1920. Subsequent principal fisheries are shown by the dramatic shift from a harvest founded on Atlantic cod *Gadus morhua* (~ 1920-1970) to the present-day harvest of northern shrimp *Pandalus borealis* (Smidt 1983). The harvest levels of these stocks are projected to switch again in coming years as a consequence of ocean warming (ACIA online).

The redfish stocks (*Sebastes* spp.) in the Atlantic Arctic gateway are at a historical low reinforced by recruitment failures during 1991-2005. Slow growth and late maturation in these species makes their stocks particularly vulnerable to overfishing and as bycatch in other commercial fisheries. A fishing moratorium is presently in effect, and beaked redfish *Sebastes mentella* and golden redfish *Sebastes norvegicus* (Fig. 6.14) are now included in the Norwegian Red List (Gjøsæter *et al.* 2010). Furthermore, legitimate management is confounded by the fact that redfishes are controversial both in terms of species identification and the demarcation of populations (cf. Cadrin *et al.* 2011 for further discussion). Surprisingly, the genetic population structuring of Atlantic cod is still disputed (Nordeide *et al.* 2011), although convincing and acknowledged genetic markers have been developed and employed to discriminate between stocks, for example between the migratory NE Atlantic cod stock and the resident coastal cod stocks of northern Norway (cf. Section 6.3.5.2; Sarvas & Fevolden 2005, Fevolden *et al.* 2012 and references therein).

Demersal or groundfish fisheries harvest near the seabed, whereas pelagic fisheries harvest the water column. Several technologies are employed in the AOAS fisheries, but bottom trawls for groundfishes together with purse seine nets and midwater trawls in the pelagic fisheries are undoubtedly among the most widely used gears. Bottom trawls are almost the sole gear used by Russia in the fisheries for groundfishes in the Barents Sea (Wienerroither *et al.* 2011b). Abundance trends for selected AOAS stocks are shown in Tab. 6.11. In general, the pelagic stocks show negative or highly variable trends. By contrast, groundfishes in both the Atlantic and Pacific sectors seem to be in a strong positive development. Given these prospects, intensified bottom trawling for groundfishes in upcoming Arctic fisheries will inevitably have a direct and instant effect on the sea bed and will boost the bycatch of non-targeted native fishes. Importantly, the term ‘bycatch fishes’ is exclusively anthropocentric and comprises species and sizes of no immediate commercial interest. But ‘bycatch fishes’ also includes species that are indispensable to the structuring and functioning of marine ecosystems.

Abrupt shifts in biodiversity and abundance trends are signs of ecosystem perturbation. Unfortunately, bycatch statistics from commercial fisheries are notoriously poor. In Greenland, the fishery for northern shrimp *Pandalus borealis* forms the local socioeconomic base, and in 2011 the scientific TAC was set to 120,000 tonnes (Fig. 6.15; GINR online). Bycatches are estimated to be about 1% of the shrimp catches and consist almost solely of the vulnerable redfishes. In the Bering Sea, there are no targeted fisheries for spotted spiny dogfish and Pacific sleeper shark *Somniosus pacificus*. Nevertheless, these cartilaginous fishes constitute a significant part of the bycatch in the fisheries for Alaska pollock and Pacific cod *Gadus macrocephalus*.

The Kamchatka or red king crab *Paralithodes camtschaticus* is a valuable fisheries resource and a natural component of the Bering Sea biota. In the Barents Sea, on the other hand, the red king crab is an alien species that was effectively introduced by the former Soviet Union in 1961 to establish a regional fishery along the Murman coast and the eastern Barents Sea (Orlov & Ivanov 1978). Since then, the red king crab has successfully invaded the coastal waters of Troms and Finnmark counties, northern Norway, on the west (Falk-Petersen *et al.* 2011).

In Norway, the management strategy for red king crab is ambivalent, because the species is handled both as an asset and a pest: the fisheries for crab are regulated by quotas in the eastern part of Finnmark, and a free fishery is encouraged outside the regulated areas on the west. On one hand, to serve socioeconomic demands the crab is considered an important commercial resource for the coastal fleet and, therefore, the stock should be maintained at a sustainable level. On the other hand, to serve conservation aims for native fauna, the crab is viewed as a potentially harmful alien invasive species that should be eradicated or the population minimized outside the regulated areas (see Lassuy & Lewis, Chapter 16). Red king crab is omnivorous, and recent studies show that predation from the crab has significant adverse effects on the Barents Sea bottom fauna, including egg clusters from demersal fishes (Oug *et al.* 2011; see also Josefson & Mokievsky, Chapter 8 and Michel, Chapter 14). Among the fishes at risk from additive and harmful stressors are the species-rich snailfishes, sculpins and eelpouts (Section 6.3.5.1), which are all likely to be severely affected both by upcoming Arctic fisheries, as unwarranted and unprecedented bycatch, and regionally, as prey for the invasive red king crab. In essence, an alleged benthic and resident life-style combined with a long generation time (Section 6.3.7.1; Hildebrandt *et al.* 2011) adds a completely new dimension to the vulnerability of the native Arctic marine fishes and the harmful effects that will stem from bycatch fisheries and habitat destruction caused by conventional fishing operations.

Fisheries also elicit biological phenomena that are less obvious and that may have direct and lasting implications for both targeted and non-targeted AOAS fishes. Fluctuation in abundance is a natural trait among fish populations. However, harvesting *per se* apparently amplifies abundance variability, leading to destabilized populations (Anderson *et al.* 2008, Stenseth & Rouyer 2008). Furthermore, fisheries target the phenotype and also truncate gene pools, which again may cause irreversible changes in life history traits, i.e. 'fisheries-induced evolution,' among populations (Kuparinen & Merilä 2007, Enberg *et al.* 2012, Borrell 2013).

The ecological effects of oil spills in Arctic waters are practically unknown (Sutherland *et al.* 2013), and studies of the toxicity of petroleum in Arctic marine fishes are scarce (Christiansen *et al.* 2010 and references therein). The implications of seismic activities in sub-zero waters are of particular concern, because exposure to air-guns and other human-generated noises may change migration patterns and cause species-specific physiological responses in fishes, ranging from negligible to massive tissue damage (Popper & Hastings 2009, Malakoff 2010, Slabbekoorn *et al.* 2010). This clearly calls for caution against making uncritical generalizations across fish species and marine eco-zones.

The Arctic is a sink for man-made pollutants (Macdonald *et al.* 2005), and negative consequences of human activity are demonstrated even in the remote Antarctic region (Aronson *et al.* 2011). It is noteworthy, therefore, that the highly adapted physiologies that have evolved in polar fishes in pristine environments may turn out to be disadvantageous as novel pollutants enter the Arctic Ocean (Christiansen *et al.* 1996). The seasonal build-up of large energy-rich lipid stores will inevitably boost the binding of lipophilic pollutants, and long life spans are likely to promote the accumulation of mercury and other detrimental metals (Dietz *et al.* 2009, Kirk *et al.* 2012).

To sum up the repercussions of human intervention for Arctic fisheries in particular, one should bear in mind the divergent assumptions of management practitioners and conservation biologists (Redpath *et al.* 2013). The former group regards fishes mainly as a commodity (i.e. targeted species) whereas conservationists consider the entire range of biodiversity (i.e. non-targeted and targeted species alike). Also, it is essential to acknowledge that the Arctic region is neither 'remote' nor a 'frontier' but the very centre of livelihood for indigenous peoples and, in light of the poleward displacement of commercial fish stocks, conflicts between subsistence and high-tech fisheries are imminent. For obvious legitimate reasons, Arctic indigenous peoples demand due respect for their perception and utilization of natural resources, and calls for joining traditional knowledge and science have increased (Huntington 2011). Traditional ecological knowledge (TEK) is not science *per se* but holds important complementary information to conservation biology, as it often detects local changes in climate and wildlife much faster than does science. Furthermore, TEK integrates knowledge of species, ecosystems and environments across and beyond scientific disciplines (Chapman 2007). Examples of TEK-derived information of vital scientific value include timing of biological events (phenology; Høye *et al.* 2007), changes in habitats and species distributions and identification of sites in biodiversity monitoring (cf. CAFF-Circumpolar Biodiversity Monitoring Program (CBMP); Saslis-Lagoudakis & Clarke 2013).

## 6.3.8. Conclusions and possible conservation actions

### 6.3.8.1. Key knowledge gaps

Once patterns of biodiversity emerge, it is essential to identify the underlying processes to counteract negative trends. Still, patterns remain fragmentary for the majority of fishes in the Arctic Ocean and adjacent seas (AOAS). The following issues are suggested to increase present knowledge to a point where sensible hypotheses may be proposed and tested, credible forecasts made and legitimate actions executed (Christiansen *et al.* 2013):

1. Long-term time series of real-world and diagnostic data are essential for forecasting biological and environmental trends. Therefore, key sites and baseline transects for long-term studies of functional biodiversity should be identified in the AOAS (cf. CBMP online).
2. Natural history collections (NHC) hold essential information for studies of biodiversity (Harrison *et al.* 2011, Lister *et al.* 2011), and information from fishery logbooks has proven valuable in historical analysis of population trends (Alexander *et al.* 2009). Therefore, NHCs should be continuously upgraded and archival data critically examined and employed to reconstruct long-term time series for specific AOAS regions.
3. Taxonomy and conservation are two sides of the same coin. Classic taxonomy is a critically endangered science and a craft that cannot be substituted by DNA profiles and gigabytes (Bacher 2012, Deans *et al.* 2012, Scotland & Wood 2012). Therefore, training programs in taxonomy *sensu lato* and biogeography for young researchers should be encouraged.
4. Habitats of particular significance for conservation, such as breeding grounds and biodiversity hotspots, should be identified in time and space and protected accordingly, cf. the debate on Marine Protected Areas (MPAs) (Henriksen 2010, Barry & Price 2012, Rice *et al.* 2012).
5. Fishing gear technology designed for sustainable fisheries in Arctic waters is poorly developed. Multidecadal datasets from the North Sea unequivocally demonstrate that conventional bottom trawl fisheries for groundfishes are extremely efficient but also

highly damaging to the environment, as they impoverish, perturb and change the functional composition of benthic communities (Tillin *et al.* 2006, Thurstan *et al.* 2010). Arctic fish species are largely bottom-living and territorial (Karamushko 2012), and since Arctic groundfish fisheries are expected to increase in coming years, less harmful fishing technologies should be developed and used to minimize bycatch and seabed destruction.

6. Abrupt shifts in abundance trends are warning signals for conservation. Therefore, accurate bycatch statistics in upcoming Arctic fisheries are crucial and call for adaptive monitoring plans and policies to meet conservation aims (Lindenmayer *et al.* 2012). A range of management policies for marine fisheries are in operation worldwide (Pitcher & Lam 2010), and fisheries founded on balanced rather than selective harvesting are currently debated (Garcia *et al.* 2012, Borrell 2013). No single harvesting practice is foolproof. But any management policy would be desireable if it relies on the principle of full accountability – that is a procedural change from the present-day selective fishing and fixed landing quotas of targeted species to catch quotas that embrace the entire biomass extracted from the sea, i.e. targeted and non-targeted species alike. For example, catch quota management (CQM) seems a promising policy that has been tentatively implemented in the North Sea fisheries (Kindt-Larsen *et al.* 2011, Schou 2011). Combined with taxonomic expertise on non-targeted Arctic species, CQM may well be the immediate and first step toward obtaining credible and urgently needed bycatch data as a precautionary measure for upcoming Arctic fisheries.
7. Traditional ecological knowledge (TEK) and citizen science (Hochachka *et al.* 2012) would generate valuable and complementary information that should be critically scrutinized to increase the legitimacy of biodiversity assessments across the marine Arctic. This would require a completely new setting, and a designated forum of TEK-informants and scientists is called for, to ensure that trust-building and respectful and equal sharing of information and methods are also put into practice.
8. An ambitious interdisciplinary science plan should be outlined and implemented as a precautionary and fundamental measure to meet large-scale human intervention in understudied Arctic waters (cf. PEG 2012).

#### 6.3.8.2. Other key messages

Taxonomic inventories for marine fishes (cf. Appendix 6.2) are not mere ‘stamp collections’ but an absolute necessity for biodiversity and conservation biology. However, their completeness differs vastly both geographically and among marine habitats (Mora *et al.* 2008). Arctic societies are based on living natural resources, and any socioeconomic progress is inevitably rooted in sound ecosystems. The data available for the AOAS fishes are admittedly precarious, and lack of proper species identifications, demarcations of populations, and data on functional biodiversity are the most severe shortcomings for conservation and credible management of the Arctic seas. Hence, scientific uncertainty (Dankel *et al.* 2011) is a key factor in Arctic marine biodiversity assessments and underlines the importance of precautionary approaches. Issues of marine biodiversity, conservation and the ecological effects of climate change and human intervention are addressed by several international forums such as the Arctic Council, ICES, PICES, Census of Marine Life, Ramsar Convention on Wetlands and numerous NGOs (Bluhm *et al.* 2011). A much stronger coordination among and within these bodies is needed to harmonize assessments and facilitate the transition from general principles to operational conservation actions for the AOAS fishes.

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Appendix 6: www.abds.is/aba-2013-appendix-6

The mirid bug *Chlamydatus pullus* feeding in a flower head of the dandelion *Taraxacum croceum* in the preserved herb field of Østerlien near Arctic Station at Godhavn/Qeqertarsuaq on Disko Island, W Greenland. Photo: Jens J. Böcher.

## *Chapter 7*

# Terrestrial and Freshwater Invertebrates

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## Contents

> **Big new insects have appeared, beetles that fly.**
>
> [American buring beetle]
> Jolene Nanouk Katchatag an Inupiaq from Unalakleet, Alaska;
> Mustonen & Mustonen 2009.

> **Now the black flies appear before the mosquitoes, this is something new.**
>
> Komi Irina Kaneva from the Krasnochelye wilderness village
> on the Kola Peninsula;
> Mustonen 2011.

> **Judging by the last year there are almost no mosquitoes left in Lovozero [Luujavre]. It can be real evidence that climate is changing. Even some species of southern bugs and spiders appeared in tundra.**
>
> Vladimir Galkin, a member of the Sámi community Piras
> on Lovozero Lake in the Murmansk region of Russia;
> Mustonen & Zavalko 2004.

## SUMMARY

The known terrestrial and freshwater invertebrate faunas of the Arctic comprise several thousand described species, representing over 16 major phyla. Many other species remain to be discovered and/or described. Arctic endemic species occur in many invertebrate groups. A significant proportion of Arctic species have circumpolar distributions. By comparison with better known groups such as vertebrates and plants, the invertebrates exhibit much higher biodiversity at all taxonomic levels and attain greater population densities in favorable habitats. Springtail (Collembola) numbers, for example, sometimes exceed $0.5 \times 10^6/m^2$ and eelworm (Nematoda) populations reach over $7.0 \times 10^6/m^2$ in areas of Taimyr.

Little is know about the detailed distribution and biology of most species, and good long-term population data on individual species, sufficient to indicate population trends, are almost entirely lacking. Predictions of how Arctic invertebrate communities may respond to climate change are, of necessity, based on extrapolations from experimental and/or distributional studies based on a few selected species or species groups in a restricted range of habitats.

This chapter brings together, and highlights for the first time, baseline information on the biodiversity of all Arctic terrestrial and freshwater invertebrates. It evaluates the importance of habitat diversity, climatic severity and biogeography, particularly historic patterns of glaciations, as determinants of invertebrate biodiversity. The significance of the Beringia refugium for biodiversity in several groups is stressed. Invertebrates are key players in a range of ecosystem services within the Arctic, including herbivory, decomposition, nutrient cycling, pollination, parasitism and predation.

Changes in invertebrate communities, perhaps involving new invasive species, may have important impacts on several of these processes, particularly through interactions with other groups of organisms. The key environmental factors (drivers) determining species success in an era of climate warming are likely to be mean summer and winter temperatures, soil-moisture availability, length of growing season and the frequency of freeze/thaw events that may disrupt preparation for and emergence from the overwintering state.

Several recommendations for future action are listed. Highest priority should be given to establishing an inventory of Arctic invertebrate species, including their distribution, habitat preference and ecological function. This list should be used to identify true Arctic endemic taxa, classify species according to IUCN Red Book criteria and identify the vulnerability of species and their habitats. Key indicator species that are responsive to habitat change should be identified and monitored. For a group as diverse as the invertebrates, conservation action should focus on the maintenance of habitat diversity coupled with the selection of ecologically important flagship species that can provide a focus for raising the profile of invertebrates as a whole.

## 7.1. INTRODUCTION

The observations by indigenous peoples given on the title page of this chapter, often made in association with traditional activities such as reindeer herding, hunting and fishing, clearly suggest that profound changes are occurring in the invertebrate faunas of the Arctic regions. This chapter attempts to set a baseline for invertebrate biodiversity within the Arctic, to document the scientific evidence for such change and to provide a prognosis and recommendations for the future.

Even within the scientific community, the biodiversity of invertebrates inside the Arctic is poorly understood by non-specialists and is thus frequently underplayed or sometimes ignored. The CAFF Habitat Conservation Report No.4 (Principles and Guidelines), for example, states that “invertebrate fauna in the Arctic is scarce” (CAFF 1996), a statement far removed from reality. Collectively, the number of Arctic invertebrate species greatly exceeds that of all other non-microbial eukaryotic species groups combined, including the plants and the vertebrates. Furthermore, invertebrates are often found at densities of several hundred thousand, and occasionally several million, per square meter. Arctic invertebrate faunas are thus far from simple, but their complexity is less overwhelming than for many tropical ecosystems, and their diversity is perhaps more readily understandable (Danks 1990, Vernon *et al.* 1998).

The mistaken idea of an overly ‘simple’ Arctic invertebrate food web almost certainly owes its origin to a summarizing diagram of the nutrient flow pathways through the ecological community of Bjornøya, Svalbard, published by Charles Elton in 1923 (Hodkinson & Coulson 2004). This diagram, erroneously interpreted as a ‘simple’ food web, still holds sway in several modern ecology textbooks. In such diagrams, it is assumed that individual species within related invertebrate groups are ecologically interchangeable, performing similar ecological functions or responding in similar ways to environmental change. They are in consequence usually consigned together, for example to a ‘box’ labeled ‘ciliates’ or ‘Collembola’. This assumption of species equivalence is mistaken, and important components of biodiversity become hidden when species are aggregated and compartmentalized in this way. Take for example the unicellular ciliates, a group whose biodiversity is poorly known within much of the Arctic. Despite their relatively simple body form, the freshwater ciliates of Svalbard fall into eight different trophic groups, each feeding on different microscopic prey categories representing various trophic levels and with individual species performing different ecological roles (Petz 2003). Similarly, species within several of the larger groups of Arctic invertebrates such as eelworms (Nematoda), springtails (Collembola), mites (Acari), flies (Diptera) and ground beetles (Coleoptera), to name but a few, display a similarly wide range of multi-trophic feeding specializations and adpatations (Chernov 1996, Rusek 1998, Chernov 2002, Makarova & Böcher 2009, Peneva *et al.* 2009). Trophic, behavioral and physiological divergence among related species is thus an important yet frequently overlooked component of invertebrate biodiversity within the Arctic.

Many invertebrate species are endemic to the Arctic and display highly restricted distributions. However, being small and lacking the charisma of their vertebrate and floral counterparts, few have received special conservation status, despite their vulnerability to climate change. A notable exception is the round spine tadpole shrimp *Lepidurus couesii* found in the American Arctic and listed as 'endangered' in the IUCN Red Data List. By contrast, many other Arctic invertebrate species are broadly distributed across a wide circumpolar range and display unusually wide within-species genetic diversity, or differences in their methods of reproduction, throughout their geographical range (Hobaek & Weider 1999, Reiss *et al.* 1999, Hessen *et al.* 2004, Wheat *et al.* 2005). Because of their small size and mobility, terrestrial and freshwater invertebrates are well-adapted to the multiplicity of different microhabitats generated by macro- and microtopographic variations in the landscape, interacting with climatic differences and the contrasting biotic environments created by different plant species and communities (Coulson 2000). Many species show strict fidelity to particular restricted microhabitat types, whereas others are more generally distributed across a range of habitats. Such variation in habitat occupancy is an important facet of biodiversity within the Arctic.

This chapter seeks to present a balanced assessment of invertebrate biodiversity and population trends within the Arctic regions. The quantitative data presented represent the best estimates available, but it should be recognized from the outset that our knowledge of Arctic invertebrates is far from complete, especially for many of the microscopic soil-dwelling forms. Our current understanding of their biodiversity rests on the extent and quality of available data and the reliability of the methods used to obtain those data. For many invertebrate groups, our knowledge of their distribution is based on a few samples taken from selected habitats at a few well-studied sites. Often these inadequacies are compounded by taxonomic problems, particularly a lack of critical comparison of species across different regions of the Arctic. Furthermore, large areas of the Arctic remain under-sampled for many invertebrate groups. Current sampling methods may also fail to record all species present, as evidenced by divergence between studies of soil fauna using traditional extraction techniques coupled with morphological taxonomy versus those based on the direct extraction of animal DNA from soil (Wu *et al.* 2009). Among ciliates and testate amoebae, for example, the number of described species may represent only a fraction of the total number of species present (Foissner *et al.* 2008, Smith *et al*. 2008). Even in relatively well-known groups such as the springtails, molecular techniques are also beginning to reveal the presence of sibling species not discernible by traditional taxonomy based on morphology (Hogg & Hebert 2004).

Species abundance distributions for invertebrate communities normally follow patterns in which the community is dominated by a few common species supported by a long tail of less common species, as for example in the Arctic testate amoebae on Richards Island, Canada (Dallimore *et al.* 2000). From a biodiversity perspective, this tail is highly significant but is rarely adequately sampled. The Arctic can also still produce surprises, as evidenced by the relatively recent discovery of *Limnognathia maerski*, a representative of an entirely new Class of animal, the Micrognathozoa, in a cold spring on Disko Island, W Greenland (Kristensen & Funch 2000). This species has subsequently been found on the sub-Antarctic Crozet Islands and is probably much more widely distributed than is currently recorded (De Smet 2002).

Population density estimates exist for many terrestrial and freshwater Arctic invertebrates in a variety of habitats (e.g. Hammer 1944, Coulson 2000, Sorensen *et al*. 2006), but these are often spot estimates, and there are few if any data sets that reliably indicate population trends over extended recent time periods. Even the more detailed population studies, with repeated sampling, rarely extend for periods greater than 3-5 years (e.g. Addison 1977, Hodkinson *et al.* 1998, Søvik 2004). Frequently, such population estimates have been made for taxonomic groups combined, such as for the total springtails or oribatid mites, rather than for individual species. It is thus difficult to identify shorter term trends in individual species populations associated with environmental change, and it is here that manipulation experiments are important. Such experiments, measuring experimentally the response of invertebrate populations to climate manipulation and ideally linked to laboratory-based physiological studies, probably give us the best clues as to the direction of potential future change (Hodkinson *et al.* 1998). The woolybear caterpillar *Gynaephora groenlandica* in Canada provides a good example of such a study (Kukal & Dawson 1989, Morewood & Ring 1998, Bennett *et al.* 1999). However, where a vertebrate ecologist might regard a drop of 25% in a species population density as significant, invertebrate ecologists struggle to estimate mean population densities of even the commoner species with an associated statistical error of less than 25%. Furthermore, invertebrate populations are often highly aggregated and frequently display wide natural fluctuation over short time scales and across topographically diverse landscapes (e.g. Høye & Forchhammer 2008). Their densities and the associated fluctuations are thus normally expressed on the logarithmic rather than the more sensitive linear scale. Invertebrates are also capable, within limits, of shifting their population center to more suitable habitat in response to deteriorating conditions. Several species of springtails, for example, track optimum soil moisture status across a drying landscape within a given season, confusing population estimates at any one fixed point (Hayward *et al.* 2001).

Despite the limitations listed above, the stratigraphy of subfossil remains of invertebrate groups within the Arctic such as beetles, chironomid midge (Chironomidae) larvae, testate amoebae and ostracod crustaceans (Ostracoda) have successfully been used to indicate past climatic conditions and the way these conditions have changed over time (e.g. Bobrov *et al.* 2004, Wetterich *et al.* 2005, Zinovjev 2006, Thomas *et al.* 2008, Porinchu *et al.* 2009, Elias 2000a, 2000b, 2009a, 2009b). Comparison of the species composition of these subfossil assemblages with the known distribution and environmental preferences of the same species today indicates the likely conditions that prevailed when the subfossil invertebrates were deposited. Examination of the different temporal assemblages in successive strata permits the reconstruction of changing palaeoclimatic conditions at a given locality over historical time.

Large areas of the Arctic are occupied by mesic and wet tundra, grading into shallow pools, ponds and lakes where the transition between terrestrial and aquatic habitats becomes blurred. Several important groups of organisms, notably ciliates, testate amoebae, rotifers (wheel animals), tardigrades (water bears), nematodes (eelworms) and enchytraeid worms, are commonly found in both terrestrial and aquatic habitat types, and several nominally terrestrial arthropod species are typical of the marine littoral zone. Some Arctic taxa, usually thought of as aquatic, such as chironomid midge larvae, contain terrestrial species, as in the genus *Smittia*. Similarly, the predominantly 'terrestial' springtails contain 'aquatic' species such as *Heterosminthurus aquaticus*, *Podura aquatica* and *Sminthurides aquaticus* (Babenko & Fjellberg 2006, Deharveng *et al.* 2008). For these reasons the non-marine Arctic invertebrates are considered here as an integrated whole rather than split artificially into terrestrial and aquatic groups. Invertebrates that are endoparasites of other terrestrial, freshwater and marine animals are considered by Hoberg & Kutz, Chapter 9.

Emphasis within this chapter is, of necessity, placed on documenting, essentially for the first time, the true biodiversity and abundance of the entire terrestrial Arctic invertebrate fauna and the driving factors that determine that diversity. Available knowledge of these organisms is sparse, precluding prediction of future population trends for the majority of species. Nevertheless, potentially important indicator groups are highlighted wherever possible and recommendations for future action are given.

## 7.2. STATUS OF KNOWLEDGE

To appreciate fully the biodiversity of invertebrates within the Arctic and how it might respond to environmental change, we initially need to

- Comprehend the wide diversity of life forms that are likely to be present in any one area at a given time.
- Appreciate how and why the Arctic fauna varies in composition and abundance among habitat types and across the different geographical regions of the low and high Arctic.
- Consider how and why invertebrate diversity in the Arctic differs from that of other life zones and the potential for colonization of the Arctic by invertebrates from further south.

The following sections address these issues.

### 7.2.1. Terrestrial Arctic invertebrate biodiversity

#### 7.2.1.1. An invertebrate biodiversity profile for a high Arctic region, Svalbard

Probably the most complete inventory of the invertebrate fauna for any Arctic region is for the high Arctic Svalbard archipelago (Tab. 7.1) (Coulson 2000, 2007, Coulson & Refseth 2004). This list illustrates the taxonomic profile of diversity across all invertebrate groups and carries a number of caveats. It is primarily based on a literature survey, which is prone to problems of misidentifications and synonymies (Danks 1981). Sampling on Svalbard, moreover, has historically been concentrated around accessible sites along the west coast, whereas the more remote eastern islands tend to be undersampled. Nevertheless, despite the fact that the climate of Svalbard is relatively warm for its latitude, the inventory is highly typical and displays the general taxonomic profile observed throughout the Arctic regions.

The terrestrial and freshwater invertebrate fauna of Svalbard, while containing fewer individual species than the equivalent faunas of the low Arctic and of the temperate and tropical regions, is still complex. It currently contains 1308 species and 556 genera spread across 16 phyla and 27 classes. For those unfamiliar with invertebrate classification, the insects, perhaps the most familiar group, represent a single Class within the Phylum Arthropoda. The dominant groups in terms of species representation are amoebae, ciliates, rotifers, tardigrades, nematodes, mites, springtails and insects, particularly those belonging to the order of flies (Diptera). Chernov (2002) highlights the dominance of the more 'primitive' groups of invertebrates within such faunas, at the expense of more advanced forms. He argues that the more 'primitive' (phylogenetically basal) forms are better able to adapt to the severe conditions and that the more advanced groups such as the insects, because of their evolved specialisms such as close dependence on specific host plants, find adaptation to Arctic conditions more difficult. He notes that worldwide there are 130 and 16 times more species of insect than of springtails and Arachnida (spiders, mites etc.), respectively. In the low Arctic, however, these ratios shrink to eight and three, and in the high Arctic numbers of springtails and Arachnida species often equal or exceed those of the insects. Similarly, only slightly more than half of the insect orders are represented in the low or high Arctic. In large insect orders like the flies and ground beetles, family representation is only 40 out of 130 and 17 out of 170, respectively (Chernov 2002). Even within speciose groups like the dipteran flies, which may make up 75% of the insect fauna of polar deserts, the dominant families/superfamilies such as the chironomid midges and craneflies (Tipuloidea) tend to fall within the less specialized lower dipteran flies, although some higher Diptera, e.g. house flies (Muscidae) and root-maggot flies (Anthomyiidae), are also well represented (Brodo 1990, Chernov 1996). The most abundant dipteran flies are almost invariably species with aquatic or semi-aquatic stages. Chernov (2002) argues that the Arctic invertebrate fauna results not merely from a gradual species impoverishment occurring as part of a latitudinal trend in diversity among higher taxa, but also from the realization of the adaptive potentials of certain, albeit more 'primitive' or basal, phyletic lineages that increase in dominance. The Arctic fauna, he contends, should be considered distinctive, with its own characteristic composition related to the adaptive success of some of the constituent taxa.

A striking feature of high Arctic faunas that reflects this adaptational trend is the greatly reduced numbers of above-ground herbivores, particularly insects, feeding on the higher terrestrial plants and the decreasing proportion of terrestrial versus aquatic insects (mainly dipteran flies) (Fig. 7.1) (Danks 1992). On Svalbard, for example, the invertebrate herbivores are dominated by 2-3 aphid (plant lice; Aphididae) species, a few sawflies (Tenthredinidae) and a single weevil (Curculionoidea) (Hodkinson & Coulson 2004). The great majority of the invertebrate species, at least during their immature stages, inhabit the soil surface or live variously within soil or aquatic habitats.

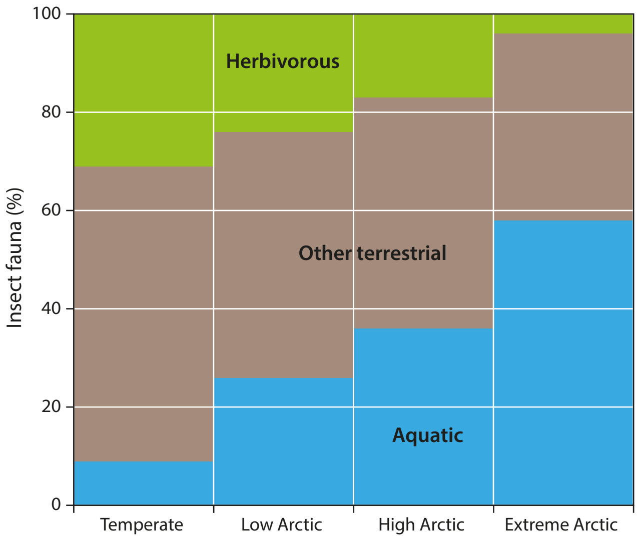

**Figure 7.1.** The changing relative percentages of herbivorous, aquatic and other terrestrial insect species groups with respect to increasing climate severity within the Arctic regions of North America. Note that the aquatic species are predominantly dipteran flies with larval aquatic stages and water beetles (redrawn from Danks 1992).

### 7.2.1.2. A biodiversity profile for a selected group, Arctic insects within the Nearctic region

Having established the general composition of a typical Arctic fauna across all taxa, we will examine the diversity *within* an example of one of the most widely represented taxa, the insects. The most wide-ranging and complete inventory of Arctic arthropods and their distribution is Danks's monumental work on the Arctic arthropods of North America (Danks 1981, Danks & Smith 2009). While this is inevitably dated with respect to both nomenclature and species completeness, the information it contains allows a more detailed analysis of major patterns of general biodiversity within an important component of the Arctic fauna over a wider area. Tab. 7.2 summarizes the diversity for insects, arranged by families with the number of genera and species indicated. There are 143 families spread over 14 orders. The large number of families represented indicates that the Arctic fauna is a derived assemblage of species representing many major evolutionary lines. There are no endemic Arctic orders or families. Many of the families, which are highly speciose in temperate/tropical regions, are represented by a single genus, and many of the genera are represented by a single or just a few species. This suggests that a wide diversity of insect taxa reach their limits of distribution and adaptational tolerance within the low Arctic. Over 60% of the families present in the low Arctic are absent from the high Arctic. There is a proportionate reduction in the average number of species per family present from 11.0 in the low Arctic to 5.8 in the high Arctic. This reduction, however, is not uniform across families. If we set a criterion of a minimum of 20 species per family, the most speciose insect families present in the low Arctic are lice (Philopteridae), aphids, ground beetles, water beetles (Dytiscidae), rove beetles (Staphylinidae), craneflies, black flies (Simuliidae), chironomid midges, empid flies (Empididae), thick-headed flies (Dolichopodidae), hover flies (Syrphidae), house fly type groups (Muscidae and Anthomyiidae), looper-moths (Geometridae), noctuid moths (Noctuidae), sawflies and ichneumon parasitoid wasps (Ichneumonidae).

The generality of these trends is reinforced by data from Svalbard, Greenland and the Palearctic region in general (Coulson 2000, Konstantinov *et al.* 2009, Böcher & Kristensen in press). For example, beetles of the families Carabidae (ground beetles), Staphylinidae (rove beetles) and Dytiscidae (water beetles) are the dominant beetle groups in Arctic mainland Norway and Russia, but Latridiidae (minute scavenger beetles) and Chrysomelidae (leaf beetles) become more significant elements in the fauna at the highest latitudes (Chernov *et al.* 2000, 2001, Olsvik *et al.* 2001, Chernov 2002, Chernov & Makarova 2008). Craneflies (inc. Limoniidae), chironomid midges, empid flies, thick-headed flies, hover flies and house flies are listed by Chernov (1996) as the most common Arctic dipteran fly families.

**Table 7.1.** A typical biodiversity profile across invertebrate taxa for a high Arctic region: the diversity of the terrestrial and freshwater invertebrates of Svalbard, listing the number of families, genera and species for each known group. Data are based on revised versions of Coulson (2000, 2007) and Coulson & Refseth (2004). The list includes occasional presumed vagrants and introductions. The table retains the animal classification used in the original work: more recent updates of the classification for some groups, such as the rotifers, are given in Tab. 7.3.

| Phylum | Class | Order | Families | Genera | Species |
|---|---|---|---|---|---|
| **Sarcomastigophora** (flagellates) | Heliozoea | | 3 | 3 | 3 |
| | Zoomastigophorea | | 1 | 1 | 2 |
| **Rhizopoda** (amoebae) | Filosea | Gromiida | 5 | 11 | 53 |
| | Lobosea | Amoebida | 1 | 1 | 1 |
| | | Arcellinida | 13 | 23 | 145 |
| **Ciliophora** (ciliates) | Kinetofragminophorea | Colpodida | | 4 | 4 |
| | | Cyrtophorida | | 2 | 2 |
| | | Nassulida | | 3 | 3 |
| | | Pleurostomatida | | 2 | 2 |
| | | Prostomatida | | 7 | 7 |
| | | Suctorida | | 1 | 1 |
| | | Synhymeniida | | 1 | 1 |
| | Oligohymenophorea | Hymenostomatida | | 4 | 6 |
| | | Peritrichida | | 5 | 7 |
| | | Scuticociliatida | | 3 | 3 |
| | Polyhymenophorea | Heterotrichida | | 3 | 3 |
| | | Hypotrichida | | 6 | 9 |
| | | Oligotrichida | | 4 | 5 |
| **Apicomplexa** (sporozoans) | Sporozoea | Coccidea | | 3 | 3 |
| **Rotifera** (rotifers) | Digononta | Bdelloidea | 3 | 8 | 38 |
| | Monogononta | Collothecacea | 1 | 1 | 5 |
| | | Flosculariacea | 2 | 2 | 3 |
| | | Ploimida | 12 | 30 | 122 |
| **Gastrotricha** (gastrotrichs) | | Chaetonotida | 1 | 1 | 1 |
| **Nematoda** (eelworms) | Adenophorea | Enoplia | 3 | 3 | 5 |
| | Penetrantia | Dorylaimida | 4 | 8 | 24 |
| | | Enoplida | 4 | 4 | 10 |
| | Secernentia | Ascaridida | 2 | 4 | 5 |
| | | Rhabditida | 4 | 11 | 18 |
| | | Spirurida | 1 | 3 | 3 |
| | | Strongylida | 1 | 6 | 11 |
| | | Tylenchida | 5 | 13 | 16 |
| | Torquentia | Araeolaimida | 2 | 5 | 19 |
| | | Chromadorida | 3 | 3 | 3 |
| | | Monohisterida | 1 | 3 | 6 |
| **Acanthocephala** (spiny-headed worms) | Palaecanthcephala | Polymorphida | 1 | 1 | 1 |
| **Platyhelminthes** (tapeworms & flukes) | Cestoda | Cyclophyllidea | 5 | 10 | 16 |
| | | Proteocephalidea | 1 | 1 | 1 |
| | | Pseudophyllidea | 2 | 2 | 4 |
| | Trematoda | Opisthorchiida | 1 | 1 | 1 |
| | | Plagiorchiida | 1 | 1 | 3 |
| | | Strigeata | 1 | 1 | 3 |
| **Annelida** (whiteworms) | Oligochaeta | Haplotaxida (all Enchytraeidae) | 1 | 9 | 42 |

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| Phylum | Class | Order | Families | Genera | Species |
|---|---|---|---|---|---|
| **Tardigrada**<br>(tardigrades) | Eutardigrada | Apochela | 1 | 1 | 1 |
| | | Parachela | 3 | 16 | 74 |
| | Heterotardigrada | Arthrotardigrada | 1 | 4 | 16 |
| **Bryozoa**<br>(moss animalcules) | Phylactolaemata | Parachela | 1 | 1 | 1 |
| **Chelicerata**<br>(mites & spiders) | Arachnida | Acari:Acariformes | 38 | 76 | 133 |
| | | Acari:Parasitiformes | 10 | 14 | 27 |
| | | Araneae | 4 | 14 | 21 |
| **Hexapoda**<br>(springtails & insects) | Collembola | Arthropleona | 7 | 27 | 65 |
| | | Neelipleona | 1 | 1 | 1 |
| | | Symphyleona | 2 | 3 | 6 |
| | Insecta | Phthiraptera (Anoplura+Mallophaga) | 3 | 14 | 38 |
| | | Ephemeroptera | 1 | 1 | 1 |
| | | Hemiptera (all aphids) | 2 | 4 | 4 |
| | | Thysanoptera | 1 | 1 | 1 |
| | | Mallophaga | 2 | 12 | 36 |
| | | Coleoptera | 12 | 18 | 21 |
| | | Diptera:Chironomidae | 1 | 25 | 92 |
| | | Diptera:other | 19 | 39 | 69 |
| | | Hymenoptera:Symphyta | 1 | 4 | 10 |
| | | Hymenoptera:Parasitica | 4 | 20 | 21 |
| | | Lepidoptera | 6 | 12 | 12 |
| | | Siphonaptera | 1 | 2 | 2 |
| | | Trichoptera | 1 | 1 | 1 |
| **Crustacea**<br>(water fleas, ostracods and shrimps) | Branchiopoda | Cladocera | 4 | 7 | 9 |
| | | Ctenopoda | 1 | 1 | 1 |
| | | Notostraca | 1 | 1 | 1 |
| | Copepoda | Calanoida | 2 | 2 | 2 |
| | | Cyclopoida | 1 | 3 | 4 |
| | | Harpacticoida | 3 | 3 | 3 |
| | | Siphonostomatoida | 1 | 1 | 2 |
| | Malacostraca | Amphipoda | 1 | 1 | 2 |
| | | Mysidacea | 1 | 1 | 1 |
| | Ostracoda | Podocopida | 4 | 8 | 10 |
| **Total** | | | | **556** | **1,308** |

Among the dominant low Arctic families, most are still represented in the high Arctic. However, number of species is greatly reduced, with only lice, chironomid midges, house flies and ichneumon parasitoid wasps still meeting the 20 species criterion. The black flies, whose larvae live in flowing water, are lost from the fauna and ground beetle numbers are reduced from 85 to one species. The most successful insect families (i.e. those with species numbers in the high Arctic > 50% of those in the low Arctic) are the bird lice (Philopteridae), which are parasites of warm-blooded vertebrates, and the chironomid midges that breed in aquatic habitats and wet soils.

The relative abundance of ichneumonid parasitoid wasps is perhaps surprising at first, given their dependence on the availability of particular invertebrate prey species, the susceptibility of their life cycles to disruption through the direct effect of lethal cold temperatures and the potential breakdown of temporal synchrony with their host species (Hance *et al.* 2007). However, it is the other abundant species groups, notably dipteran flies, spiders (Araneae), aphids and sawflies that provide the majority of hosts for these parasitoids. Parasitism also probably takes place on other species *within* the family Ichneumonidae (parasitoid wasps) (Danks 1981, Roininen *et al.* 2002, Hodkinson & Coulson 2004).

**Table 7.2.** Number of genera and species of insect within each family across the Nearctic region illustrating further the taxonomic biodiversity within a selected class of Arctic invertebrate. Data are from Danks (1981) and should be viewed with the caveats noted in the text. Note also that the boundary between the high and low Arctic in the Canadian Arctic Archipelago differs slightly from that used in other sections of the Assessment.

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| Order | Arctic families | Arctic genera | High Arctic species | Low Arctic species |
|---|---|---|---|---|
| **Ephemeroptera** | Metretopodidae | 1 | 0 | 1 |
| | Baetidae | 1 | 0 | 7 |
| | Heptageniidae | 1 | 0 | 1 |
| | Leptophlebiidae | 1 | 0 | 1 |
| | Ephemerellidae | 1 | 0 | 1 |
| **Odonata** | Aeshnidae | 1 | 0 | 4 |
| | Coenagriidae | 1 | 0 | 1 |
| | Corduliidae | 1 | 0 | 1 |
| **Plecoptera** | Pteronarcidae | 1 | 0 | 1 |
| | Chloroperlidae | 3 | 0 | 3 |
| | Perlodidae | 5 | 0 | 5 |
| | Perlidae | 2 | 0 | 2 |
| | Capniidae | 1 | 0 | 6 |
| | Nemouridae | 3 | 0 | 5 |
| **Orthoptera** | Acrididae | 3 | 0 | 4 |
| **Phthiraptera** | Philopteridae | 21 | 23 | 37 |
| | Trichodectidae | 1 | 0 | 1 |
| | Menoponidae | 7 | 5 | 10 |
| | Ricinidae | 1 | 2 | 2 |
| | Echinophthiriidae | 2 | 2 | 2 |
| | Linognathidae | 1 | 0 | 1 |
| | Pediculidae | 1 | 0 | 1 |
| | Hoplopleuridae | 2 | 1 | 2 |
| | Polyplacidae | 1 | 0 | 2 |
| **Hemiptera** | Lygaeidae | 1 | 0 | 1 |
| | Miridae | 4 | 0 | 8 |
| | Anthocoridae | 1 | 0 | 1 |
| | Saldidae | 4 | 1 | 9 |
| | Corixidae | 2 | 0 | 3 |
| | Cicadellidae | 7 | 0 | 9 |
| | Delphacidae | 1 | 0 | 1 |
| | Psyllidae | 2 | 0 | 9 |
| | Aphididae | 17 | 3 | 20 |
| | Coccidae | 1 | 0 | 1 |
| | Orthezidae | 1 | 0 | 1 |
| | Pseudococcidae | 3 | 1 | 2 |
| **Thysanoptera** | not stated | 3 | 1 | 2 |
| **Neuroptera** | Chrysopidae | 1 | 0 | 1 |
| | Hemerobiidae | 1 | 0 | 2 |
| **Coleoptera** | Carabidae | 16 | 1 | 85 |
| | Halipliidae | 1 | 1 | 2 |
| | Dytiscidae | 7 | 2 | 24 |
| | Hydrophilidae | 2 | 0 | 6 |
| | Silphidae | 3 | 0 | 3 |
| | Staphylinidae | 17 | 4 | 23 |
| | Byrrhidae | 3 | 0 | 5 |
| | Bupestridae | 1 | 0 | 1 |
| | Elateridae | 2 | 0 | 7 |
| | Cantharidae | 2 | 0 | 2 |
| | Dermestidae | 1 | 0 | 1 |
| | Cucujidae | 1 | 0 | 1 |
| | Coccinellidae | 5 | 0 | 6 |
| | Lathridiidae | 2 | 1 | 2 |
| | Cerambycidae | 5 | 0 | 5 |
| | Chrysomelidae | 6 | 0 | 13 |
| | Curculionidae | 9 | 1 | 14 |
| **Diptera** | Trichoceridae | 1 | 2 | 5 |
| | Tipulidae | 13 | 9 | 52 |
| | Dixidae | 1 | 0 | 1 |
| | Chaoboridae | 2 | 0 | 2 |
| | Culicidae | 2 | 3 | 17 |
| | Simuliidae | 6 | 0 | 28 |
| | Ceratopogonidae | 4 | 3 | 4 |
| | Chironomidae | 62 | 93 | 159 |
| | Bibionidae | 1 | 0 | 1 |
| | Scatopsidae | 2 | 0 | 3 |
| | Mycetophilidae | 9 | 9 | 17 |
| | Sciaridae | 4 | 5 | 3 |
| | Cecidomyiidae | 2 | 2 | 2 |
| | Rhagionidae | 2 | 0 | 2 |
| | Tabanidae | 1 | 0 | 4 |
| | Empididae | 4 | 7 | 20 |
| | Dolichopodidae | 7 | 2 | 31 |

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### 7.2.1.3. Biodiversity of Arctic invertebrates, the best collective estimates

Tab. 7.3 lists the numbers of species for each of the main groups of invertebrates recorded from the low and high Arctic regions of the Nearctic and Palearctic regions, together with the number of known endemics. This table is based on our collective knowledge derived from literature and museum collections. Greenland data, where possible, are disaggregated from the Nearctic region, as the zoogeographical origins of the Greenland invertebrate fauna remain uncertain. This list is our best current estimate of invertebrate biodiversity within the Arctic, although there may be omissions, taxonomic uncertainties and other inadequacies. Data for many groups are absent, unreliable or unavailable in a form that can easily be mapped onto the table format. Some groups present particular problems. The eelworms, for example, are one of the most numerically abundant groups of Arctic invertebrate and are undoubtedly species diverse within the Arctic regions, but most studies record biodiversity at the generic rather than the species level. For example, generic diversity associated with hair grass tussocks *Deschampsia sukatschewii* ssp. *borealis* across sites on Bol'shevik Island, Severnaya Zemlya and the Putorna Plateau, Taimyr, ranged from 18 to 28

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| Order | Arctic families | Arctic genera | High Arctic species | Low Arctic species |
|---|---|---|---|---|
| **Diptera** (continued) | Platypezidae | 1 | 0 | 1 |
| | Phoridae | 2 | 1 | 4 |
| | Syrphidae | 13 | 6 | 21 |
| | Pipunculidae | 1 | 0 | 1 |
| | Micropezidae | 2 | 0 | 3 |
| | Piophilidae | 4 | 5 | 7 |
| | Acartophthalidae | 1 | 1 | 1 |
| | Agromyzidae | 7 | 5 | 18 |
| | Milichiidae | 1 | 1 | 2 |
| | Sciomyzidae | 4 | 0 | 6 |
| | Heleomyzidae | 5 | 1 | 9 |
| | Sphaeroceridae | 2 | 0 | 3 |
| | Drosophilidae | 2 | 0 | 2 |
| | Ephydridae | 5 | 2 | 10 |
| | Chloropidae | 2 | 0 | 2 |
| | Scathophagidae | 9 | 5 | 28 |
| | Anthomyiidae | 19 | 7 | 138 |
| | Muscidae | 25 | 21 | 166 |
| | Calliphoridae | 12 | 4 | 12 |
| | Oestridae | 2 | 0 | 3 |
| | Sarcophagidae | 1 | 0 | 1 |
| | Tachinidae | 8 | 6 | 8 |
| **Siphonaptera** | Pulicidae | 1 | 1 | 1 |
| | Leptopsyllidae | 2 | 0 | 2 |
| | Ceratopsyllidae | 5 | 3 | 9 |
| **Lepidoptera** | Incurvariidae | 1 | 0 | 1 |
| | Gelechiidae | 1 | 0 | 1 |
| | Plutellidae | 1 | 0 | 1 |
| | Tortricidae | 10 | 3 | 19 |
| | Hesperiidae | 2 | 0 | 2 |
| | Papilionidae | 2 | 0 | 3 |
| | Pieridae | 4 | 2 | 13 |
| | Lycaenidae | 5 | 2 | 5 |
| | Satyridae | 3 | 0 | 17 |
| | Nymphalidae | 7 | 3 | 12 |
| | Pterophoridae | 3 | 1 | 3 |
| | Pyralidae | 7 | 0 | 7 |
| **Lepidoptera** (continued) | Geometridae | 16 | 2 | 24 |
| | Sphingidae | 1 | 1 | 1 |
| | Lymantriidae | 1 | 2 | 2 |
| | Arctiidae | 4 | 0 | 5 |
| | Noctuidae | 15 | 5 | 28 |
| **Trichoptera** | Ryacophilidae | 1 | 0 | 1 |
| | Glossosomatidae | 1 | 0 | 1 |
| | Hydroptilidae | 1 | 0 | 1 |
| | Phryganeidae | 2 | 0 | 2 |
| | Brachycentridae | 1 | 0 | 2 |
| | Limnephilidae | 9 | 1 | 15 |
| | Leptoceridae | 1 | 0 | 1 |
| **Hymenoptera** | | | | |
| Symphyta | Tenthredinidae | 9 | 8 | 39 |
| | Siricidae | 2 | 0 | 2 |
| Parasitica | Braconidae | 10 | 3 | 14 |
| | Ichneumonidae | 78 | 35 | 131 |
| | Mymaridae | 1 | 0 | 1 |
| | Eulophidae | 1 | 1 | 1 |
| | Encyrtidae | 3 | 2 | 2 |
| | Ptermomalidae | 4 | 2 | 2 |
| | Chalcidae | 1 | 1 | 0 |
| | Figitidae | 1 | 0 | 1 |
| | Alloxystidae | 3 | 0 | 4 |
| | Cynipidae | 1 | 0 | 1 |
| | Proctotrupidae | 2 | 0 | 2 |
| | Diapriidae | 1 | 0 | 1 |
| | Scelionidae | 1 | 0 | 1 |
| | Platygastridae | 1 | 0 | 1 |
| | Ceraphronidae | 1 | 0 | 1 |
| Aculeata | Formicidae | 1 | 0 | 1 |
| | Vespidae | 1 | 0 | 2 |
| | Megachilidae | 1 | 0 | 1 |
| | Apidae | 1 | 3 | 12 |
| **Total** | | **677** | **330** | **1,567** |

genera, comparable with the 29 and 40 genera listed for Cape Chelyuskin, Taimyr, and the Devon Island Plateau, Canada (Peneva *et al.* 2009). At least 73 genera have been recorded from within the whole Arctic region (Tab. 7.3). Where specific studies of small regional areas have been made, such as for Lake Hazen, Canada, and the low Arctic tundra on Taimyr, species numbers range from 60 to 162 (Danks 1981, Kuzmin 1976).

### 7.2.1.4. Variation within species

Modern molecular techniques are beginning to reveal high levels of genetic variation within Arctic populations of several of the invertebrate taxa named above, both across their geographical range and within local populations. These variations often provide strong evidence for genetic polymorphism within species populations and provide insights into the local adaptation and dispersal history of species. Studies have focused particularly on genetic variation at different spatial scales within and among metapopulations of aquatic species, notably the waterfleas *Daphnia* spp. (Cladocera), tadpole shrimps (Notostraca) and ostracod crustaceans, in the mosaic of lakes, ponds and pools scattered over the landscape (Dufresne & Hebert 1995, 1997, Van Raay & Crease 1995, Weider *et al.* 1996, 1999a, 1999b, 2010, Little

| Group | Palearctic low Arctic | Palearctic high Arctic | Total Palearctic | Nearctic low Arctic | Nearctic high Arctic | Total Nearctic | Greenland | Total Arctic | Arctic endemic |
|---|---|---|---|---|---|---|---|---|---|
| **Testate amoebae** | 190 | 185 | 229 | 210 | 121 | 243 | 128 | 319 | 9 |
| **Rotifera** (rotifers) | | | | | | | | | |
| Monogononta | 97 | 137 | 191 | 220 | 97 | 191 | | 327 | 12 |
| Bdelloidea | 0 | 68 | 68 | 10 | 6 | 15 | | 80 | |
| **Micrognathozoa** | | | | | | | 1 | 1 | |
| **Tardigrada** (water bears) | 132 | 126 | 182 | 106 | 70 | 123 | | 215 | 10 |
| **Cladocera** (water fleas) | 85 | 16 | 86 | 74 | 17 | 79 | 32 | 110 | 6 |
| **Copepods** (copepods) | | | | | | | | | |
| Calanoida | 19 | 8 | 19 | 35 | 12 | 35 | 4 | 39 | 11 |
| Cyclopoida | 7 | 2 | 7 | 14 | 3 | 12 | 8 | 19 | 0 |
| Harpacticoidea | 5 | 3 | 15 | 14 | 1 | 14 | 9 | 21 | 2 |
| **Anostraca** (shrimps etc) | 5 | 8 | 9 | 5 | 4 | 6 | 2 | 12 | 6 |
| **Notostraca** (tadpole shrimps) | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 |
| **Ostracoda** (ostracods) | 34 | 30 | 34 | 40 | 27 | 40 | 12 | 47 | 4 |
| **Enchytraeidae** (white worms) | | | 73 | | | 48 | 32 | 85 | 16 |
| **Nematoda** (eelworms) | | | | | | | | 73+ (genera) | |
| **Araneae** (spiders) | 250 | 100 | | | 50 | 200 | | 450 | 50 |
| **Acari** (mites) | | | | | | | | | |
| Mesostigmata | 182 | 37 | 188 | 68 | 33 | 80 | 63 | 231 | 72 |
| Prostigmata | | | 94 | | | 111 | 72+ | | |
| Oribatida | 271 | 97 | 283 | 174 | 46 | 177 | 110 | 372 | 69 |
| Astigmata | | | 8 | | | | 10 | | |
| **Collembola** (springtails) | 347 | 132 | 348 | 162 | 49 | 174 | 94 | 425 | 14 |
| **Insecta** (insects) | | | | | | | | | |
| Plecoptera | | | | | | | | 72 | 0 |
| Hemiptera | | | | | | | | | |
| Psylloidea | 7 | | 7 | 11 | | 11 | 3 | 14 | 6 |
| Aphidoidea[2] | | | | 21 | 6 | 27 | 23 | (407)[2] | > 12 |
| Coleoptera | | | | | | | | | |
| Carabidae | | 10 | | | 4 | | | | |
| Staphylinidae | | 28 | | | 9 | | | | |
| Dytiscidae | | 2 | | | 6 | | | | |
| Chrysomelidae | | 5 | | | 4 | | | | |
| Curculionidae | | 5 | | | 1 | | | | |
| Diptera | | | | | | | | | |
| Tipuloidea | | | 131 | 128 | 53 | 139 | | | 32 (Nearctic) |
| Chironomidae | 235 (695) | 155 (235) | 235 (695) | 165 (450) | 81 (165) | 235 (695) | | 360 (760) | ? |
| Culicidae | | | | | | 36 | 2 | | |
| Anthomyiidae | 98 | 15 | 98 | 141 | 22 | 142 | 32 | 143 | c10 |
| Muscidae | 140 | 37 | 145 | 224 | 21 | 224 | 35 | | |
| Lepidoptera (total) | | | 105 | | | 165 | | 270 | 25 |
| Butterflies[1] | | | 91[1] | 21 | 7 | 61[1] | | 106[1] | 6 |
| Hymenoptera | | | | | | | | | |
| Symphyta | 17 | 25 | 37 | 46 | 5 | 46 | | 71 | 8 |
| Parasitoidea | | | | see Tab. 7.2 | | | | | |

1) Chernov & Tatarinov 2006; 2) Stekolshchikov & Buga 2009.

**Table 7.3.** Number of species in the dominant or relatively well-studied groups of invertebrates in the major biogeographical regions of the low and high Arctic. Greenland, in addition to being included within the traditional Nearctic region, is also considered as a separate unit as its fauna cannot be considered as being solely derived from the Nearctic region. Data are partly compiled from Babenko & Fjellberg (2006), Chernov & Makarova (2008), Chernov & Tatarinov (2006) and Stekolshchikov & Buga (2009), but mainly from original data assembled by the contributing authors. Data on butterflies and Anostraca (shrimps, etc.) are for the whole of the Arctic region including the sub-Arctic zone and may, in the case of the butterflies, include some migrant species – about 40% of the 106 species of butterflies numbered are typically Arctic. For the midge family Chironomidae the first number in each cell is an estimate of the total number of species present, the figure in parentheses is the total number of species known to occur north of the Arctic Circle, many of which are likely to be found in the low Arctic. Within this highly diverse group a revised and updated species list is only currently available for the subfamilies Podonominae, Tanypodinae, Diamesinae, Prodiamesinae and Telmatogetoninae within the Arctic (see Ashe & O'Connor 2009). The ratio of Arctic to total Holarctic species in these taxa has been extrapolated to arrive at a revised estimate of the number of species in the remaining subfamilies. For the aphids, the Nearctic data are reliably compiled from published accounts, whereas the data given for the Total Arctic (inluding the sub-Arctic and thus placed in parenthesis) are taken from Stekolshchikov & Buga (2009), but the original source is not known. A major omission is the parasitoid Hymenoptera wasps (predominantly Ichneumonoidea), which are relatively diverse but for which up to date data in the required format are not easily accessible. Tab. 7.2 should be consulted for older data on their biodiversity in the Nearctic region.

& Herbert 1997, Weider & Hobaek 2003, Hessen *et al.* 2004). More limited data are available for terrestrial groups such as ground beetles (Ashworth 1996, Reiss *et al.* 1999), sulfur butterflies *Colias* spp. (Wheat *et al.* 2005) and selected springtails (K. Hedlund pers. com.).

Several species of Arctic invertebrates, e.g. Svalbard aphids, show diversity in their method of reproduction, switching between sexual and parthenogenetic modes. The seed bug *Nysisus groenlandicus* exists as both parthenogentic and sexually reproducing populations at Zackenberg (74° 30' N, 20° 30' W), NE Greenland (Böcher & Nachman 2011). Other invertebrates, e.g. some waterfleas and chironomid midge species, may be obligatorily parthenogenetic (Armitage *et al.* 1995, Dufresne & Hebert 1995, Strathdee *et al.* 1995, Gillespie *et al*. 2007). Parthenogenetic reproduction leads to the creation of genetically distinct clones or haplotypes whose distinctness is frequently reinforced by polyploidy (Dufresne & Hebert 1995, Van Raay & Crease 1995). The waterflea *Daphnia middendorfiana* in Canada appears to have evolved polyploidy independently in several separate geographical areas, possibly as a result of nuclear introgression between haplotypes or hybridization with haplotypes of related species (Dufresne & Hebert 1997, Weider *et al.* 1999b). By contrast, high genetic similarity occurs in some species that display high levels of morphological plasticity, such as the tadpole shrimp *Lepidurus arcticus* (Hessen *et al.* 2004).

Waterflea species show a high clonal diversity within the Arctic, contradicting the assumption that genetic variation in Arctic species is limited and suggesting a high degree of population fragmentation and isolation (Weider *et al*. 1996, Weider & Hobaek 2000). The tadpole shrimp, by contrast, had just two haplogroups (A and B), identified by mitochondrial 12SrDNA, across 48 populations. The distribution of these haplogroups, nevertheless, provides intriguing insights into species disperal. Both haplogroups occur over wide geographic ranges, including northern Norway, suggesting efficient long distance dispersal. However, populations on Svalbard consisted entirely of haplogroup A, while those on neighbouring Bjørnøya were almost all of haplogroup B (Hessen *et al.* 2004).

Studies of waterflea mitochondrial DNA and allozyme variation have also provided insights into the phylogeography of species complexes within the Arctic and evidence for relationships between waterflea clone distributions and the position of old Pleistocene glacial refuges. The highest levels of haplotype diversity within the waterflea *Daphnia pulex* complex have been found in areas that were within the unglaciated Beringian refuge during the Pleistocene, namely NE Siberia and NW North America. The contrast is most striking in N Canada where haplotype diversity is highest along the eastern edge of the Beringian refuge, reaching a maximum on Banks Island. The more recently deglaciated parts of the eastern Canadian Arctic support a much lower diversity of haplotypes, with diversity decreasing significantly with distance from the edge of the Beringian refuge (Weider & Hobaek 1997, 2003). These data suggest a longer uninterrupted period of haplotype development within the refuge followed by only limited dispersal into the surrounding geographical areas as the ice sheets retreated. A similar pattern is found in the ground beetle *Amara alpina* as indicated by DNA restriction-site variation, which is greatest in the Beringian regions of Alaska and northern British Columbia and lowest in the area of Hudson Bay (Reiss *et al.* 1999).

On the more local scale, genetic studies are beginning to reveal shifts in the parameters of genetic diversity over short time intervals. For example, allozymic studies on waterfleas in 131 rock pools at Churchill, Manitoba, Canada indicate dynamic changes in the clonal structure of populations occurring over time intervals as short as 20-25 years (Dufresne & Hebert 1995, Weider *et al.* 2010). The number of populations with melanic clones fell from 131 to 90, 59% had an unchanged clonal structure, 33% showed some clonal replacement and 8% showed total clonal replacement (Weider *et al.* 2010).

It is often assumed that species generally show reduced genetic diversity with increasing latitude as a result of population extinction followed by limited recolonization events associated with expanding and retreating ice sheets. Evidence for three genes that code for the metabolic enzymes phosphoglucose isomerase, phosphoglucomutase and glucose-6-phosphate dehydrogenase in sulfur butterflies, however, suggests that, at least for some genes, high heterozygosity is maintained into the highest latitudes (Wheat *et al.* 2005).

## 7.2.2. Historical overview

Changes in subfossil Arctic invertebrate assemblages, in conjunction with pollen and diatom stratigraphy, have been widely used as proxies for past climatic conditions within the Arctic (e.g. Andreev *et al.* 2004, Sher *et al.* 2005). They illustrate the magnitude and time scales for past changes of the Arctic climate and provide a baseline for assessing future trends in both climate and biodiversity (Kaufman 2009). Key indicator taxa for particular climatic regimes can be identified and the boundaries of shifting climatic zones can be mapped.

Subfossil beetle assemblages in permafrost provide some of the earliest proxy evidence for Arctic climate conditions across a wide region, with many identifiable beetle species surviving virtually unchanged since the late Miocene (Elias *et al.* 2006). Changes in such assemblages have been particularly useful in resolving the past climates of N Greenland, E and W Beringia, and the Bering Land Bridge (Böcher 1995, Elias 2000a, 2000b, Elias & Mathews 2002). Elias (2000a, 2000b), for example, identified 147 Pleistocene species of predatory or scavenging beetles (mainly ground beetles, water beetles and rove beetles) that were particularly important for climate reconstruction in Alaska and the Yukon Territory. For each species, he described Mutual Climatic Range, a climate envelope defined by the mean temperature range of the warmest (TMAX) and coldest (TMIN) months at sites where the species occurred today. This allowed species to be classified with respect to the breadth/narrowness of their TMAX and TMIN ranges and grouped according to their likely distributional responses to climate change. Species assemblages from other sites representing more recent stages within the Holocene could then be compared with this species preference list to gain an idea of the likely climate under which they existed. Cold-adapted beetles, such as ground beetles, have tracked climate change since the Pleistocene, through dispersal and differential survival (Ashworth 1996).

Freshwater ostracod crustaceans and soil testate amoeba species assemblages, similarly preserved in permafrost, provide examples of the longest continuous data sets for the climate within Arctic regions. On the Bykovsky Peninsula, Siberia, near the mouth of the Lena, the ostracod crustaceans and testate amoeba record extends over nearly 60,000 years. Six ostracod crustacean zones, based on 15 species within seven genera, track stadial-interstadial variations in climate from the Late Quaternary through to the Late Holocene, reflecting repeated changes from cold to warm and/or wet to dry (Wetterich *et al.* 2005). Variations in the testate assemblage, totaling 86 taxa, were less indicative but suggest cold, dry conditions during the Late Pleistocene and warm wet conditions throughout most of the Holocence (Bobrov *et al.* 2004). Presence/absence of rare amoeba species, e.g. those of the genus *Argynnia*, and shifts in dominance among the commoner groups such as species in the genus *Difflugia* are useful indicators of change.

Available data series for freshwater chironomid midge communities, based on head capsule analyses, are usually of shorter duration, from < 10,000 BP to the present, although much earlier spot samples exist for lakes in NW Greenland (Brodersen & Bennike 2003). Care is needed in extrapolating data from single sites, however, as local climates may differ from regional averages or there may be a lag in community response to climate change (Wooller *et al.* 2004, Rolland *et al.* 2008). Chironomid assemblages for lakes on Southampton Island in the eastern Canadian Arctic, for example, provide evidence for recent cooling, contrary to the general trend of Arctic warming (Rolland *et al.* 2008). Stable isotope $\delta^{18}O$ values derived from chironomid head capsules within sediment cores taken from Fog Lake, Baffin Island, and Qipisarqo Lake, S Greenland, correlate strongly with mean annual temperature. Such data can be used further to support observations on changes in species assemblages associated with shifting climate (Wooller *et al.* 2004).

Chironomid data from the Canadian Arctic Islands exemplify identifiable trends during the late Holocene deglaciation. Three major stratigraphic zones that reflect variations in temperature and productivity have been recognized in a core sample from Lake V57 on Victoria Island (Porinchu *et al.* 2009). The basal zone (0-1600 AD) is characterized by high abundance of the genera *Heterotrissocladius*, *Tanytarsus* and *Micropsectra*, with narrowly cold-adapted taxa such as the genera *Pseudodiamesa*, *Abiskomyia*, *Sergentia* and *Zalutschia*, and a species of the *Parakiefferiella nigra* type also present at low densities. The second zone (1600 – c. 1850 AD) is dominated by a species of the *Corynocera ambigua* type, a *Psectrocladius sordidellus* type and *Micropsectra*; several of the narrowly cold adapted taxa named above have disappeared. From 1850 onwards the community is characterized by high proportions of *Tanytarsus* and a *C. ambigua* type, by increases in a *C. olivieri* type, *Hydrobaenus/Olivieridia*, *Orthocladius* and Pentaneurini, and a decline in *Heterotrissocladius*, *Paracladius* and *Paratanytarsus*. Chironomid data from Lake CF8 on northeastern Baffin Island similarly forms part of multi-proxy evidence for very rapid climate change within the last 200 years, during which time productivity increased 20-fold. The chironomid communities show the most marked changes post 1950. Two narrowly cold-adapted genera *Oliveridia* and *Pseudodiamesa* declined rapidly, disappearing from the community by 1980, while other taxa with higher temperature optima, especially *Abiskomyia* and Tanytarsini, increased in abundance (Thomas *et al.* 2008). These four genera had formed part of the community continuously for over 5,000 years. Changes in testate amoebae assemblages in cores from Richards Island, Canada similarly suggest shifts in local climate within the last 3,000 years (Dallimore *et al.* 2000).

## 7.2.3. Regional considerations

The overwhelming diversity of invertebrate species, many of which display circumpolar distributions, coupled with the influence of microclimate and habitat type on species distribution and diversity, makes any strict compartmentalized analysis of regional invertebrate faunas relatively uninstructive. Here we examine how various driving factors influence the biodiversity of invertebrate communities on different spatial scales, from the local to the circumarctic.

### 7.2.3.1. Habitat specificity and its implications for biodiversity

Many Arctic invertebrate species have specific requirements that restrict their distribution to particular habitats within their broader geographical range. Other related species may be more broadly distributed across habitat types. This ensures that different habitat types tend to support communities of differing species composition, an important consideration when measuring total biodiversity. It is, however, impractical to list all habitat types that support characteristic species assemblages; examples will suffice to illustrate the general principles.

Testate amoebae communities of soil, moss, water and lichen habitats on Devon Island, Canada, have been classified into 18 separate species assemblages based on 75 species in 19 genera (Beyens & Chardez 1994). Six of these assemblages are linked to specific habitats, notably soil (*Plagiopyxis callida* association), moss (*Assulina-muscorum-Corythion dubium* and *Euglypha rotunda* assemblages) and water (*Trinema lineare* and *Paraquadrula irregularis-P. penardi*); the remaining assemblages occupy more than one habitat. Fig. 7.2 shows the generality of this trend, illustrating the percentage of testate amoeba species that are unique to these habitats throughout Svalbard, Jan Mayen, Greenland and the North American Arctic combined (Beyens *et al.* 1986a, 1986b, Beyens & Chardez 1994). Even among common aquatic testates, species such as *Centropyxis aerophila*, *Paraquadrula irregularis* and *Trinema lineare* are characteristic indicators of acid-oligotrophic, alkaline-mesotrophic and waters of intermediate pH conditions, respectively (Beyens *et al.* 1986a). Ciliate species similarly show differences in habitat choice, resulting in clear differences in biodiversity between habitats. On Svalbard, diversity was higher in stagnant versus running water. Highest species numbers were associated with cyanobacterial mats and aquatic moss beds; lowest diversity occurred in sediments and among species associated with encrusting plants or filamentous green algae (Petz 2003).

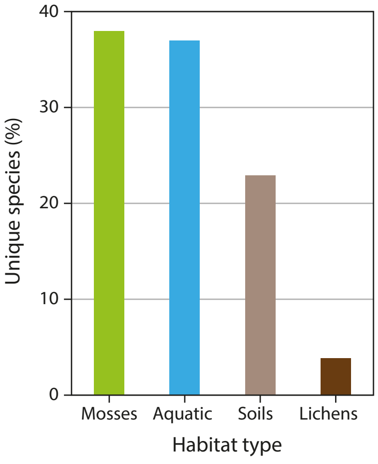

**Figure 7.2.** The number of species of testate amoebae unique to particular habitat types, expressed as a percentage of the total species found within that habitat. Data are from several sites spread across the Arctic compiled by Beyens & Chardez (1995).

The influences of water chemistry, temperature, and lake size and depth are important determinants of species composition for communities of chironomid midges in Arctic water bodies (Brodersen & Anderson 2002, Walker *et al.* 2003, Gajewski *et al.* 2005, Nyman *et al.* 2005). Differences in the characteristics of surrounding bedrock, soil and plant community combine to determine the invertebrate species assemblages present. Nitrogen, phosphorous and organic matter content, together with water temperature and pH, are frequently the important explanatory variables. For lakes in W Greenland, midges of the genera *Heterotrissocladius*, *Micropsectra*, *Ablabesmyia* and *Chironomus* are those most strongly influenced by such differences in environmental conditions, making them the best predictors of lake nutrient status. They are, however, not necessarily the most abundant taxa (Brodersen & Anderson 2002). Among stream-dwelling chironomids, water origin, distance from source and level of disturbance, including channel stability and sediment load, are major influences shaping communities at the landscape scale (Lods-Crozet *et al.* 2007).

Terrestrial and freshwater tardigrades are another group that contains both habitat specialists and generalists. Several species are typically associated with homothermal springs, notably on Disko Island, W Greenland. The area around the warmest (c. 17 °C) of these springs, Puilassoq, supports 18 species of Eutardigrada and three Heterotardigrada, with species variously associated with wet soil, mud, algae, hydrophilic mosses and moss-on-stone habitats (Heide-Jørgensen & Kristensen 1999). Comparison of the soil-dwelling tardigrade communities at three separate locations on Disko Island showed a distinctive community at each, with only four of 13 species common to all three locations (Stark & Kristensen 1999). A separate study along two transects, however, showed little evidence that altitude and bedrock type strongly influenced species composition (Peters & Dumjahn 1999).

Perhaps the most unique habitats supporting invertebrate life, including tardigrades, are the water-filled dust holes (cryoconites) that form on the surface of Arctic glaciers. White Glacier at 79° N on Axel Heiberg Island, Canada supports a mixed cryoconite community of unidentified flagellates, ciliates, rotifers and tardigrades (Mueller *et al.* 2001). Tardigrades and sometimes rotifers occur frequently in cryoconites on Disko Island, Greenland, and Svalbard glaciers (De Smet & Van Rompu 1994, Grøngaard *et al.* 1999, Séméria 2003). Invertebrates in eight cryoconite holes on Hyrnebre, Svalbard, included seven rotifer species in six genera, the tardigrades *Diphascon recamieri* and *Isohypsibius granulifer* and at least four species of ciliates (De Smet & Van Rompu 1994). Most of the species involved are not unique to cryoconites but are often widely distributed elsewhere in non-glacial habitats and some are cosmopolitan (McFatter *et al.* 2007).

Higher plant species are often good indicators of soil conditions, particularly the depth and content of organic matter and water availability. These same factors strongly influence soil invertebrate biodiversity. At Zackenberg, NE Greenland, different assemblages of testate amoebae species are associated with polargrass *Arctagrostis* sp. and bilberry *Vaccinium* sp. (high soil moisture, thicker active layer), mountain heather *Cassiope* sp. and willow *Salix* sp. (low soil moisture) and meadow-grass *Poa* sp. (high organic content, shallow active layer) (Trappeniers *et al.* 2002). Enchytraeid worm communities in the same area show comparable changes in species composition between vegetation/soil types (Sorensen *et al.* 2006), and even within individual species there may be diversity in life cycle duration between vegetation types (Birkemoe *et al*. 2000). There are similar differences in community structure of springtail and mite communities in soils beneath willow, saxifrage *Saxifraga*, mountain avens *Dryas*, wood-rush *Luzula* and mountain heather growing together in a mixed vegetation mosaic on Svalbard (Coulson *et al.* 2003b). Even within ostensibly similar plant communities, parameters of diversity may shift along short environmental gradients. Microathropod communities on Svalbard associated with a *Dryas*-dominated plant community changed along a snow-melt transect of 135 m in response to differences in temperature, annual heat accumulation and soil moisture characteristics (Dollery *et al*. 2006). Furthermore, over greater latitudinal distances there is often little overlap at the species level in springtail communities occupying similar vegetation, as demonstrated by comparing areas such as Severnaya Zemlya in the high Arctic with areas farther south in Siberia (Babenko 2000).

At the highest latitudes, local invertebrate biodiversity may be linked to restricted microtopographical features that create slightly more favorable microclimatic conditions that extend the growing season, e.g. well-drained slopes, raised areas and river terraces. The chrysomelid beetle *Chrysolina septentrionalis* and the latridiid beetle *Dienerella elegans*, for example, are found only in turf growing on lemming mounds on Severnaya Zemlya and Ellef Ringnes Island, respectively (Chernov & Makarova 2008). Populations of the rove beetle *Micralymma brevilingue* are also highest on these mounds (Makarova *et al.* 2007). Similarly, springtail communities associated with the different microhabitat topographies created during different stages of the frost-boil cycle in Taimyr, Russia, differ markedly in their species composition over short distances (Babenko 2009).

**Table 7.4.** Habitat preferences of common Arctic springtail species selected to illustrate variation in the range of habitats utilised, often by related species. Data are from Fjellberg (1994) with nomenclature updated from Babenko & Fjellberg (2006).

| Species | Habitats |
|---|---|
| *Hypogastrura viatica* | Wet areas rich in organic matter |
| *Hypogastrura tullbergi* | Dry upland, grassy meadows, lichen heath |
| *Hypogastura concolor* | Moss, lichens, grass tussocks |
| *Anurida polaris* | Wet mossy areas |
| *Megaphorura arctica* | Bird colonies, sea shore |
| *Oligaphorura groenlandica* | Wet mossy sites, bird cliffs |
| *Tetracanthella arctica* | Beach meadows, bird cliffs, lagoon edges |
| *Folsomia sexoculata* | Salt meadows, littoral |
| *Folsomia quadrioculata* | Ubiquitous across a wide range of habitats |
| *Isotoma anglicana* | Both wet and dry areas |
| *Isotoma tshernovi* | Wet meadows, moss by ponds, snowfields |
| *Lepidocyrtus lignorum* | Dry meadows, bird cliffs |
| *Sminthurides malmgreni* | Very damp habitats |
| *Sminthurinus concolor* | Rocky dry sites |

Tab. 7.4 illustrates diversity in habitat usage by springtails and shows the habitat preferences of selected common species on Svalbard. Most notably the springtails occupy a multiplicity of habitats from marine littoral through wet tundra to dry polar desert, with several species commonly associated with seabird colonies. Mites almost invariably co-occur with springtails and selectively occupy the same wide range of habitats, including association with nesting birds and/or lemming mounds and burrows (Makarova 1999, 2002b, Lebedeva *et al.* 2006). Furthermore, mesostigmatid mites are among the main predators of springtails and other invertebrates and several Meso- and Astigmata mite species show phoretic associations with flying insects such as flies (Diptera) of the families Anthomyiidae (root-maggot flies), Muscidae (house flies) and Trichoceridae (winter craneflies) across a variety of habitats (Makarova 1999, Makarova & Böcher 2009). Prostigmata mites, by contrast, are usually associated with spiders of the family Linyphiidae. As a consequence of habitat specialization by constituent species, the composition of springtail and mite communities varies between habitats. For example, mesic and dry heath at Zackenberg, NE Greenland, share several species in common, but their relative densities often differ widely between habitats, and some species are unique to each habitat type (Sorensen *et al.* 2006).

Some taxa show a shift in their habitat preference with latitude, perhaps in response to reduced competition. For example, species of oribatid mite of the widely distributed genus *Ameronothrus* are typical of marine intertidal habitats. However, the Arctic species occupy an uncharacteristically wide range of habitats from supralittoral to terrestrial, with one Arctic species, *A. dubinini*, found only in terrestrial habitats (Marshall & Convey 2004). Compared with temperate regions, most species of oribatid mite within the Arctic are associated with soil surface, moss and lichens, rather than living deep within the soil (Behan-Pelletier 1999).

The general conclusion to be drawn from these examples is that extensive sampling in a wide range of habitats is necessary to establish the true invertebrate biodiversity even at a single location. When the whole of the Arctic is considered, the task becomes immense. The level of variation in habitat selection and usage among taxa makes generalization across the invertebrates exceedingly difficult.

### 7.2.3.2. Biodiversity changes along latitudinal gradients

The broad general trend of decreasing biodiversity with increasing latitude described previously for many insect groups has often been, as might be expected, correlated with decreasing temperature, which acts progressively to limit the northern distributions of species, many of which occur south of the low Arctic (Gaston 1996). Fig. 7.3 shows an example of this trend among the well-studied ground beetles along a north-south transect through the low Arctic tundra of the Taimyr Peninsula, Russia. As mean July temperature declines from 12.5 to 4.0 °C, the number of ground beetle species declines from 59 to three (Chernov 1995, Chernov & Makarova 2008). Equivalent data showing similar trends are available for spider and butterfly assemblages in Middle Siberia and Russian Beringia (Chernov 1995). The pattern is repeated, if less dramatically, among ground beetles in Arctic Alaska and Norway (Nelson 2001, Olsvik *et al.* 2001) and leaf beetles (Coleoptera: Chrysomelidae) in the Palearctic tundra (Chernov *et al.* 1994, Medvedev 1996, Makarova *et al.* 2007).

The ground beetles appear more strongly temperature restricted than the other group of smaller predatory/scavenging beetles, the Staphylinidae (Chernov & Makarova 2008). Among the 341 spider species of the Russian Arctic tundra, 41 are restricted to the Arctic zone, 34 are Arctic-alpine and 266 are also found in zones farther south (Marusik & Eskov 2009). In addition, as for many invertebrate groups, the family composition of spiders changes with latitude. At high Arctic sites such as Svalbard, Linyphiidae make up 93% of the species. This percentage declines to 59% at Kevo, N Finland and 36% in W Germany (Koponen 1993). A similar trend occurs within mesostigmatid mites, with the family Ascidae becoming progressively more dominant with increasing latitude (Makarova 2002a, 2009). Nearly all known Arctic species of sawflies (Symphyta) belong to the family Tenthredinidae, and all the high Arctic species fall within the subfamily Nematinae. Apart from Nematinae, the ranges of only a very few species of other tenthredinid subfamilies such as Selandriinae, Allantinae, Heterarthrinae, Tenthredininae and Cimbicidae reach into the low Arctic.

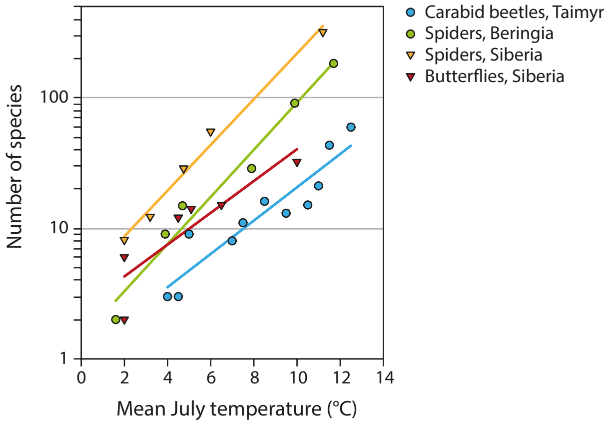

**Figure 7.3.** Relationship between numbers of spider, carabid beetle and butterfly species and mean July temperature at sites along south to north transects in Taimyr, Middle Siberia and Beringia (based on data from Chernov 1995, Chernov *et al.* 2000, Chernov & Makarova 2008).

Among many other groups that are poorly represented in the Arctic, e.g. thermophilous bumble bees *Bombus* spp., the few Arctic species represent the extreme northern branches of much larger and more broadly distributed phylogenetic lines (Pekkarinen & Teräs 1993, Hines 2008). The 27 Arctic *Bombus* species are scattered thinly across the subgenera *Bombus* sensu stricto, *Pyrobombus*, *Alpinobombus*, *Melanobombus*, *Thoracobombus*, *Tricomibombus*, *Psithyrus*, *Megabombus* and *Subterraneobombus* (Hines 2008).

A detailed analysis of the distribution of the abundant and well-adapted springtails along a north-south transect through the central Siberian Arctic reveals a far more complex picture. At first sight the pattern appears similar to the ground beetles, with a decline in number of species from the northern taiga/southern tundra zone to the polar desert, albeit at a slower rate (Babenko 2003a, 2003b, 2009). This trend, however, masks greater subtleties with important consequences for biodiversity. At each point along the transect the fauna is made up of varying proportions of different faunal elements, each with a different characteristic distribution pattern. Important elements include high Arctic species associated with polar desert, separate faunal elements typically occupying the northern and mid zones of the low Arctic tundra, and a faunal element typical of the southern tundra and forest-tundra zones. Only a small proportion of species occurred across all zones. Unlike the ground beetles, the number of species across the entire transect greatly exceeded the number of species within the more southerly zones (Babenko 2003a, 2003b, 2009).

Some groups show an opposite trend in diversity. Host-plant-specific sawflies, for example, exhibit increasing species richness into the low Arctic, before declining in the high Arctic (Kouki *et al.*1994, Kouki 1999). This appears to be associated with the diversity and abundance of suitable host-plants, especially willows, on which the majority of Arctic sawflies feed in the larval stages (Viitasaari 2002). Willows are themselves unusual, reaching their highest species diversity in high northern latitudes.

Enchytraeid worms, a group particularly associated with the abundant wet organic soils of the low Arctic tundra, exhibit a similar inverse trend in diversity with increasing latitude. Species richness in the Palearctic tundra is only marginally lower than in the temperate regions. Only 13 of the 56 species known from Palearctic tundra occur further south (Christensen & Dózsa-Farkas 1999). Four genera, *Mesenchytraeus*, *Henlea*, *Cognettia* and *Bryodrilus*, exhibit higher species diversity in the tundra than in temperate regions. This general pattern is repeated among enchytraeids in NE Greenland and the Canadian Arctic Archipelago (Christensen & Dózsa-Farkas 2006).

Lumbricid earthworms, by contrast, are strictly temperature limited and scarce, with only two freeze-tolerant species, *Dendrobaena octaedra* and *Eisenia nordenskioldi*, found in areas with permafrost. *D. octaedra* is widespread in W Greenland up to Disko, but also found on Novaya Zemlya and low areas of W Siberia. *E. nordenskoldi* occurrs relatively commonly at sites at Maria Pronchitsheva Bay and Tareya on the Taimyr Peninsula (MacLean 1981, Holmstrup *et al.* 2007, Overgaard *et al.* 2007). However, in sub-Arctic, permafrost free soils of southern Greenland several other earthworm species occur quite frequently, some of them probably introduced with Nordic settlers (M. Holmstrup unpubl.). Among the oribatid mite species of North America, nearly 50% of species are known only from boreal and Arctic areas, suggesting a distinctive high latitude faunal element with its own provenance (Behan-Pelletier 1999, Behan-Pelletier & Schatz 2009). Genera of the tiger moth family Arctiidae of the Arctic tundra are similarly relatively distinct from those of the adjacent areas of the Palearctic and Nearctic regions, albeit based on a small number of species present (Dubatolov 2008).

Freshwater and terrestrial tardigrades (Tardigrada) in the North American Arctic form another characteristic species assemblage distinct from that of the remaining Nearctic region (Meyer & Hinton 2007). Chironomid midges show a parallel trend along a north-south transect through the Yukon, Canada, with genera such as *Abiskomyia, Mesocricotpus*, *Pseudochironomus* and *Polypedilum* being restricted to the Arctic tundra section of the transect (Walker *et al.* 2003). Chironomid community composition also tracks apparent north-south temperature anomalies. For example, in the Canadian high Arctic islands chironomid communities of the relatively warmer northern and southern islands are more similar than those of the cooler intervening central areas, notably Devon and Cornwallis Islands (Gajewski *et al.* 2005).

In several groups of herbivorous insects the effects of temperature along latitudinal transects in the Arctic are mediated through their host plant's range and phenology. Jumping plant lice (Hemiptera: Psylloidea), for example, are host-plant specific and develop on a number of woody shrubs, including many willow species, dwarf birch *Betula nana* sensu lato and Labrador tea *Rhododendron tomentosum* ssp. *decumbens* across a broad distribution within the low Arctic, including Alaska, the Chukotka Region of NE Russia and Scandinavia. Numbers of species decline with increasing latitude within the low Arctic, but in nearly all cases the host plant extends further north than the insect (Hodkinson & MacLean 1980, MacLean & Hodkinson 1980). Furthermore, several psyllid species drop out at a similar point along the transect. Their disappearance appears to result from a breakdown of phenological synchrony with their host, resulting from a failure to develop sufficiently quickly to complete their usual annual life cycle within a prescribed developmental window set by the plant (Hodkinson *et al.* 1979). One W Greenlandic species, *Cacopsylla groenlandica*, progressively sheds willow host-plants in this manner with increasing latitude before itself disappearing from its last surviving host grayleaf willow *Salix glauca* at the northern limit of its distribution (Hodkinson 1997). It is thus the differential effect of temperature on interacting insect and plant development that limits distribution, rather than the direct effect of cold temperature *per se*.

Such phenological limitation of distribution within the Arctic probably applies to many phytophagous groups with annual life cycles, including many of the sawflies (Høye & Forchammer 2008). However, more polyphagous herbivores with the ability to extend life cycle duration such as chrysomelid beetles and some Arctic moths (Lepidoptera) such as woolybear caterpillars *Gynaephora* spp. are unlikely to be restricted in this manner (Chernov *et al.* 1994, Medvedev 1996, Morewood & Ring 1998, Chernov & Makarova 2008). Among Finnish butterflies the proportion of species capable of overwintering in the extendable larval stage increases significantly at the highest latitudes (Virtanen & Neuvonen 1999).

Some Arctic insects exhibit restricted distributions relative to those of their host-plant along local rather than latitudinal microclimatic gradients, sometimes over relatively short distances. The aphid *Acyrthosiphon svalbardicum*, for example, feeding on eight-petal mountain-avens *Dryas octopetala* on W Spitsbergen, Svalbard is absent from its host at colder sites on the outer Kongsfjord but becomes progressively more abundant at warmer and more sheltered sites on the inner fjord. The distribution is related to the availability of sufficient 'degree-days' for the aphid to complete its life cycle (Strathdee & Bale 1995).

#### 7.2.3.3. Geographical and regional variations in biodiversity

The present compositions of the regional invertebrate faunas of the Arctic are determined by a multitude of factors. They represent an amalgam of taxa that survived the Pleistocene glaciations in Arctic glacial refuges, such as Beringia, intermixed with taxa that have at various times and with varying degrees of success colonized the Arctic from different geographical source areas lying farther to the south. Different taxa have dispersed at different rates, with climatic and geographical barriers to dispersal, such as mountain ranges, proving more effective for some taxa than others (Varga & Schmitt 2008, Ávila-Jiménez & Coulson 2011). The overall outcome is expressed as differences and similarities in faunal biodiversity among different regions of the Arctic and groups of invertebrates.

Danks (1981) predicted that invertebrate species with Holarctic distributions would tend to form a greater proportion of the fauna in the boreal/Arctic zones than elsewhere. Transholarctic, circumboreal, northern circumpolar and cosmopolitan species do indeed comprise a significantly large proportion of most Arctic faunas. Some Arctic bug species (Hemiptera) exemplify such wide-ranging and common northern Holarctic species. These include the seed bug *Nysius groenlandicus* (Lygaeidae) and the shore bugs *Chiloxanthus arcticus* and *Calacanthia trybomi* (Saldidae) (Danks 1981, Makarova & Makarov 2006, Böcher & Kristensen in press). However, even though some large taxa often contain several Holarctic species they may also contain other, often closely related, species that display widely disjunct distributions. Such distributions, as found in many springtail species, are often more difficult to interpret (Babenko 2005). Furthermore, the proportion of Holarctic species within the fauna may vary among the different regions of the Arctic and across invertebrate groups. Oribatid mites, for example, generally contain a high proportion of Holarctic species, with the majority of species found in the North American high Arctic and eastern low Arctic having Holarctic distributions (Behan-Pelletier 1999). Similarly, several important dipteran fly families within the Arctic, such as the winter craneflies (Trichoceridae), mosquitoes (Culicidae), root-maggot flies (Anthomyiidae) and blow-flies (Calliphoridae), contain at least 68% Holarctic species (Danks 1981). By contrast, surprisingly few (28%) Holarctic species of spider have Arctic or boreal ranges (Marusik & Koponen 2005). A similarly low proportion of Holarctic species also occurs in some aquatic insect groups, such as the stoneflies (Plecoptera), which tend to be largely restricted to the low Arctic. The declining percentage of Holarctic species with decreasing latitude is illustrated by moths of the family Noctuidae (noctuid moths) in which the percentage falls from 100%, in the high Arctic, to around 42% at lower latitudes in Iceland and the Yukon (Mikkola *et al.* 1991). For Arctic lepidopterans as a whole, the proportion of Holarctic species is around 13%.

**Table 7.5.** The number of species of springtail and butterfly species recorded from the different sectors of the Arctic (from Babenko 2005 and Chernov & Tatarinov 2006). Data for the high Arctic springtails alone are given in parentheses. Note that not all sectors have been sampled with equal thoroughness. For butterflies, the Ural and Western Siberian sectors are combined.

| Sector | Collembola | Butterflies |
|---|---|---|
| A Western European | 201 (71) | 51 |
| B Eastern European | 97 (14) | 74 |
| C Ural | 65 (51) | 57 |
| D Western Siberian | 178 (37) | |
| E Eastern Siberian | 105 (43) | 60 |
| F Northeastern Siberian | 152 (62) | 59 |
| G Western American | 155 | 59 |
| H Eastern American | 115 (49) | 47 |
| I Greenland | 89 | 6 |

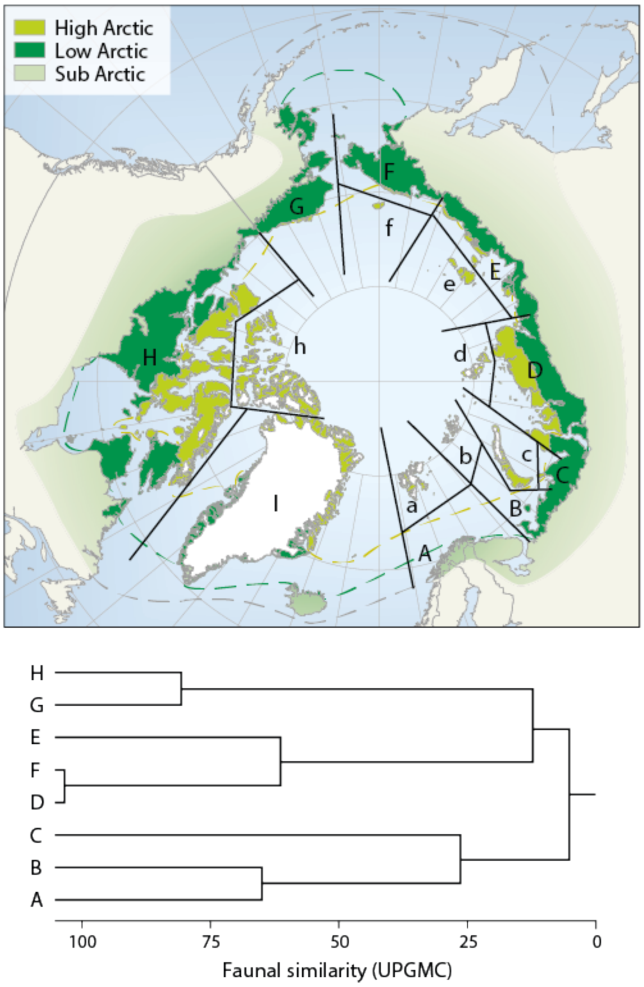

**Figure 7.4.** Biodiversity of springtail species within and among biogeographic sectors of the low (upper case letter) and high Arctic (lower case letter). Data in Tab. 7.5 are based on the divisions in the map: A Western Europe, B East Europe, C Ural, D West and Middle Siberia, E Eastern Siberia, F North East Asia, G Western America, H Eastern America, I Greenland. The lower dendrogram summarises the similarity of the faunas in eight of the different sectors (from Babenko 2005, Babenko & Fjellberg 2006). Clustering was carried out using the Unweighted Pair Group Method with Centroid Averaging (UPGMC).

Differences in biodiversity across geographical regions are well illustrated by a comparison between a well-adapted and diverse but flightless group, such as the springtails, and an assemblage, such as the butterflies, in which species are capable of flight but are more strongly restricted by climate and consequently contain a smaller proportion of high Arctic species. The overall patterns of diversity also differ in that for Arctic butterflies over 50% of species belong to just four genera *Colias* (sulfur butterflies), *Boloria* (fritillaries), *Oeneis* (graylings) and *Erebia* (mountain ringlets), a pattern most accentuated at higher latitudes (Chernov & Tatarinov 2006). Springtail species are, by contrast, more widely spread across a wider set of genera (Babenko & Fjellberg 2006). Tab. 7.5 shows the distribution of the 425 species (102 genera in 16 families) of springtails and 106 species of butterflies (36 genera in six families) across nine sectors of the low and high Arctic as defined in Fig. 7.4 (Babenko 2005, Babenko & Fjellberg 2006, Chernov & Tatarinov 2006). The numerically most important groups of springtail species present within the high Arctic, based on their known geographical distributions, are, in descending importance, Transholarctic and cosmopolitan > TransPalearctic > European and W Palearctic > E Palearctic > Beringian > Nearctic > Amphi-Atlantic species (Babenko 2005).

Patterns of glaciation have left strong residual effects on the biodiversity of invertebrate communities in different regions of the Arctic. Zooplankton crustaceans, for example, display higher diversity in lakes that remained unglaciated during the Pleistocene such as on the Chukotski Peninsula, Russia; Point Barrow, Alaska; and Disko Island, Greenland, compared with lakes in recently glaciated areas such as the Canadian Shield and parts of Siberia (Samchyshyna *et al.* 2008). The old Beringian refuge still casts its shadow today on invertebrate biodiversity, with many invertebrate species exhibiting an Amphi-Beringian distribution and the Beringian region being a diversity hotspot for several Arctic invertebrate groups such as chrysomelid beetles, weevils, craneflies, noctuid moths, spiders and particular groups of oribatid mite, such as the Ceratozetoidea (Danks 1981, Chernov & Makarova 2008, Behan-Pelletier & Schatz 2009, Elias 2009a, 2009b). Wrangel Island and the adjacent Chukotka Region are particularly rich in spider species, although Novaya Zemlya is also a hotspot for spider diversity.

The Bering Strait generally represents a less significant faunal disjunction than certain physiographic barriers within continental North America. For many arthropod groups, there is a strong faunal disjunction between the western and eastern sectors of the North American Arctic (Danks 1993). Several groups show a progressive decline in biodiversity as one moves from the Arctic west of the Mackenzie through the region between the Mackenzie and Hudson Bay to the area east of Hudson Bay (Danks 1981, Danks & Smith 2009). The reason for this is unclear. Notable examples include spiders; beetles of the families Carabidae (ground beetles) and Chrysomelidae (leaf beetles); flies of the families Tipulidae (craneflies), Anthomyiidae (root-maggot flies) and Muscidae (house flies) and butterflies of the families Pieridae (whites and sulfurs) and Nymphalidae, including the Satyrinae (fritillaries and browns). Several groups of Hymenoptera with strongly contrasting biologies, such as the leaf-eating sawflies Tenthredinidae, the parasitoid wasp family Ichneumonidae and the social bees Apidae, follow a similar trend (Danks 1981). Likewise, the number of mite species in the low Arctic of western North America is almost double that of the eastern part of the continent and the high Arctic combined (Behan-Pelletier 1999). There are also significantly more springtail species in NE Siberia and the western North American Arctic than in adjacent areas of W Siberia and eastern North America (Babenko 2005).

By contrast with the higher invertebrate groups, many of the lower invertebrate taxa within the Arctic are much more cosmopolitan in their distribution. This has been attributed to their small size and abundance facilitating dispersal and the maintenance of persistent populations (Segers & De Smet 2008). Of the 70 species of rotifers collected in ponds on Devon Island, Canada, only two species, *Notholca latistyla* and *Proales kostei*, are restricted to the Arctic, and a significant majority are cosmopolitan (De Smet & Beyens 1995). This dominance by cosmopolitan species is repeated in the 69 species from samples collected in W (Kangerlussuaq) and E (Ammassalik) Greenland (De Smet & Beyens 1993). The ciliates similarly contain high proportions of cosmopolitan species (Foissner *et al.* 2008). Forty-four of the 210 ciliate species found on Svalbard are also found in Antarctica, although other species have a more restricted distribution (Petz 2003, Petz *et al.* 2007). Around 13% of species in Petz's Arctic samples were new to science, and some may represent rare endemics (Petz *et al.* 2007).

Greenland forms an especially interesting sector of the Arctic as it is geologically a part of the North American continent and has traditionally been included within the Nearctic zoogeographical realm. However, Greenland presents a good example of how typical Arctic invertebrate faunas comprise an admixture of several biogeographical elements. It has long been recognized that the Greenland invertebrate fauna is not exclusively and typically Nearctic (Danks 1981). Some have suggested that it might represent a distinct zoogeographical unit containing characteristic faunal elements that survived the Pleis-

**Table 7.6.** Wider distribution patterns of species within selected arthropod taxa from Greenland, showing affinities with the Holarctic, Nearctic and Palearctic regions (from Makarova & Böcher 2009).

| Taxon | Species in Greenland | Holarctic + semicosmopolitan + cosmopolitan | Nearctic + Nearctic-W Beringian | Palearctic + European |
|---|---|---|---|---|
| Oribatid mites | 109 | 78 | 15 | 11 |
| Mesostigmatid mites | 59 | 28 | 5 | 21 |
| Areneae | 74 | 37 | 25 | 8 |
| Collembola | 89 | 50 | 7 | 31 |
| Coleoptera | 37 | 20 | 1 | 15 |
| Lepidoptera | 42 | 14 | 22 | 6 |
| Diptera: Muscidae | 37 | 26 | 10 | 0 |
| Trichoptera | 8 | 1 | 6 | 1 |

tocene glaciations in addition to the later colonizers from various geographic sources (Böcher 1988, Bergersen 1995). The presence of endemic species, often associated with the homothermal springs, lends some weight to this argument (Bergersen 1995). Tab. 7.6 shows that for several important arthropod groups, three distinctive elements can be recognized within the Greenland fauna (i.e. Holarctic, Nearctic and Palearctic), in addition to the endemic and cosmopolitan species. These data suggest that Greenland has been repeatedly colonized from the north, east and west. Even among closely related taxa within groups such as the mites there may be differences in the geographical origins of different subgroups. The moss mites (Oribatida), for example, show the strongest affinities with Nearctic faunas, whereas the Mesostigmata mites display clearer affinities with the Palearctic fauna (Makarova & Böcher 2009).

#### 7.2.3.4. Endemic species

Despite the widespread presence of transholarctic and cosmopolitan invertebrate species within the Arctic fauna, many other species are apparently endemic (Tab. 7.3). Some of these endemics are widespread within the Arctic, such as the springtails *Ceratophysella longispina* and *Bonetogastrura nivalis*, but others are restricted to small specific regions (Babenko & Fjellberg 2006). Even among primarily cosmopolitan groups, e.g. testate amoebae and rotifers, eight and twelve Arctic endemics, respectively, have been identified (e.g. De Smet & Beyens 1995). Interestingly, centers of endemism of some groups, e.g. rotifers (Monogononta), tardigrades and testate amoebae, include Svalbard and NE Canada, areas not noted for high endemicity among arthropods.

Some Arctic endemics have very highly restricted distributions. The aphid *Sitobion calvulus*, for example, despite extensive searches, is known only from a few scattered localities adjacent to the inner parts of Kongsfjord, W Spitsbergen, Svalbard (Gillespie *et al.* 2007). Another aphid, *Acyrthosiphon svalbardicum*, is more locally abundant but still endemic to Svalbard (Strathdee & Bale 1995). The primary host-plants of these aphids, polar willow *Salix polaris* and mountain-avens respectively, are however widespread within the Arctic. Endemicity is especially common among Arctic aphids, with around 37% of the Nearctic species apparently endemic to the region and a particular concentration of endemic species in the eastern Canadian Arctic (Tab. 7.3).

In general, the Arctic endemic invertebrate species tend to be scattered across a wide range of taxa. For example, the number of endemic species within numerically important groups of arthropod in Greenland is: springtails 1, aphids 9, scale insects (Coccoidea) 5, chironomid midges 13, fungus gnats (Mycetophilidae) 2, parasitic wasps of the families Braconidae 8 and Ichneumonidae 28, ground beetles 1, spiders 3, moss mites 4, Prostigmata mites 11 and Mesostigmata mites 5 (Böcher & Kristensen in press). The enchytraeid worms represent a group especially rich in Arctic endemic species, particularly within the Palearctic tundra and in the Amphi-Beringian region, with a strong dominance by species of the genera *Mesenchytraeus* and *Henlea* (Christensen & Dózsa-Farkas 1999). The Amphi-Beringean region, notably the tundra steppe region of NE Siberia, is particularly rich in endemic species in many taxa, including spiders, oribatid mites, lepidopterans, craneflies, weevils and ground beetles, chrysomelid and rove beetles (e.g. Mikkola *et al.* 1991, Ryabukhin 1999, Marusik & Koponen 2002, Chernov & Makarova 2008, Konstantinov *et al.* 2009). Arctic endemic species of flightless leaf beetles belonging to the genus *Chrysolina*, for example, are typical of eastern Siberia and adjacent islands (e.g. Wrangel Island) and northern Alaska, but are absent from the Canadian Arctic Islands and Greenland (Chernov & Makarova 2008). It is notable that several species of insect living in the eastern Siberian steppe desert today, such as the pill beetle *Morychus viridis* (Byrrhidae), are remnants of an Early Pleistocene fauna that have survived in similar unglaciated habitats for around 2.5 million years (Berman 1990, Elias 2009a).

Care is needed, however, in interpreting available data on endemicity. For example, existing data suggest that 68% of anthomyiid flies are Holarctic and the remainder is Nearctic endemics. This is unlikely to be the case and merely reflects a paucity of data on this group from the Russian Arctic (A. Pont, unpubl.).

## 7.3. STATUS AND TRENDS

### 7.3.1. Species richness and distribution

The lack of long-term studies on most invertebrate species leads to a paucity of empirical data on their response to climate change across the Arctic regions, despite some knowledge about their existing distributions. Much evidence for natural change, including that noted earlier by indigenous peoples, is primarily based on records of species that appear to have become more abundant or extended their range. For example, the moth *Apamea zeta* (= *maillairdi*) appears to have become more abundant around Longyearbyen, Svalbard, and the thrip *Aptinothrips rufus* has been recorded from Svalbard for the first time (Hodkinson 2004). The latter record, however, illustrates a further problem of knowing whether a species is newly establishing or whether it is a mere vagrant. The Greenland ladybird *Coccinella transversoguttata* appears to have recently pushed its distributional limit about 100 km northwards in E Greenland, and the aphid *A. svalbardicum*, previously thought to be apterous, is now commonly producing winged forms (Simon *et al.* 2008, Böcher 2009). Observations by indigeneous peoples, notably the Saami in Finland, provide many records of apparent longer-term changes in insect abundance, particularly in association with reindeer herding. These involve changes in the numbers of biting flies, such as mosquitoes and black flies, and of parasites such as caribou nostril flies and gadflies. They also extend to a wider range of species, including bees, wasps, butterfly and beetle species (Salin *et al.* 2004, Mustonen 2004, Mustonen & Zavalko 2004, Mustonen & Mustonen 2009, 2011).

Probably the best quantitative evidence for change within the last hundred years comes from studies on aquatic chironomid midges, where community composition can be reconstructed from subfossil records. Chironomids in high Arctic ponds on Ellesmere Island, Canada, for example, have shown a marked increase in both population density and diversity associated with shifts in diatom populations and reduced ice cover (Quinlan *et al.* 2005).

Glacial retreat in many parts of the Arctic is exposing new habitats for colonization by invertebrates. Studies of the past chronology of colonization and community assembly indicate how and why future changes in biodiversity may take place. For example, a study of the progressive colonization of the glacier foreland of Midtre Lovénbreen, Svalbard, with respect to elapsed time since exposure, showed that colonization by pioneer species is rapid, but that it may take up to 2000 years for the full complement of species found in the surrounding non-glaciated areas to establish, particularly the species associated with deeper soils (Hodkinson *et al.* 2004). Invertebrate species fell into eight groups with respect to colonization success, based on ecophysiological tolerances, the need for facilitation, or a dependence on other species. The earliest colonizers were predators and detritus feeders, including spiders, surface-active springtails and drought resistant oribatid mites, which established before vascular plants arrived and soil developed. Later colonizers required facilitation and soil development. Equivalent data for associated glacial streams shows similar rapid early colonization by cold-adapted aquatic faunas, especially chironomid midges, followed by gradual community change as conditions become more stable (Lods-Crozet *et al.* 2007). Such glacier retreat chronosequences show that the development of biodiversity is time dependent but deterministic, and that this process is likely to accelerate within a warming Arctic.

These local changes in biodiversity should, however, be viewed against the broader background of a changing Arctic, the ability of existing species to survive change and the potential for the invasion by dispersal of 'new' species from outside. Arctic invertebrates, despite their small size and absence of specialized adaptations, frequently display highly effective dispersal mechanisms. For many of the smallest invertebrates with cold/drought resistant egg or other resting stages, often coupled with asexual reproduction (e.g. rotifers, tardigrades, ostracod crustaceans and testate amoebae), dissemination by wind or water is commonplace. The use of yellow sticky traps and water traps reveals a significant and continual dispersal of flying, wind-blown and ballooning (spider) invertebrate species across the Arctic landscape, with chironomid midges usually the dominant faunal component (Coulson *et al.* 2003a, Hawes 2008). Springtail and mite species appear to disperse effectively on the surface of, and occasionally submerged within, both fresh and salt water (Coulson *et al.* 2002a). Phoretic association of several, such as oribatid mites, with flying Diptera and birds may also enhance their wider dissemination (Lebedeva & Lebedev 2008, Coulson 2009). The sporadic mass arrival within the high Arctic of a wide diversity of living non-indigenous insect species, such as the moth *Plutella xylostella*, resulting from the movement of atmospheric depressions from lower latitudes, suggests that a mechanism is already in place for colonization by more southerly species as climate ameliorates (Coulson *et al.* 2002b). However it also indicates that conditions must become suitable for sustained activity, growth, development and reproduction before establishment can occur. For example, *P. xylostella*, which has yet to establish known self-sustaining populations within the high Arctic, has a development threshold of 7 °C and an activity threshold of 18 °C for sustained flight compared with a current maximum mean monthly temperature of 6 °C and a maximum air temperature of 17 °C at sites on Svalbard where it has been found (Coulson *et al.* 2002b). However, the successful colonization by *P. xylostella* of the sub-Antarctic Marion Island, with a similar summer climate to Svalbard, suggests that classical physiological thresholds may not always reflect true adaptational ability.

Changes in Arctic biodiversity in response to changing climate at any site will in all probability result from a re-sorting of existing Arctic species as they shift their distributions and potentially begin to interact with incomer species. Different organisms, however, will tend to move at different rates. Their success in adapting to change will depend largely on their ability to track changes in their habitat and match their ecophysiological requirements to those of their new surroundings. The key environmental factors determining their success are likely to be mean summer and winter temperatures, moisture availability, length of growing season and the frequency of freeze/thaw events that may disrupt preparation for, and emergence from, the overwintering state (Hodkinson *et al.* 1996a, 1998, Ávila-Jiménez *et al.* 2010, Bale & Hayward 2010, Ayres *et al.* 2010). While warmer summer temperatures may adversely affect some Arctic invertebrate species such as stenothermal ground beetles and spiders, many are likely to respond positively to such temperature increases, provided other conditions remain suitable. For example, populations of the aphids *A. svalbardicum* and *S. calvulus*, despite their status as high Arctic endemics, both respond rapidly and positively to increased summer temperature under experimental manipulation (Strathdee *et al.* 1995, Gillespie *et al.* 2007). The response, however, may occur differentially among ostensibly similar taxa. The larvae of tenthredinid sawflies, for example, appear to develop and molt more rapidly at low temperatures than those of lepidopterans, suggesting that their responses to increased temperature will also differ (Bogacheva 1994). Similarly, several springtail and oribatid mite species may respond positively to increased temperatures, but many springtail species are also highly susceptible to reduced moisture availability (Hodkinson *et al.* 1998). Oribatid mites, by contrast, appear more drought resistant and better able to withstand lower soil moisture, but are less responsive to increased temperature. Soil dwelling invertebrates such as enchytraeid worms, eelworms, ciliates, testate amoebae, rotifers and tardigrades, which either live in the soil water film or possess cuticles that are highly permeable to water, are the organisms that are the most likely to be adversely affected by a drying of the tundra associated with increased temperatures (e.g. Maraldo *et al.* 2009).

It is unlikely, however, that the overall effect of climate amelioration on Arctic invertebrates will be simple, with high Arctic species disappearing to be replaced in an orderly manner by species diffusing up from the south. Change will at least initially involve resorting and reordering of taxa within existing communities. Much of the terrestrial high Arctic is comprised of island archipelagos that are separated from areas farther south by marine/pack ice barriers. While many colonizing invertebrate taxa and species are easily capable of jumping these barriers, they will do so at different rates and with a significant element of stochasticity in their order of arrival and establishment (Hodkinson *et al.* 1998). A more gradual northward diffusion of species is most likely in the continental low Arctic tundra areas of northern Russia, Canada and Alaska, but even here topographic diversity should ensure that diffusion proceeds in a punctuated manner. In mountainous regions there is a strong possibility that Arctic arthopods, together with their host plants, will move to and survive at higher elevations (Hodkinson 2005). Equilibrium communities will take a long time to develop, if they become established at all.

#### 7.3.1.1. The importance of species interactions

Arctic invertebrate species do not live in isolation, but rather interact with other species to form food chains and webs of varying complexity. Increasing biodiversity implies increased food web complexity, with implications for species interdependence, ecosystem function, resilience and stability (Wall 2009). Interactions can take many forms, including predation, parasitism and pollination, all of which are susceptible to modification in a changing climate. For interacting species to co-exist in space and time, they must share similar ecophysiological tolerances and habitat requirements. Phenological asynchrony or mismatched environmental tolerances may lead to the breakdown of interactions between the species, especially in the harsh and unpredictable climates of the Arctic (Hance *et al.* 2007).

The success of seed set in many common Arctic dicotyledenous plants, such as Arctic willow *Salix arctica*, purple saxifrage *Saxifraga oppositifolia* and entire-leaved mountain-avens *Dryas integrifolia* at Lake Hazen, Ellesmere Island, is totally or partially dependent on pollination by insects (Kevan 1972, Danks 1986). Bumblebees, the important pollinators at temperate latitudes, are generally scarce within Arctic ecosystems where a wide variety of nectar/pollen feeding dipteran flies are the main pollinators (Pont 1993, Elberling & Olesen 1999, Larson *et al.* 2001). Butterflies, e.g. the fritillaries *Boloria* spp., are less common pollinators, but parasitoid wasps are frequently associated with flowers, although their precise role in pollination is less clear (Klein *et al.* 2008).

Arctic plant-insect pollinator networks can be complex. For example, seven pollinator networks at sites located between latitudes 66-82° N involved 15 to 31 plant species, 26 to 118 insect pollinators, and 63-286 recorded insect plant interactions per site (Lundgren & Olesen 2005). However, the extent to which these networks are flexible and able to accommodate new invading species in an era of warming climate remains unclear and probably depends on the extent of the mutual specificity of the relationships among incoming species (Klein *et al.* 2008). Some plants with specialized floral anatomy, e.g. the lousewort *Pedicularis* spp. and legumes, appear more closely linked to pollination by bumblebees and hoverflies (Kevan 1972, Klein *et al.* 2008). Established pollinators may thus be unable to facilitate the establishment of such specialized plants.

Communities of Arctic arthropods contain at first sight a surprisingly high proportion of predatory and parasitic species relative to prey species (Hodkinson & Coulson 2004). Spiders, predatory mesostigmatid mites and parasitoid wasps are an abundant and ubiquitous element of faunas throughout the Arctic. Among beetles, predatory ground beetles and rove beetles often predominate, particularly in the low Arctic. The precise food/host interrelationships of many of these predators and parasitoids remain unknown, although existing data suggest that food chains are not as short as some have suggested. A four link chain, for example, springtail → spider → ichneumon wasp → bird is not uncommon (Hodkinson & Coulson 2004).

Levels of predation by beetles and predatory hover fly larvae are frequently reduced at higher latitudes as these less well adapted predator species become temperature limited and fail to exploit the full range of their potential hosts. For example, the distribution of the rove beetle, *Atheta graminicola*, in NW Spitsbergen is confined to thermally favorable microsites, and it is absent from the coldest areas despite an abundance of suitable prey. Similarly, the Greenland willow psyllid *Cacopsylla groenlandica* suffers reduced predation by hover fly larvae in the northern part of its range (Hodkinson 1997). Communities of *Eupontania* species of gall-forming sawflies in the Russian Arctic support fewer parasitoids and suffered lower overall parasitism at northern compared with southern Arctic localities (Roininen *et al.* 2002). A warming climate will begin to alter the balance of these relationships.

Many tundra-nesting bird species depend for their reproductive success on the availability of a diverse assemblage of invertebrates on which to feed their young. A reliable and sufficient food supply, which is sustained throughout the breeding season, requires a seasonal progression of invertebrate species, particularly insects, becoming successively available through the summer. There is some evidence that, at least initially, a warmer summer may lead to accelerated emergence of insect species, notably chironomid midges and mosquitos, such that the availability of food is increased early in the season but becomes restricted later in the year (MacLean 1980, Hodkinson *et al.* 1996b, Tulp & Schekkerman 2008). Larval chironomids also provide a prime source of food for some freshwater fish species.

### 7.3.2. Population sizes and densities

Population densities of both individual species and higher taxa of invertebrate vary greatly among habitat types, and it is not possible to quote typical density values. Likewise it is difficult to predict future trends. It is more apposite to emphasize the variation that occurs across a range of habitats. For example, on Svalbard total springtail numbers may range from less than 2,000/m$^2$ in impoverished habitats to over 260,000/m$^2$ in damp grassland and 590,000/m$^2$ in enriched wet moss sites below bird cliffs (Coulson 2000). Similarly, numbers of eelworms vary between 400,000 and 7,000,000/m$^2$ among sites at Tereya on the Taimyr Peninsula, Russia (Chernov 1972). Proportions of individual species within the total population also vary considerably among habitats. The mite *Camisia anomia*, for example, comprises over half the total oribatid mite population in polar semi-desert communities on Svalbard but less than 10% in tundra heath (Webb *et al.* 1998). Tab. 7.7 shows the range in mean population densities recorded for some of the numerically dominant groups of soil invertebrates at selected sites throughout the Arctic. Variation among habitats within sites is frequently as great as that among sites.

Other invertebrate groups are usually present at much lower densities. However, certain groups, such as the larvae of craneflies, sawflies and butterflies can, because of their larger individual size, make highly significant contributions to total invertebrate biomass (Bogacheva 1977, MacLean 1980). Craneflies, for example, are especially important in wetter low Arctic habitats such as at Barrow, Alaska (MacLean 1980). Earthworms, although unevenly distributed, can in some hotspot areas reach moderately high densities and contribute substantially to the biomass of the soil biota. *E. nordenskioldi* populations in the Taymyr peninsula reach densities of 80 individuals/m$^2$, and biomass varies between 25 and 65 g fresh weight/m$^2$ (Matveyeva *et al.* 1975). *D. octaedra* in Greenland may attain densities of 10-20 individuals/m$^2$, but the distribution is patchy (M. Holmstrup unpubl.). Total Diptera larval densities across habitats ranged from 0 to 668/m$^2$ at Zackenberg, NE Greenland, 10 to 2,500/m$^2$ on Svalbard, 8 to 99/m$^2$ at Tereya, Taimyr, and 171 to 915/m$^2$ at Barrow, Alaska (Chernov 1972, MacLean 1980, Coulson 2000, Sorenson *et al.* 2006). Equivalent data for beetle numbers are 0 to 60/m$^2$ on Svalbard and 0 to 107/m$^2$ at Tereya, and for spiders 0 to 100/m$^2$ on Svalbard and 35.9/m$^2$ on the Yamal Peninsula, Russia (Danilov 1972, Coulson 2000).

The population densities of biting flies found within some areas of the Arctic, notably mosquitoes and black flies, have strong impacts on a range of human activities, particularly reindeer herding and tourism. They also have important implications for the breeding success of native mammals and birds. These may involve positive effects, such as the provision of food for birds, but also negative impacts, such as the disruption of normal patterns of behaviour in both birds and mammals. Despite their often high abundance, the biting flies are not particularly species rich. Nevertheless, they have the potential to act as vectors of disease in both humans and a range of bird and mammal species. The introduction of novel or more virulent forms of insect-borne disease may thus become more likely because of climate-change effects on biting fly distribution and density.

It is notoriously difficult to estimate accurate population densities for microscopic soil animals and data, when recorded, are usually expressed per gram of soil rather than per square meter. Testate amoebae populations ranged from 20 to 40 individuals/g soil across four vegetation types at Zackenberg, NE Greenland, while 'Protozoa' (naked amoebae + flagellates) numbered 7,000 to 11,000 individuals/g soil at sites ranging from mesic to dry heath (Trappeniers *et al.* 2002, Sorensen *et al.* 2006).

## 7.4. CONCLUSIONS AND RECOMMENDATIONS

### 7.4.1. Sensitive areas and hotspots

In addition to the known major biodiversity hotspots within the Arctic, e.g. Beringia, there are many smaller biodiversity hotspots or oases with features favorable to invertebrates. Such sites may, for example, have a particu-

**Table 7.7.** Mean population densities (1,000/m$^2$) of the numerically dominant soil invertebrate groups across a variety of habitats and dates at selected Arctic sites. Data are compiled from existing summaries, which should be consulted for more detailed information and original source references (see Chernov 1972, Bliss 1987, MacLean 1980, 1981, Coulson *et al.* 1996, Webb *et al.* 1998, Coulson 2000, Sorensen *et al.* 2006).

| Site | Springtails | Mites | Enchytraeidae | Nematoda |
|---|---|---|---|---|
| Svalbard | 0.6-592 | 0.3-248 | 0.2-100 | 2.3-376 |
| Devon Island, Canada | 2-30 | 10-20 | 20-30 | 40-50 |
| Point Barrow, Alaska | 24-171 | 9-83 | 11-93 | 46-723 |
| Prudhoe Bay, Alaska | 1-70 | 1-80 | 10-40 | - |
| Tereya, Taimyr, Russia | 14-119 | 2-45 | 1-24 | 400-76,000 |
| Zackenberg, Greenland | 30-130 | 39-46 | 0.3-3.5 | 65-250/g soil |

larly favorable microclimate, habitat diversity or nutrient status. These sites are more likely to attract new colonizing species and to harbor source populations from which species may spread as conditions become more favorable in the surrounding areas. Several thermally favorable 'oases' are sheltered south or west facing sites, often with a reflective body of water in front and cliff behind (Mikkola 1992). Consequently, such sites occur most frequently at the sheltered heads of fjords or adjacent to sea coasts where climate is ameliorated by a warmer ocean current.

Examples of oases for invertebrates in the Canadian Arctic include Lake Hazen and Alexandra Fjord on Ellesmere Island and Truelove Lowland on Devon Island (Bliss 1987, Svoboda *et al.* 1994, Ring 2001). Greenland sites include low Arctic Disko Island with its homothermal springs, the sub-Arctic inner fjord region around Narsarsuaq on the west coast, and the high Arctic Zackenberg adjacent to Young Sund on the northeast coast (Høye & Forchammer 2008). These sites, because of their perceived diversity, have frequently been the subject of the most intensive investigations. On Svalbard, Ossinsarsfjellet oasis at the head of Kongsfjord in NW Spitsbergen supports a relatively rich flora and fauna. The moth *Pyla fusca*, a more typical denizen of temperate regions, is persistently found here. This is an excellent example of a species that has managed to establish a toehold within a Svalbard oasis, albeit at a single favorable site (Coulson *et al.* 2003c). Wrangel Island is an important biodiversity hotspot within the Russian high Arctic.

The areas on, below and in front of nesting seabird cliffs that receive high subsidies of nutrients from bird droppings, and allochthonous detritus often have greater diversity of invertebrates such as beetles. These areas may also support atypically high population densities for several invertebrate species. High total populations of mites and springtails, however, are often associated with lowered species diversity within these groups.

There is a danger that because diversity hotspots often coincide with areas of climatic favorability or historic glacial refugia, any conservation focus on such areas may result in the cold-adapted, true Arctic species with wide ranging distributions being ignored.

### 7.4.2. Key knowledge gaps and recommendations

Our fragmentary knowledge of the biodiversity of many Arctic invertebrate taxa and the lack of good long-term data on population trends suggests the following important priorities for Arctic invertebrate diversity research:

- There is a pressing need for an increased recognition within CAFF that the invertebrates play a significant and essential role in the functioning of Arctic ecosystems. Given their dominant contribution to Arctic biodiversity and their role in providing key ecosystem services such as energy flow, decomposition, nutrient cycling and pollination (e.g. Wall *et al.* 2008), it is surprising how little attention has been paid to them in previous syntheses on the impact of climate change on the Arctic biota. For example, the *Arctic Climate Impact Assessment* barely touches on their biodiversity and makes few suggestions as to how they might respond to changing climate (Callaghan *et al.* 2004, 2005). Furthermore, their interaction with other organism groups through pollination (higher plants), ecto- and endo-parasitism (birds, mammals and other invertebrates) and their role as food for tundra-nesting birds or fish species at critical stages of their life cycle further emphasizes their importance to the functional health of Arctic ecosystems.
- A comprehensive inventory should be compiled for invertebrate species within the Arctic, listing their known distribution, abundance, habitat preference and functional role within the ecosystem. Traditional knowledge and expertise should be incorporated wherever feasible. Initially, this inventory should be based on existing literature. It is recognized that this will be fraught with difficulties and will require the resolution of many taxonomic and nomenclature problems. This latter issue might be tackled by utilizing and further developing molecular methodologies such as the DNA Barcode of Life (BOL) initiative at the University of Guelph, Canada (www.dnabarcoding.ca).
- There is a pressing need for further field survey work throughout previously neglected areas of the Arctic to ensure that the species inventory is as complete as possible and to establish more clearly the distribution patterns of species, particularly among the neglected invertebrate groups such as the eelworms and most lower invertebrates. Potential sites for long-term monitoring should be identified within these areas.
- The inventory should be used to identify and list the number and distribution patterns of the true Arctic endemic species, spread across many higher taxa, which are most likely to be most affected by a warming climate. All species, where possible, should be classified using the IUCN Red List Categories and Criteria. The inventory should also be used to identify or confirm areas of high diversity and endemism at various taxonomic levels across the invertebrates.
- There is an urgent need to establish a longer-term program monitoring population trends for selected indicator species that are likely to show both adverse and positive reactions to changing climate. It is essential that both above-ground and soil-dwelling species are included as they are likely to respond to climate change at different rates. Lake/pond dwelling species may similarly exhibit a buffered response to temperature changes. Compared with vertebrates and plants, many species/communities of invertebrates posses the attributes to act as highly sensitive indicators of changing climate. Their often effective powers of dispersal, coupled with rapid development rates leading to short generation times, ensure that they are able to rapidly shift location and re-establish populations as conditions permit (Hodkinson & Bird 1998). The potential exists to identify key indicator species/communities that may be used, through changes in

phenology and distribution, to track climate changes and their impacts over time. Such changes may have cascading effects within ecosystems. Indicator species could include generalist, temperature-limited predators/scavengers such as ground and rove beetles and cold-adapted spiders including the genus *Erigone* (dwarf spiders), or species of host-specific herbivorous insect, such as psyllids (jumping plant lice) or leaf beetles, which currently do not occupy the full range of their host plant. The former group would be particularly easy to monitor as baseline data on their distribution along north-south transects already exist, and their common and widespread host-plants are easy to locate. Monitoring should also examine longer term population/genetic trends in indicator species/communities at fixed locations. The indicator species should include both Arctic endemics and widespread Arctic species across a range of sites. Candidate species/groups might include chironomid midges and water beetles in lakes, herbivorous terrestrial species such as the aphid *Acyrthosiphon svalbardicum* on Svalbard and the woolybear caterpillar in Canada, and certain widespread springtail species such as *Folsomia quadrioculata* and *Hypogastrura tulbergi*, soil-dwelling and surface-active species respectively. Inclusion of species with a long continuous history within the Arctic, such as the Beringean pill beetle *Morychus viridis*, could provide the longer-term context for change.

- Community change in the Arctic is likely to be driven in part by newly arrived incomer species. It would be instructive to set up a sampling program to analyze the species composition and abundance of the aerial invertebrate plankton that is carried into the Arctic from farther south by northwards-moving weather systems. These are the potential colonizing species. An inventory of newly establishing species should be developed and the extent of human mediated introductions of species into the Arctic assessed.
- The effects of climate change on economically significant biting fly populations should be evaluated throughout the Arctic in relation to alterations in the hydrology of habitats and rising temperatures. This is particularly important for the indigenous peoples of the Arctic, especially with respect to reindeer herding and other traditional activities. It also has implications for the tourism industry. Assessment should be made of the potential spread of important arthropod vector-borne diseases of humans, other mammals and birds into the Arctic.

### 7.4.3. Recommended conservation actions

Because of the sheer number of species, it is impractical to take a species-based approach to conservation of Arctic terrestrial and freshwater invertebrates. Conservation actions should focus on the maintenance of habitat diversity and protection. Nevertheless, invertebrate conservation in the Arctic has suffered from a lack of focal species that can be used to highlight the problems of conservation. Focal species, however, must be chosen for their uniqueness or for their importance in ecological processes rather than for their aesthetic appeal. Examples of the former might include the flightless aphid *Sitobion calvulus* with its highly restricted distribution on Svalbard or chrysomelid beetles on the high Arctic islands. Examples of the latter could include a typical widely-distributed, surface-active springtail such as *Hypogastrura tullbergi* or widespread Arctic species of enchytraeid worms.

### 7.4.4. Other key messages

Our knowledge of the invertebrates as a group lags far behind that of higher plants, mammals and birds, yet the invertebrates represent the dominant group in terms of species-based biodiversity. This deficiency is reflected in the paucity of data concerning numerical trends, drivers and stressors presented in the preceding sections. Invertebrates are small and, to many, aesthetically unappealing, but they are almost invariably the numerically dominant group of organisms (excluding microorganisms) at sites in the Arctic, where they serve a wide variety of ecological functions and are key players in important ecosystem processes. There is danger in overstating the importance of larger, more charismatic vertebrate species with conservation appeal at the expense of those lesser invertebrates with greater functional significance for the well being of Arctic ecosystems.

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With the acidification expected in Arctic waters, populations of a key Arctic pelagic mollusc – the pteropod *Limacina helicina* – can be severely threatened due to hampering of the calcification processes. The Greenlandic name, Tulukkaasaq (the one that looks like a raven) refers to the winged 'flight' of this abundant small black sea snail. Photo: Kevin Lee (see also Michel, Chapter 14).

*Chapter 8*

# Marine Invertebrates

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## Contents

> **» There are areas where the salmon is expanding north to the high Arctic as the waters are getting warmer which is the case in the Inuvialuit Home Settlement area of the Northwest Territories of Canada. Similar reports are heard from the Kolyma River in the Russian Arctic where local Indigenous fishermen have caught sea medusae in their nets.**
>
> Mustonen 2007.

## SUMMARY

This chapter brings together baseline information on the diversity of marine invertebrates in the Arctic Ocean and discusses the importance of factors that have shaped patterns of biodiversity.

The Arctic Ocean is here defined as the areas north of the Bering Strait on the Pacific side and areas with consistent seasonal sea ice cover on the Atlantic side. The known marine invertebrate fauna of this area comprises c. 5,000 species, representing at least 24 phyla with representatives in all three marine realms: sea ice, pelagic and benthic. About 50% of the Arctic Ocean overlays continental shelf areas at water depths ranging from 0-500 m. This Arctic Shelf constitutes 31% of the total shelf area of the world. More than 90% of the known Arctic invertebrate species occur in the benthic realm. As for terrestrial environments, the most species rich taxon in all realms is Arthropoda, with most species among crustaceans, i.e. >1,500 species according to a recent estimate. Other species-rich taxonomic groups are Annelida, mainly bristle worms (Polychaeta), moss animals (Bryozoa) and Mollusca, including bivalves (Bivalvia) and snails (Gastropoda). Among the meiobenthos (small-sized benthic metazoans, < 1 mm) the predominant groups are free-living nematodes (Nematoda), followed by harpacticoids (Copepoda: Harpacticoida). In terms of abundance and biomass, nematodes and harpacticoid copepods typically dominate the meiofauna (as they do elsewhere), while polychaetes, bivalves and amphipods typically dominate the macrofauna, and echinoderms and crustaceans dominate the megafauna.

The number of known marine invertebrate species in the Arctic Ocean is very likely to increase in the future, because vast areas, particularly the deep-sea basins, are under-sampled. For example, a recent estimate suggests that several thousand benthic species have been missed to date. Contrary to paradigms of an impoverished Arctic fauna due to a harsh environment, as seen in the terrestrial realm, the Arctic shelf fauna is not particularly poor, but considered to be of intermediate richness, similar in overall species richness to some other shelf faunas, such as the Norwegian shelf. The pattern of declining species richness with increasing latitude, obvious in the terrestrial realm, is controversial among marine invertebrates and conclusions depend on the taxon and geographic scale studied. A latitudinal decline from the tropics to the Arctic was seen in shelf molluscs, while arthropods seem to show higher diversity in some Arctic areas compared with some non-Arctic areas.

Due to the turbulent geological history with repeated glaciation events over the last 3.5 million years, together with in ineffective isolation from adjacent oceans, *in situ* evolution of species has been hampered, and as a consequence there are few Arctic endemics, at least on the continental shelves. However, bryozoans contain more endemics than many other groups, possibly partly related to poor dispersal in this group.The present-day invertebrate fauna in the Arctic is a mixture of species with different origins, where the majority have distributions reaching outside the Arctic, i.e. the boreal parts of the adjacent oceans. By and large the Arctic Ocean is a sea of immigrants that have dispersed from adjacent oceans both in historical and in recent time.

Today’s biogeographic drivers of Arctic diversity are clearly seen in the distributions of origins in relation to the two major gateways into the Arctic, i.e. from the Atlantic Ocean and the Pacific Ocean. On the continental shelves, the proportions of present-day Pacific and Atlantic species decrease with increasing distance from the Bering Strait and the NE Atlantic, respectively. Current inventories indicate that the Barents Sea has the highest species richness, being ‘enriched’ by sub-Arctic and boreal species. Today’s Arctic deep-sea floor fauna is most closely related to the present North Atlantic fauna, which in a geological time perspective contains a strong Pacific influence.

Like other faunal elements in the Arctic, marine invertebrates are affected by climate warming. The most obvious effects will be on the fauna of the permanent ice (sympagic fauna) which will lose its habitat. However, detecting effects in the other realms is difficult, mainly because there are only few time series data available. It is expected that the fauna with strong boreal influence may show (perhaps temporarily) increased diversity, due to a combination of anticipated increased food availability for the benthos and immigration of species adapted to warmer waters. Signs of borealization are already seen in marginal areas of the Actic Ocean. Long-term estimates of climate change effects on diversity are challenging because of the complex interactions of changes on multiple levels of the Arctic system.

It is recommended that conservation actions are targeted towards whole systems rather than individual species. Since system-focused conservation efforts typically focus on limited regions, we need to know more about diversity patterns at a high spatial resolution, in particular the distribution of Arctic endemics in order to conserve as many unique species as possible. Also we need to identify the ‘biodiversity hotspots’ – the areas which harbor high numbers of unique species due to habitat complexity and other factors.There is a demand for research to get a better understanding of the factors and processes that affect diversity. To achieve this, regional and taxonomic gaps need to be closed, and time series are needed to address temporal dynamics and changes in biodiversity. However, since time is probably short before severe effects of climate change will appear, we cannot wait for a high frequency mapping of the whole Arctic. Instead we suggest the establishment, or in some cases continuation, of time series monitoring at selected sites in species rich Arctic areas close to the major gateways, as well as in some areas distant from the gateways into the Arctic. We also suggest protection of areas with the highest proportion of Arctic endemic species, as well as the productive polynyas where pelagic-benthic coupling

is strong and that are of high importance for higher taxonomic life.

## 8.1. INTRODUCTION

In this chapter, we consider the diversity of invertebrates from the entire benthic, pelagic and sea-ice realms of the Arctic Ocean, broadly defined as areas north of the Bering Strait on the Pacific side and areas with consistent seasonal sea ice cover on the Atlantic side (Bluhm *et al.* 2011a). This corresponds broadly to the delineation of the Arctic waters made in Fig. 6.4 in the fish chapter (Christiansen & Reist, Chapter 6), but excluding the Bering and Norwegian Seas. We recognize, however, that the literature cited below does not always follow this delineation.

The present invertebrate diversity in the Arctic Ocean area is the net result of many factors acting both in historical and recent time. Like in other systems on Earth, species diversity in the Arctic is influenced by niche-based factors, such as adaptation to different environmental conditions and by dispersal based factors, such as immigration from species pools. The relative importance of these two types of factors is not always easy to disentangle and may vary with scale and the degree of connectivity to other ecosystems.

Niche-based factors like adaptation to different environmental conditions are likely to account for a significant part of biodiversity in the Arctic because it is far from homogeneous. In each of the three realms, invertebrate species inhabit a multitude of different habitats. The pelagic realm contains downwelling or upwelling areas, frontal zones and polynyas with a varying degree of coupling with the benthic realm below. The recent permanent ice-cover in the Central Arctic and seasonal ice in the rest of Arctic act as a specific habitat for sea-ice associated life, and within the ice realm habitats vary from highly productive ice edge areas to more oligotrophic zones in brine channels in the ice, as well as the ice-water interface on the underside of the ice.

The sea floor contains considerable large scale topographic heterogeneity, for instance intertidal coastal areas, semi-enclosed fjords with fjord basins, estuaries of different sizes, an expanded shelf zone with a number of canyons (Voronin, St. Anna) and inner isolated depressions (like Novaya Zemlya Trench), and the deep sea with several basins separated by deep-sea ridges. At smaller scales, benthic areas contain different sediment habitats such as sand and mud as well as harder substrata like boulders and bedrocks. The Arctic Ocean covers a large area, of which about 50% overlays shelf zones, which in turn constitute 31% of the total shelf area of the world (Jakobsson *et al.* 2004). It is well known that diversity generally increases with the extent of an area (MacArthur & Wilson 1967). If so, we would expect a high total diversity in particular of Arctic shelf fauna relative to deep sea areas.

A conspicuous feature of the sea areas of the Arctic is the strong gradient in salinity, both horizontally from river mouths out into the open sea as well as vertically, from close to fresh near the surface to fully marine at depth. Hence, in addition to seasonal ice melt, salinity gradients are highly influenced by freshwater inputs from mainly the Russian rivers, but also the MacKenzie and Yukon rivers in the western part of the Arctic Ocean. These large rivers together with smaller ones create estuarine systems of different spatial sizes which often harbor a peculiar set of species adapted to cold water of low salinity. The area of most intensive fresh water impact is regarded as a specific zoogeographical unit (Siberian brackish shallow province by Filatova 1957). A consequence of high freshwater inputs is also the permanent stratification of the central Arctic Ocean with a surface salinity of less than 32‰ and a deep water salinity of 34‰ (Gradinger *et al.* 2010a), thus providing different habitats for planktonic invertebrates, because pelagic organisms, like benthic ones, have differerent tolerances for low salinity.

Furthermore, different parts of the Arctic have different levels of productivity (Michel, Chapter 14), which also may affect diversity (Currie 1991). Productive areas often have more species than unproductive areas, but the causal relationships are still unclear (Currie *et al.* 2004) and firm evidence is also lacking for such effects on marine benthic diversity, although hump-shaped relationships have been reported between chlorophyll *a* and Arctic benthos richness (Witman *et al.* 2008). An example of an oligotrophic area is the Beaufort Gyre, as compared with a productive area in the Chukchi Sea shelf (Gradinger 2009) or Barents Sea shelf (Sakshaug 1997, Denisenko & Titov 2003).

The Arctic Ocean may be regarded as an open system where the strength of the connections with adjacent oceans has changed over the last 4 million years. Water currents facilitate dispersal from sub-Arctic and boreal parts of adjacent oceans, through the Fram Strait and the Barents Sea from the Atlantic, and the Bering Strait from the Pacific Ocean (e.g. Węsławski *et al.* 2011). While the connection with the Pacific has opened and closed over time due to varying sea levels, the deep Atlantic entrance has been widely open. At present, there is some 10 times more Atlantic water than Pacific water flowing into the Arctic Ocean (Loeng *et al.* 2005).

In addition to habitat complexity and the importance of recent dispersal from adjacent oceans, the turbulent geological history has also been important in shaping present day diversity of Arctic invertebrates. In the comparatively young Arctic Ocean, the evolutionary origin of marine invertebrates reflects a Pacific origin dating back to the opening of the Bering Strait 3.5 million years ago (Adey *et al.* 2008). Throughout most of the Tertiary, the Arctic Ocean region supported a temperate biota, and fully Arctic conditions developed only during the latest part of this period. Sea ice cover formed c. 3-5 million years ago (Briggs 2003). Over the last 3-5 million years, a series of glaciation periods with intermittent de-glaciations has created an unstable environment with a series of extinction and immigration events shaping present day diversity. These extinction events are thought to have precluded extensive local evolution or endemism on the shelves (Dunton 1992). Furthermore, events during the last 3.5 million years have allowed great re-distributions of species in the boreal part of the northern hemisphere likely still affecting Arctic diversity today. The most pervasive change occurred during the late ice-free Pliocene, after the opening of the Bering Strait, when extensive transgressions of invertebrates species across the Arctic occurred (Vermeij 1989, 1991, Mironov & Dilman 2010), mainly from the species-rich Pacific center of diversity (Briggs 2003) to the Northern Atlantic, an event called 'The Great Trans-Arctic Biotic Interchange' (Briggs 1995). As contended by Briggs (2007), there is little evidence from the marine realm that invasions have decreased native diversity, but rather that they have added to the native diversity, resulting in an overall increased diversity. A result of this major transfer was therefore likely an enrichment of the Northern Atlantic pool of species with Pacific species. This pool of species may be the source of immigration into the Arctic Ocean in recent time.

Against this background we expect that invertebrate diversity in the Arctic Ocean has been shaped to a high degree by dispersal based factors like immigration and a low degree of endemism. We expect the Arctic Ocean to be dominated by wide-range boreal species. In this respect, it is interesting to compare the degrees of endemism in the Arctic with those in the Antarctic, another cold region with similar glaciation history (Krylov *et al.* 2008), but which has been much more isolated from adjacent oceans by the strong Antarctic Circumpolar Current (ACC). The ACC, formed in the Miocene, is the only current on Earth extending from the sea surface to the sea floor, unimpeded by any landmasses (Hassold *et al.* 2009). We certainly would predict a much higher degree of endemism in the Antarctic, which as we will see is in fact the case. Furthermore, given that connectivity is strong between the Arctic Ocean and the boreal parts of the Pacific and the Atlantic oceans, we would not expect a markedly lower richness in the Arctic, but fairly similar levels of species richness as in the other oceans, at least in proximity to the two gateways.

In addition to the natural structuring factors, diversity patterns in the Arctic Ocean likely are influenced by variation in sampling methods as well as sampling frequency. For instance, some areas have been extensively investigated for more than a century (Barents Sea), while other less accessible areas (deep Arctic basins) have been relatively poorly studied. This creates a challenge when estimating total numbers of species in the Arctic.

The main questions addressed in this review are:

- Is the marine invertebrate diversity in the Arctic Ocean impoverished compared with adjacent areas?
- Are there large scale diversity patterns within the AO area that can be attributed to dispersal rather than niche adaptation?
- Is the turbulent geological history and openness to adjacent oceans mirrored by a low degree of endemism?
- Are there 'hotspot' areas that by virtue of their species diversity should be protected?
- Can we predict what the effects of global warming on invertebrate species diversity will be?

## 8.2. STATUS OF KNOWLEDGE

Estimating total species richness in the Arctic is problematic mainly due to different levels of sampling effort among various regions. Furthermore, the sampling methods are selective and often only one or a few methods have been used at the same time and place. For instance, benthic infauna and mobile epifauna demand different gear to be sampled adequately. The seabed is mostly sampled by the traditional 'grab' method, but as grabs sample a limited area of the seabed, large sporadically occurring and patchily distributed epifauna species are poorly represented using this approach. For epifauna gear like trawls, sampling large areas of the seabed are needed. For example, more than 337 megafauna species have been collected by trawl sampling in the Barents Sea (Anisimova *et al.* 2011). Echinoderms, sponges and crustaceans were the dominant groups in this trawl study, in contrast to polychaetes, crustaceans and molluscs dominating grab samples (Zenkevitch 1963, Cochrane *et al.* 2009, Anisimova *et al.* 2011). This shows the importance of using both gear types (Jørgensen *et al.* 2011) to obtain a more complete estimate of the species richness of a given locality. Only very few studies also included the hyperfauna, i.e. the fauna primarily dwelling in the near-bottom water (but see MAREANO 2009). Along the Norwegian coast (Tromsø Flake) of the southern Barents Sea, 834 taxa were recorded using grab, trawl and sledge gear together at the same locality. Of this number, only 128 (15%) of the taxa were sampled with more than one of the gear types (Mortensen *et al.* 2009). Also, the meiofauna from the soft bottom sediments could only be collected correctly with the use of multicorers and box-corers, while grabs underestimated the abundance of small-sized benthic biota. There are obvious differences in sampling efforts among the different Arctic sub-areas: the Barents Sea has a long history of studies lasting over one hundred years, while the western Arctic had been poorly sampled until the last few decades. A west-east declining gradient in sampling effort is also apparent in the Russian Arctic from the Barents to Laptev Seas. Several research campains undertaken in the last decades improved the situation, to a certain extent equalizing the distribution of sampling effort across the Arctic shelf (Sirenko 2004). This has led to a significant increase in our knowledge of the spatial patterns of biodiversity in Arctic seas (Gradinger *et al.* 2010a).

There have been several attempts to estimate total invertebrate diversity both for the whole Arctic marine environment and for certain areas. Despite methodological shortcomings, such efforts are important and can provide conservative estimates. With this possible bias

**Table 8.1.** Overview of free-living invertebrate taxa in the Arctic Ocean area as defined in Fig. 6.4 in Christiansen & Reist, Chapter 6, but excluding the Bering and Norwegian Seas. Estimates based on Sirenko (2001) and updates of ArcOD researchers (from Gradinger *et al.* 2010a).

* Includes Bryozoa, ** Includes Nematoda, *** Synonymous with Tunicata.

| Taxon | Species numbers | Sea ice realm | Pelagic realm | Benthic realm |
|---|---|---|---|---|
| Porifera | 163 | | | 163 |
| Cnidaria | 227 | 3 | 83 | 161 |
| Ctenophora | 7 | | 7 | |
| Tentaculata* | 341 | | | 341 |
| Sipuncula | 12 | | | 12 |
| Platyhelminthes | 137 | >1 | | 134 |
| Gnathostomulida | 1 | | | 1 |
| Nemertea | 80 | | 2 | 78 |
| Aschelminthes** | 422 | >11 | 16 | 403 |
| Mollusca | 487 | | 5 | 482 |
| Annelida | 571 | 4 | 6 | 565 |
| Tardigrada | 7 | | | 7 |
| Arthropoda | 1,547 | >20 | 214 | 1,317 |
| Chaetognatha | 5 | | 5 | |
| Hemichordata | 1 | | | 1 |
| Echinodermata | 151 | | | 151 |
| Urochordata*** | 60 | | 3 | 57 |
| Total | 4,219 | >39 | 341 | 3,873 |

due to different use and selectivity of sampling gears, under-sampling of large areas and different taxonomic specificity in mind, marine invertebrates in the Arctic, excluding the Bering Sea, comprise about 5,000 free living species (Sirenko 2001, Gradinger *et al.* 2010a, Sirenko *et al.* 2010, Bluhm *et al.* 2011a). This comprises c. 8% in pelagic taxa and some connected to the sea ice (c. 1%), while the major proportion, (c. 90%), are benthic organisms living on or in the sea floor. Over 1,000 of these species live in the central Arctic Ocean of which c. 60% also occur on the continental shelves (Bluhm *et al.* 2011a, 2011b). About 75% of the known bottom-dwelling species are macrofauna – organisms larger than 1 mm. However, this high proportion is likely influenced by the higher taxonomic and sampling effort in this group. Comparatively, the microscopic metazoans are still under-studied. This may be a bias in particular when comparing biodiversity of shallow and deep areas, because individual sizes often decrease below shelf depths (Thiel 1975, Udalov *et al.* 2005).

The estimate by Gradinger *et al.* (2010a) arrived at c. 4,200 invertebrate species representing 17 phyla in the three Arctic marine realms (Tab. 8.1). The most species rich group in all three realms is the Arthropoda, mainly crustaceans, accounting for more than a third of all species (37%), followed by Annelida (14%), Mollusca (12%), Nematoda (10%) and Bryozoa, Phoronida and Ectoprocta (together 8%).

## 8.2.1. Regional inventories

The first complete survey of marine biodiversity in the Russian Arctic was published by Zenkevich (1963). The figures provided therein reflected both real trends in diversity along the eastern Arctic shelf and artifacts of the sampling effort. Zenkevich's review covered a half-century of studies concentrated in the western part of the Eurasian Arctic. The Barents Sea displayed the highest species diversity – with 1,851 species of free-living invertebrates, due both to the longer history of research (beginning in the late 19th century) and the significant contribution of boreal species in the fauna. The number of species was found to decrease eastward to 522 species in the Kara Sea and to increase in the Chukchi Sea (820 species) again because of the influence of the Pacific fauna (Tab. 10.1 in Gradinger *et al.* 2010a). Zenkevitch (1963) did not provide any information for the East Siberian Sea due to lack of data.

This pattern on the Eurasian shelf was still apparent in recent reviews of the macro- and megazoobenthic fauna as a whole (Fig. 8.1; Piepenburg *et al.* 2011), as well as for particular taxonomic groups (e.g Bryozoa; Fig. 8.2, see also Tab. 8.3). An increased sampling effort in the Siberian Arctic in the second half of the 20th century modified the W-E Eurasian shelf pattern to some extent. The number of known species increased drastically in the Laptev Sea from 1932 to 2004, likely a consequence of increased sampling effort (Fig. 8.3; Sirenko 2004). The results of the surveys up to the last decade of the 20th century were summarized by Sirenko (2001). The total number for taxa increased over the last two decades for selected seas by as much as twice or more (Tab. 10.1 in Gradinger *et al.* 2010a). For instance, the total diversity for the Arctic including the central Arctic Basin, but excluding the Canadian Arctic, was 4,784 species (Sirenko 2001). However, vast areas are still under-sampled, and recent estimates of hitherto missed benthic species amount to several thousands (Bluhm *et al.* 2011a, Piepenburg *et al.* 2011).

Nevertheless, these recent compilations show outstandingly high richness in the Barents Sea compared with the other Arctic regions (Fig. 8.1 and 8.2; see also Tab. 8.3). Species richness in the Chukchi Sea is comparable to that in the Laptev, East Siberian and Kara Seas.

The large-scale Arctic Ocean Diversity project (ArcOD), completed during the last decade in the framework of the Census of Marine Life, provided new species records, which have been incorporated in the world-wide on-line catalogs (OBIS 2012) and have generated new analyses of Arctic biodiversity patterns (Gradinger *et al.* 2010a, Sirenko *et al.* 2010, Bluhm *et al.* 2011a, Piepenburg *et al.* 2011). Regional species lists were erected for the Russian Arctic (Sirenko 2001), Svalbard archipelago (Prestrud *et al.* 2004), and on a smaller scale for the fjord Hornsund in Svalbard (European Marine Biodiversity All taxa Inventory site 2009), and for the White Sea at the vicinity of the White Sea Biological Station of Moscow State University (Tchesunov *et al.* 2008).

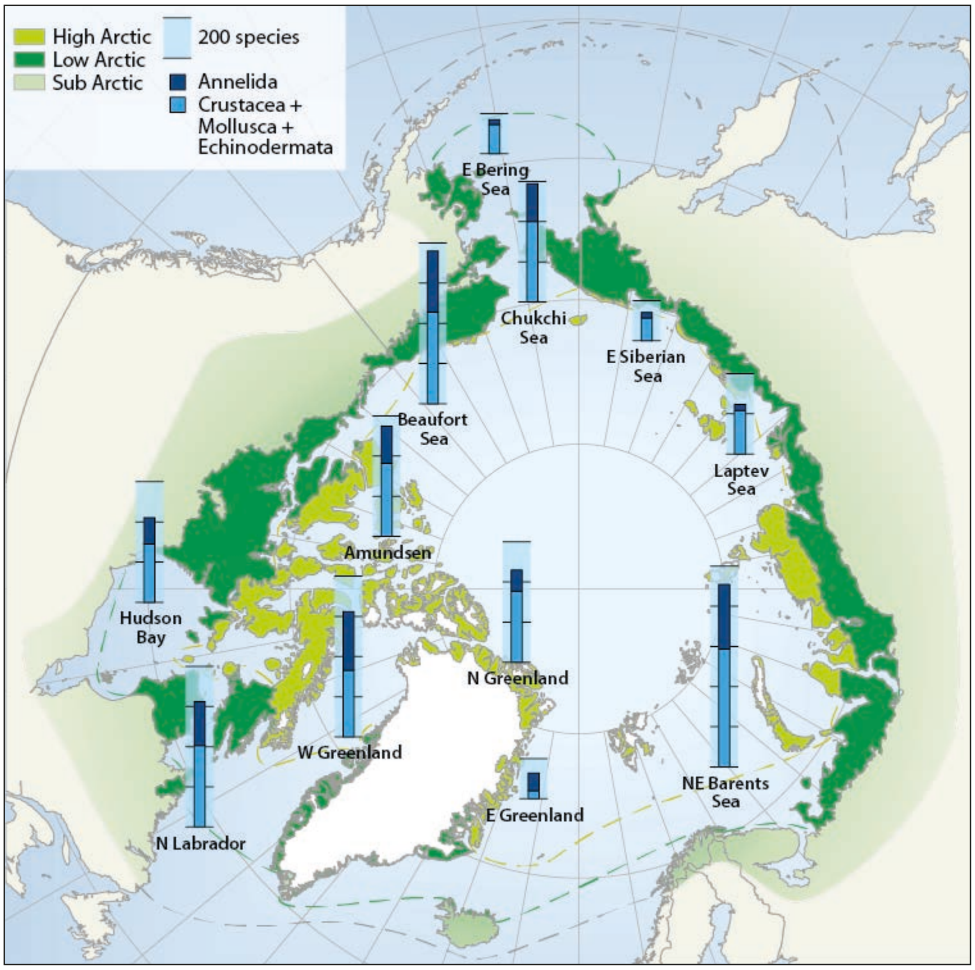

**Figure 8.1.** Map of the Arctic Ocean with superimposed stacked bars representing species numbers of macrozoobenthos from different shelf sea areas: Crustacea+Mollusca+Echinodermata (blue) and Annelida (black). Compiled by Piepenburg *et al.* (2011).

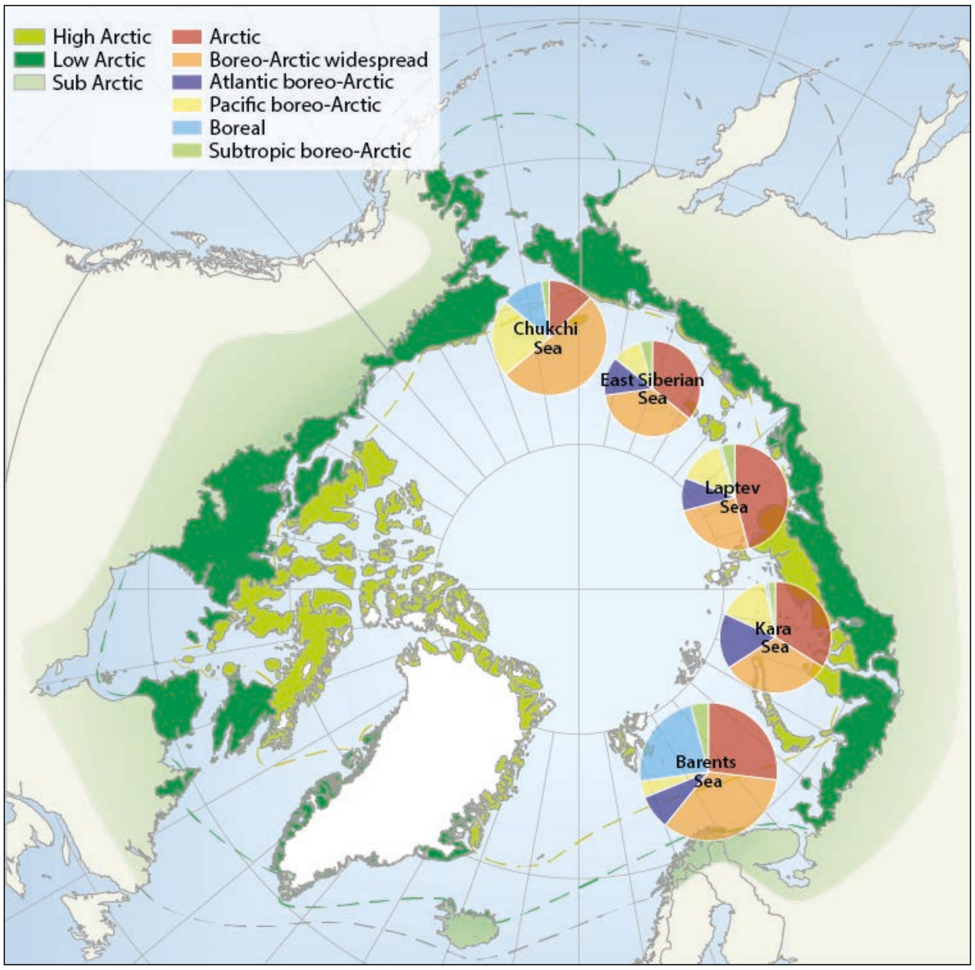

**Figure 8.2.** Map of the Arctic Ocean showing the distribution of species richness of Bryozoa for different shelf seas along the Eurasian continental shelf. Diameters of circles are proportional to the number of bryozoan species given in Tab. 8.3. Species numbers partitioned into six zoogeographical affinities are shown from the: Barents Sea (Denisenko 1990), Kara Sea (Gontar & Denisenko 1989); Laptev Sea (Gontar 2004), East Siberian Sea (Denisenko 2010), Chukchi Sea (Denisenko 2008).

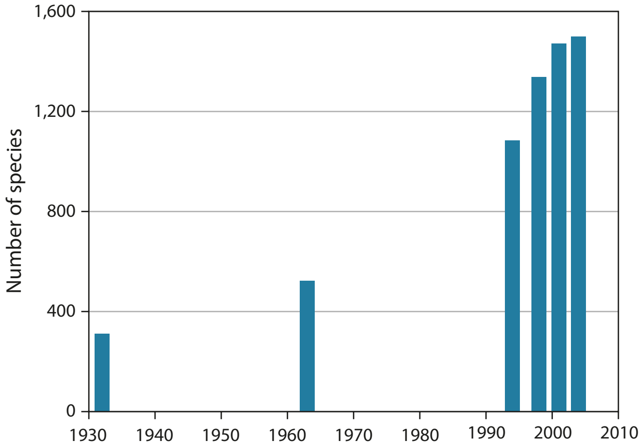

**Figure 8.3.** The number of macrofauna species in the Laptev Sea over time, likely illustrating effects of increased sampling effort.

In terms of species records, the most significant additions occurred for the Laptev Sea, the Central Arctic Basin and the Canadian Arctic. In the last of these, the Lincoln Sea is the least studied large marine area in the Arctic. The processing and analysis of this new information is still in progress, but a preliminary estimate gives a total of c. 4,600 species of benthic invertebrates (Bluhm *et al.* 2011a). The new records also enabled cell-by-cell area calculation of species diversity with a grid of 5° × 5° (Bluhm *et al.* 2011a). This indicates that the southwestern part of the Barents Sea remains among the most species rich areas. However, a second area of high diversity both in terms of observed and expected numbers of taxa was apparent within the outer shelf and slope of the Laptev Sea.

In an attempt to estimate total species richness of the macro- and megazoobenthic fauna on the Arctic Shelf, Piepenburg *et al.* (2011) compiled richness data for the groups Mollusca, Arthropoda, Echinodermata and Annelida. The total expected numbers of these four major taxa range between 2,596 and 3,116 (2,856±260) species. Assuming that these four taxa comprise 2/3 of total diversity (using calculations based on Sirenko (2001)), the authors concluded that about 3,894-4,674 (4,284 ± 390) macro- and megabenthic species can be expected to inhabit the Arctic shelf regions (Piepenburg *et al.* 2011). This was in reasonable agreement with previous findings of Sirenko (2001) who reported c. 3,000 taxa for the above-mentioned four groups.

An estimate of the total number of benthic invertebrate taxa in the Arctic deep sea by Bluhm *et al.* (2011b) was 1,125. However, as pointed out by the authors, this was a very conservative estimate, because the deep sea is still severely under-sampled. Hence it also is no surprise that over half of all benthic species listed for the deep Arctic have so far only been recorded in that area once or twice.

Another approach in estimating total species diversity is based on the All-Taxa-Biodiversity-Inventory first performed in terrestrial ecosystems (Sharkey 2001, Nichols & Langdon 2007). The first complete survey of this kind in the Arctic was done at the White Sea Biological Station situated on the Arctic Circle on the western White Sea shore (Tchesunov *et al.* 2008). The 50-year-long survey, summarized by 71 specialists, reported 6,008 extant species from an area of 40 km$^2$ that included both marine and terrestrial environments (Tchesunov 2008). Among the metazoans, 43% of the species were marine, 9% from freshwater and 48% inhabiting terrestrial biotopes. Among the marine metazoans, Arthropoda (Crustacea and Pantopoda) were the most diverse group comprising 335 species, followed by Annelida (Polychaeta, Oligochaeta and Hirudinea) with 136 species, Nematoda (mainly free-living) with 131 species, Mollusca with 113 species, Ectoprocta with 66 species and Cnidaria with 53 species. This small marine area of c. 30 km$^2$, with water depths ranging from 0 to 100 m, contained 61% of the total number of species known in the White Sea so far (Sirenko 2001, Tchesunov 2008). The macrobenthic fauna of the White Sea is close to being completely described, as species accumulation curves are close to the plateau for the whole sea and for its parts (Berger *et al.* 2001). The list of marine invertebrates is also close to being complete (Sirenko 2001).

A second ongoing program towards a complete inventory of local marine fauna is in Hornsund, Svalbard, an area of c. 50 km$^2$ from the intertidal to 280 m depth (European Marine Biodiversity All taxa Inventory site 2009). As of January 2012 more than 1,400 marine taxa have been recorded in this area, which has been regularly sampled over recent decades. The data allow extrapolations based on species accumulation curves which forecast over 2,000 metazoan species to occur in that region.

Altogether, despite differences among the different studies of sampling effort and methods, there is fair agreement among the authors with regard to the species number estimates. The existing conservative estimations for the Arctic Ocean area are approaching 5,000 metazoan species, and further increase is expected mainly in less investigated taxonomic groups (primarly meiobenthic) and areas (deep sea basins, E Eurasian and Canadian Arctic).

## 8.2.2. Diversity of species rich and better-investigated taxonomic groups

### 8.2.2.1. Crustaceans (Crustacea)

Crustaceans is probably the most species rich invertebrate group in the Arctic Ocean area, dominating the pelagic, benthic and sympagic realms. Species richness of this group in the Arctic seems to be even higher than in adjacent oceans areas of similar size (Archambault *et al.* 2010). Altogether, a recent inventory (Tab. 8.1; Gradinger *et al.* 2010a) estimated over 1,470 crustacean species in the Arctic, representing 95% of all Arctic marine arthropods. Among Crustacea the Amphipoda represents the most species rich sub-group (Tab. 8.2). However, small-sized, infaunal organisms like Harpactiocoida, Ostracoda or some families of minute Amphipoda, are little understood and every year brings discoveries of new species. Also, the number of known harpacticoid species nearly doubled from 110 in 2000 (P. Rybnikov in Sirenko 2001) to 213 in 2010 (Chertoprud *et al*. 2010). Even in the better known large epibenthic and hyperbenthic crustaceans groups like decapods, more species may be expected to be discovered in the future. The regional diversity of harpacticoids varied greatly: 179 species had been reported from the central Arctic Basin, 185 and 153 from the White and Barents Seas, respectively, and from 40-50 species for the Siberian and Canadian Seas (Chertoprud *et al*. 2010).

**Table 8.2.** Summary of the Arctic crustacean fauna inventory (based on Sirenko 2001 list) updated with new descriptions and distribution records from the Census of Marine Life (Bluhm *et al.* 2011a). Crustacea represent the largest component of the Arthropoda, which is the most speciose phylum in the Arctic.

| Class | Order | Number of species in the Arctic marine area |
|---|---|---|
| Branchiopoda | Cladocera | 4 |
| Malacostraca | Stomatopoda | 0 |
| | Nebaliacea | 1 |
| | Amphipoda | 577 |
| | Decapoda | 72 |
| | Amphionidacea | 0 |
| | Euphausiacea | 7 |
| | Cumacea | 59 |
| | Isopoda | 102 |
| | Lophogastrida | 0 |
| | Mysida | 33 |
| | Tanaidacea | 11 |
| | Mictacea | 0 |
| | Bochusacea | 0 |
| | Spelaeogriphacea | 0 |
| | Anaspidacea | 0 |
| | Bathynellacea | 0 |
| Maxillopoda | Calanoida | 114 |
| | Cyclopoida | 4 |
| | Siphonostomastoida | 1 |
| | Mormonilloida | 1 |
| | Poecilostomatoida | 14 |
| | Monstrilloida | 2 |
| | Platycopioida | 1 |
| | Harpacticoida | 207 |
| Cirripedia | Thoracica | 13 |
| Ostracoda | Halocyprida | 28 |
| | Myodocopida | 8 |
| | Palaeocopida | 0 |
| | Platycopida | 1 |
| | Podocopida | 210 |
| Remipedia | Nectiopoda | 0 |
| Pentastomida | Cephalobaenida | 0 |
| | Porocephalida | 0 |
| Total | | 1,470 |

Crustaceans play a key role in the pelagic and sea ice domains (Michel, Chapter 14), where copepods and amphipods, respectively, are the dominant metazoan taxa in terms of biomass and energy flow through the Arctic system's realms (Iken *et al*. 2005, Węsławski *et al*. 2007). Soft sediments, especially in the deep sea, contain considerable numbers of crustacean species, yet polychaete worms and bivalve molluscs are more important here than crustaceans in terms of biomass and carbon remineralization. The cold water of the Arctic generally results in slow growth and high longevity among invertebrates and seasonally abundant, but otherwise sparse, food sources. This combination has permitted several herbivores to attain record sizes within their group, namely Copepoda, Amphipoda and Mysida. High lipid content, in particular for the large pelagic copepods *Calanus hyperboreus* and *C. glacialis*, makes large crustacean herbivores a rich source of energy and high quality prey for top predators, such as whales and seabirds. A limited number of crustaceans are commercially and/or subsistence-harvested in the Arctic. Examples include fisheries of the northern shrimp *Pandalus borealis*, which brings substantial income to Greenland and Norway, and the red king crab *Paralithodes camtschaticus* fishery in the Barents Sea. In the 1960s, the red king crab was first introduced to the Russian part of the Barents Sea, and then spread naturally to the Norwegian sectors. Another crab of economic importance, the snow crab *Chionoecetes opilio,* was observed in 1969 in the Russian Barents Sea, and in 2001 in the Norwegian part of the Barents Sea. Similar to the red king crab, this species seems to be permanently established in the Barents Sea and may be a potential species for harvest in the future (Pavlov & Sundet 2011).

### 8.2.2.2. Molluscs (Mollusca)

Sirenko's (2001) compilation of invertebrates from the Eurasian Arctic seas lists 485 species of Mollusca, including 304 species of Gastropoda, 140 Bivalvia, 23 Aplacophora, two Scaphopoda, eight Polyplacophora and eight Cephalopoda. No representatives of Monoplacophora have been recorded from the Arctic seas. The majority of the mollusc species live on the sea bottom. A recent review of the macro- and megabenthic fauna of Arctic shelf seas, undertaken within the ArcOD framework by Piepenburg *et al.* (2011), yielded a total of 392 species of Mollusca, with 205 species of Gastropoda and 156 Bivalvia. These numbers represent a very small fraction of the global species richness of marine molluscs, estimated to be about 52,000 (Bouchet 2006). The clear decline of mollusc diversity in the Arctic seas compared with lower latitudes has been reported in studies of different molluscan groups at different spatial scales. Roy *et al*. (1998) reported a clear latitudinal decline from the tropics to the Arctic in species numbers of prosobranch gastropods occurring along the

Pacific and Atlantic coasts of North America. A similar pattern was described for bivalves of the North Pacific continental shelf (Jablonski *et al.* 2000). The substantial differences between Arctic and tropical mollusc diversity has also been detected on a local scale. A comprehensive assessment of shelled benthic molluscs in Kongsfjorden, W Svalbard (Włodarska-Kowalczuk 2007) reported 87 species, while a species inventory of a tropical coastal site of similar area in New Caledonia recorded as many as 2,738 species (Bouchet *et al.* 2002). Clarke (1992) noticed that widely accepted paradigms of latitudinal clines in the seas are based mostly on patterns described for taxonomic groups producing calcareous skeletons, i.e. Mollusca and Foraminifera. He hypothesized that the sharp decrease of richness of these taxa in polar waters may be at least partly explained by the high costs of calcification at low temperatures. The diversity of the Mollusca is especially low in Arctic Ocean deep basins. Bluhm *et al.* (2011b) reviewed the macrobenthic data from Arctic bottoms deeper than 500 m, resulting in a total of only 70 species of molluscs. Bouchet & Waren (1979) explained the low diversity and high endemism of molluscan fauna in northern deep-sea basins by several factors, including the young age of present-day environmental conditions, isolation from the Atlantic and Pacific pools of species, habitat homogeneity and absence of geographic isolating barriers in the Arctic abyssal area.

### 8.2.2.3. Annelids (Annelida)

Annelida is the second most species rich phylum in the Arctic, after the Arthropoda (Tab. 8.1). Most annelids in the marine realm are Polychaeta, or bristle-worms, with the remainder among the Clitellata, representing leeches and oligochaetes, with few or no bristles. The family Siboglinidae, previously treated as the phyla Pogonophora and Vestimentifera, also known as beard worms, is now recognized within the Polychaeta (Rouse 2001). Therefore, updated compilations using older species lists should take care to include these taxa within the Annelida.

Sirenko (2001) recorded 517 species of Annelida (Polychaeta, Oligochaeta and Pogonophora) for Eurasian seas and the Central Arctic Basin, updated to 571 by Gradinger *et al.* (2010a) for the whole Arctic north from Fram Strait and including the Barents Sea. Zhirkov (2001) reported 670 polychaete species in the Arctic delimited by the Faroe-Iceland Ridge from the Atlantic, accounting for c. 4.5% of the world's bristle-worm fauna. Of the species listed by Gradinger *et al.* (2010a), four species are ice-associated and six have a pelagic lifestyle, with *Tomopteris* being perhaps the most familiar of the pelagic genera. The remaining annelids are benthic, with an important role in seafloor functioning, especially in soft sediments, where their burrowing activities enhance important processes such as irrigation, oxygenation and remineralisation. On hard substrates, encrusting and suspension-feeders predominate. Areas of mixed substrates often support a high species richness, both in terms of numbers of species and functional traits (Cochrane *et al.* 2012 and references therein).

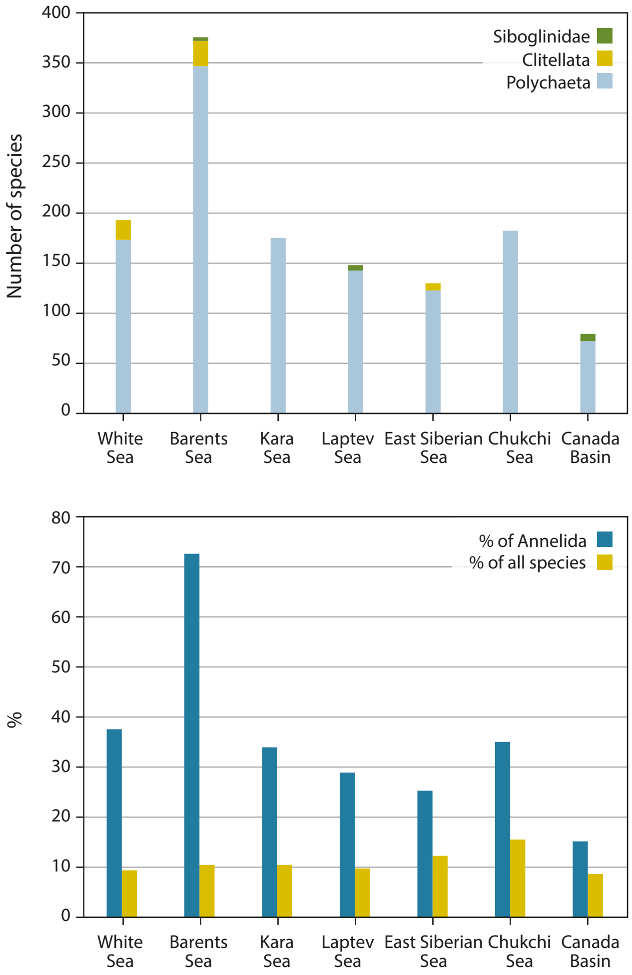

**Figure 8.4.** Upper panel: Numbers of annelid species recorded from each of seven regional Arctic seas (Sirenko 2001). Note: current values are expected to be somewhat higher, but updated records in this format are not available at this time. Lower panel: Proportions of annelid species numbers from each of seven regional Arctic seas and of the total number of all species recorded from the Arctic seas. Data source as for panel above.

Various reviews of circumpolar annelid species richness show high richness in the Barents, Beaufort and Chukchi seas, with far fewer species recorded from the East Siberian and Laptev shelf seas (Fig. 8.1, 8.4; Sirenko 2001, Piepenburg *et al.* 2011).

A decline in polychaete species richness was found along a transect with a minimum in the central Arctic basin (Renaud *et al.* 2006), but no such trend was evident between the Norwegian and Barents Seas (Renaud *et al.* 2009). Polychaete diversity (but not necessarily species richness) in the Barents Sea was highest in the northernmost, heavily ice-influenced areas, but equivalent trends were not seen in a comparative study off Greenland (Ambrose *et al.* 2009). Generally, annelids comprise about 10% of all species recorded across the study area, with the least in the central basin (9%) and most in the Chukchi Sea (16%). In the majority of areas, fewer than 40% of the total number of annelid species recorded from Arctic seas were present, whereas more than 70%

of all species were represented in the Barents Sea (Ambrose *et al.* 2009). Habitat complexity is likely to influence the number of species present in a given area, but in the case of the Barents Sea, a range of biogeographical affinities (Zenkevich 1963) most certainly also contributes to its high species richness. Examples of particularly species-rich taxa in the Barents Sea are the scaleworms of the genus *Harmothoe* and the spionid genus *Spio,* which have six and seven species occurring in the Barents Sea, respectively, but maximally two and three species, respectively in the other Arctic seas.

In a comparison of the diversity of soft-bottom polychaete assemblages in an Antarctic and two Arctic fjord localities of similar environmental settings, the total number of species and ES(50) were not significantly different, nor were the shapes of the species accumulation curves (Włodarska-Kowalczuk *et al.* 2007a). At both poles, the same families (Terebellidae, Ampharetidae, Maldanidae, Spionidae and Polynoidae) also dominated species numbers.

As in other areas, Arctic polychaetes include a diverse array of feeding types with many in the guild of deposit feeders (e.g. Iken *et al.* 2010). An interesting example of habitat adaptation is the spionid *Scolelepis squamata*, whose juveniles inhabit the seasonal fast ice to feed on the early ice algal bloom rather than spending that life stage in the water column, as elsewhere (Bluhm *et al.* 2010).

#### 8.2.2.4. Moss animals (Bryozoa)

Bryozoans are colonial suspension-feeding species attached to firm substrates such as stones, macroalgae, shells etc. They are one of the most diverse systematic groups of benthic invertebrates in the Arctic seas. Early estimates arrived at c. 340 species in the Arctic region (Gontar & Denisenko 1989). However, reviews of older literature, not previously accessible, e.g. by Osburn (1955), recent field investigations and taxonomic harmonization (Denisenko 1990, 2008, 2010, 2011, Gontar 2004, Denisenko & Kuklinski 2008), as well as descriptions of species new to science (Gontar 1996, Kuklinski & Taylor 2006, Denisenko 2009), have increased the total bryozoan species number to 370 partitioned among two classes, three orders, 42 families and 94 genera. We believe, however, that the actual species number will be higher still, as some regions in the Arctic seas are understudied due to intensive ice-cover, such as the East Siberian Sea and the Canadian Arctic Archipelago. It is also likely that identification using scanning electron microscopy will reveal new taxa of bryozoans. We selected the Bryozoa to demonstrate how species richness for an individual taxon may differ among regions of the Arctic (Tab. 8.3) and how similarities in the faunal communities can illustrate regional patterns.

As is the case for several other groups, the highest species richness is recorded in the Barents and Chukchi Seas, likely resulting from the influence of relatively warm water currents entering the Arctic Ocean from the Atlantic and Pacific Oceans (Gontar & Denisenko 1989, Denisenko 1990, 2008). The share of Arctic species is relatively high in the Laptev and East Siberian Seas (Fig. 8.2), and in the western part of the Chukchi Sea.

Gontar & Denisenko (1989), using presence-absence data, showed that the bryozoan fauna of the southwestern part of the Barents Sea differed strongly from the Siberian and adjacent seas (Kara, Laptev, East Siberian and Chukchi Seas). In another study using data with relative dominance, Denisenko (1990) demonstrated segregation of bryozoan fauna of the Laptev and East Siberian Seas from that of the Barents and Kara Seas. The bryozoan fauna of the southwestern part of the Barents Sea is closely related to that of the northern coast of Norway, and the bryozoan fauna of the Chukchi Sea had a stronger relationship (similarity) with Bering Sea fauna than with bryozoans of the East Siberian Sea (Denisenko 1990). The latter had a fauna similar to the Laptev Sea, and the Canadian Arctic Archipelago bryozoan fauna was dissimilar to the other faunas (Denisenko 2010). Visual inspections of species lists appear to show that the composition of Canadian bryozoans is similar to the bryozoan fauna of the eastern and northwestern parts of the Barents Sea and the Kara Sea. The degree of bryozoan endemism in the Arctic seems higher than in most other groups, and endemism of bryozoans is globally high, which has been attributed to restricted dispersal in this group, having demersal larvae and sessile adults (e.g. Barnes & Griffiths 2008). Compared with another cold environment, the Antarctic, endemism in the Arctic is considerably lower, maybe half of the percentage in the Antarctic (c. 60%; Barnes & Griffiths 2008). This may result from the fact that during the cold period the Antarctic has been much more isolated than the Arctic with the strong Antarctic Circumpolar Current as a dispersal barrier. The cold periods in the two polar regions seem to be of approximately the same duration (Krylov *et al.* 2008).

| Sea or area | Number of species | Source |
|---|---|---|
| Chukchi Sea | 197 | Denisenko 2008, Denisenko & Kuklinski 2008 |
| East Siberian Sea | 137 | Denisenko 2010, 2011 |
| Laptev Sea | 170 | Gontar 2004 |
| Kara Sea | 186 | Gontar & Denisenko 1989 |
| Barents Sea | 284 | Denisenko 1990, 2009, Gontar 1996, Kuklinski & Taylor 2006 |
| Canadian Arctic Archipelago | 98 | Powell 1968 |

**Table 8.3.** Species richness estimates of the bryozoan fauna in the Eurasian seas of the Arctic and in the Canadian Arctic Archipelago (Denisenko 2011).

#### 8.2.2.5. Echinoderms (Echinodermata)

Echinodermata is probably the best known phylum in the Arctic, likely because of relatively large body size and use of primarily epifaunal habitat. The current echinoderm species inventory holds a total of c. 160 species in all five living classes (Sirenko 2001, Sirenko *et al.* 2010), but depends on how the Arctic area[1] is defined. The number of sea stars is highest (c. 80), followed by brittle stars (c. 34), sea cucumbers (c. 32), and a few sea urchins (c. 13) and feather stars (4). Considering a larger undefined Arctic area, Smirnov (1994) listed 183 echinoderm species. In contrast to many other Arctic taxa, the echinoderm fauna is relatively well known, although a new species of sea cucumber, *Elpidia belyaevi*, was recently described (Rogacheva 2007).

Echinoderms typically dominate Artic epifaunal communities in abundance and often also in biomass. These are slow growing animals with usually long life cycles (Bluhm *et al.* 1998, Blicher *et al.* 2007). They represent a variety of feeding habits – many sea stars are predators, scavengers or omnivores; the basket stars *Gorgonocephalus* spp. and the Arctic feather stars are filter-feeders; *Ophiura sarsi* and other brittle stars, the mud star *Ctenodiscus crispatus*, the deep-sea urchin *Pourtalesia jeffreysii* and several sea cucumbers, such as *Kolga hyaline*, are deposit feeders (Iken *et al.* 2005). Echinoids and ophiuroids contribute greatly to benthic remineralization in coastal areas and on Arctic shelves (Ambrose *et al.* 2001, Blicher *et al.* 2009, Blicher & Sejr 2011),

Echinoids can be very abundant in coastal areas (Blicher *et al.* 2007, 2009, Gundersen *et al.* 2010), and ophiuroids can form dense beds attaining densities of > 100/m$^2$ and biomass of > 1 g C/m$^2$ on shelves and in the deep-sea (Piepenburg 2000, MacDonald *et al.* 2010, Blicher & Sejr 2011). Often one particular species contributes the majority of this dominance in a region, for example the brittle star *Ophiura sarsi* on the Chukchi and Beaufort Sea shelves (Bluhm *et al.* 2009, Rand & Logerwell 2010), *Ophiocten sericeum* on Eurasian shelves and *Ophiopleura borealis* on continental slopes (Piepenburg 2000).

### 8.2.3. The realms – diversity patterns and conspicuous taxa

#### 8.2.3.1. Sympagic realm

The sympagic realm, or the system connected to permanent sea ice, provides habitats for both macrofaunal invertebrates and meiofaunal organisms that live in brine-filled networks and pores in the ice or at the ice-water interface. Meiofauna are dominated by acoels, nematodes, harpacticoid copepods and rotifers. In coastal ice, polychaete and other larvae may be a temporary part of the fauna (Gradinger 2002). The ice-water interface under the ice provides microhabitats for endemic macrofauna, mainly gammaridean amphipods (Bluhm *et al.* 2010). Biodiversity in sea ice is low relative to water column fauna and benthic interstitial fauna, with only a few species per higher taxonomic group (Gradinger 2002). This is in part related to the extreme conditions in sea ice, with temperatures dropping below –10 °C and salinities higher than 100‰ during winter and early spring. Also, in terms of body size, organisms are constrained by the diameters of the brine channels (Krembs *et al.* 2000).

Across the entire Arctic, the most common amphipod species occurring under the ice are *Apherusa glacialis*, *Onisimus glacialis*, *O. nanseni* and *Gammarus wilkitzkii* (e.g. Gradinger *et al.* 2010b). These ice-associated crustaceans are key prey species for the macroscopic food web of the ice pack, in particular the polar cod *Boreogadus saida*, which in turn provides primary prey for ice seals. Gradinger *et al.* (2010b) suggested that sea ice pressure ridges may function as refuges for ice fauna during the summer melt period.

Ice faunal abundances vary widely in time and space and with ice thickness, with peak densities typically found in the bottom 10 cm of the cores, where environmental conditions are most favorable. Generally, densities are much higher in coastal fast ice (during peak season up to c. 250,000 individuals/m$^2$) than offshore pack ice (typically < 10,000 individuals/m$^2$) and during the spring compared with other seasons (Bluhm *et al.* 2010). A suite of grazing species takes advantage of the early ice algal bloom at times when the pelagic blooms have not yet developed.

#### 8.2.3.2. The pelagic realm

A conspicuous element of Arctic zooplankton includes large herbivorous copepods, such as *Calanus glacialis* and *C. hyperboreus*, which may occur in high abundance and biomass. While these large species have received most of the attention, there are over 100 other mostly smaller species of copepods (Kosobokova 1980). Among non-copepod groups, larvaceans may be abundant in polynyas and in the central Arctic (Kosobokova *et al.* 2011). According to Sirenko (2001) and Sirenko *et al.* (2010), the multicellular holoplankton in the Arctic consists of about 300 species, of which half are copepods, with the remainder including 50 species of cnidarians.

A zooplankton survey of the upper 100 m of the water column in the Arctic Canadian Basin (Hopcroft *et al.* 2005) showed that abundance was dominated by the small copepods *Oithona similis*, *Oncaea borealis* and *Microcalanus pygmaeus* and the larvacean *Fritillaria borealis typica*. Biomass was dominated by the large copepods *Calanus hyperboreus*, *Calanus glacialis* and *Paraeuchaeta glacialis* and the chaetognath *Eukrohnia hamata*. Later, Kosobokova & Hopcroft (2010) surveyed the mesozooplankton in the same area down to 3,000 m depth and found a diverse fauna of 111 species of which c. 50% were copepods. While most of the diversity occurred deeper

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[1] Southern boundary roughly used here: Bering Strait, Fram Strait, western border of Barents Sea, Baffin Bay.

than 100 m, c. 50% of the biomass was concentrated in the upper 0-100 m layer. Depth preferences were found to be species specific, with different species dominating in different depth layers. Zooplankton diversity in the Canadian, Nansen, Amundsen and Makarov Basins was recently reviewed by Kosobokova *et al.* (2011). They reported a total of 174 species representing the Cnidaria, Ctenophora, Mollusca, Annelida, Nemertea, Crustacea, Chaetognatha and Larvacea; 70% of the species were crustaceans, with copepods as the most diverse group. They also found a great number of unrecorded and undescribed species in the bathypelagic layers, several of them endemic to the Arctic Ocean, but distributed across the different basins, suggesting low efficiency of topographic dispersal barriers between the basins.

Ctenophores and jellyfish are understudied groups in the Arctic and yet likely important invertebrate predators in the pelagic realm. Purcell *et al.* (2010) studied the distribution of these groups in the western Arctic Ocean and found an abundant ctenophore fauna shallower than 35 m water depth. Here the characteristic species are *Dryodora glandula*, *Beroe cucumis* and *Bolinopsis infundibulum*, occurring over a stratum with the large scyphomedusae *Chrysaora melanaster*, introduced into the Arctic with warm Pacific water. Some molluscs are important in the pelagic realm. The pteropod gastropods, especially *Limacina helicina*, are a trophic link between plankton and higher trophic levels, as is the squid *Gonatus fabricii*, feeding on a variety of fish and marine invertebrates and preyed upon by sperm whales *Physeter macrocephalus*, seals, porpoises and birds (Gardiner & Dick 2010).

### 8.2.3.3. The benthic realm

More than 90% of the invertebrate species described from the Arctic are benthic, and most of these are macrofauna (Sirenko 2001, Gradinger *et al.* 2010a). The highest number of species has been recorded from the Barents Sea, partly because it has been intensively studied in the past, and partly because of enrichment by boreo-Atlantic species (Cochrane *et al.* 2009, Węsławski *et al.* 2011). Sediments are mostly muddy on the outer shelves and in the central basins, as well as in some fjord basins. This provides extensive habitats for soft sediment fauna, including infauna and some epifauna. Coarser substrates like sand and gravel dominate the inner shelves (c.f. Bluhm *et al.* 2011a and references therein). Larger and/or more extensive hard substrate occurs in some localities with strong currents, such as the Bering Strait and Barrow Canyon, where suspension-feeders occur in high numbers. Nearshore locations are often affected by ice scouring, often resulting in a relatively impoverished fauna (Conlan *et al.* 2008). Examples of benthic habitats in eastern Baffin Bay are shown in Fig. 8.5. Solid substrates like rocks, boulder fields etc. have less spatial extension than accumulation bottoms.

While the diversity of macro- and megafauna is dominated by the phyla Annelida, Arthropoda, Mollusca, Echinodermata, Bryozoa, Cnidaria and Porifera, the smaller sized meiofauna (< 0.5 mm) is dominated by Nematoda and harpacticoid Copepoda. Less common are Kinohyncha, Tardigrada, Rotifera, Gastrotricha and Tantulocarida (Mokievsky 2009a, Gradinger *et al.* 2010a).

Because of the comparatively high number of benthic invertebrate species and habitats, the benthic realm has been subdivided into the following sub-realms or major habitats: glacial fjords, intertidal zones, shelves to shelf break at c. 500 m depth, and the deep-sea.

#### Glacial fjords

Glacial fjords are deep marine inlets carved out by glacial scouring, usually longer than wide, with a restricted water circulation in deeper parts due to sills at the fjord mouth (Syvitski *et al.* 1989). The fjord basins are filled with sediments, often loose muds, while hard bottom – gravel and rocks – can be found on steep sides of the fjords and at outer banks. Tidal glaciers are often located at the heads of the fjords, such that inner basins can be heavily influenced by glacial or glaciofluvial sedimentation. The soft-bottom fauna responds to the gradients of glacial sedimentation by clear changes in species composition, diversity and functional complexity (Włodarska-Kowalczuk *et al.* 2005). Glacial bays are inhabited by the communities dominated by small, mobile, surface-detritus-feeding polychaetes and bivalves (Włodarska-Kowalczuk *et al.* 1998). Suspension feeders, sedentary and tube-dwelling animals are eliminated from glacial bays by heavy mineral sedimentation, instability of sediments and low supply of organic matter. Protobranch bivalves (*Portlandia*, *Yoldiella*) are the most common dominants near glacier areas (e.g. Syvitsky *et al.* 1989, Aitken & Fournier 1993, Renaud *et al.* 2007, Włodarska-Kowalczuk 2007). Central basins of Arctic fjords host much more diverse macrobenthic communities with tube-dwelling polychaetes (the genera *Prionospio*, *Maldane*, *Spiochaetopterus*, *Heteromastus*) and suspension-feeding bivalves (*Bathyarca*, *Astarte*) among the dominants (Holte & Gulliksen 1998, Sejr *et al.* 2000, 2010, 2011, Włodarska-Kowalczuk & Pearson 2004, Glahder *et al.* 2005, Renaud *et al.* 2007, Josefson *et al.* 2008).

Both species richness and diversity usually decrease as one move from shelf toward the fjord heads, as reported from Svalbard fjords (e.g. Holthe & Gulliksen 1998, Włodarska-Kowalczuk *et al.* 2005, Renaud *et al.* 2007, Włodarska-Kowalczuk *et al.* 2012), Greenland (Schmid & Piepenburg 1993, Sejr *et al.* 2000) and the Canadian Arctic (Farrow *et al.* 1983). These patterns are stable in time (Renaud *et al.* 2007, Kedra *et al.* 2010) and are also apparent at lower taxonomic resolution (Włodarska-Kowalczuk & Kedra 2007). The tendency of decreasing species diversity in inner fjord basins is accompanied by simplification in the composition of functional groups (Włodarska-Kowalczuk *et al.* 2005, Somerfield *et al.* 2006, Włodarska-Kowalczuk & Węsławski 2008) and a decrease in spatial heterogeneity in species distribution (Kendall *et al.* 2003, Włodarska-Kowalczuk & Węsławski 2008).

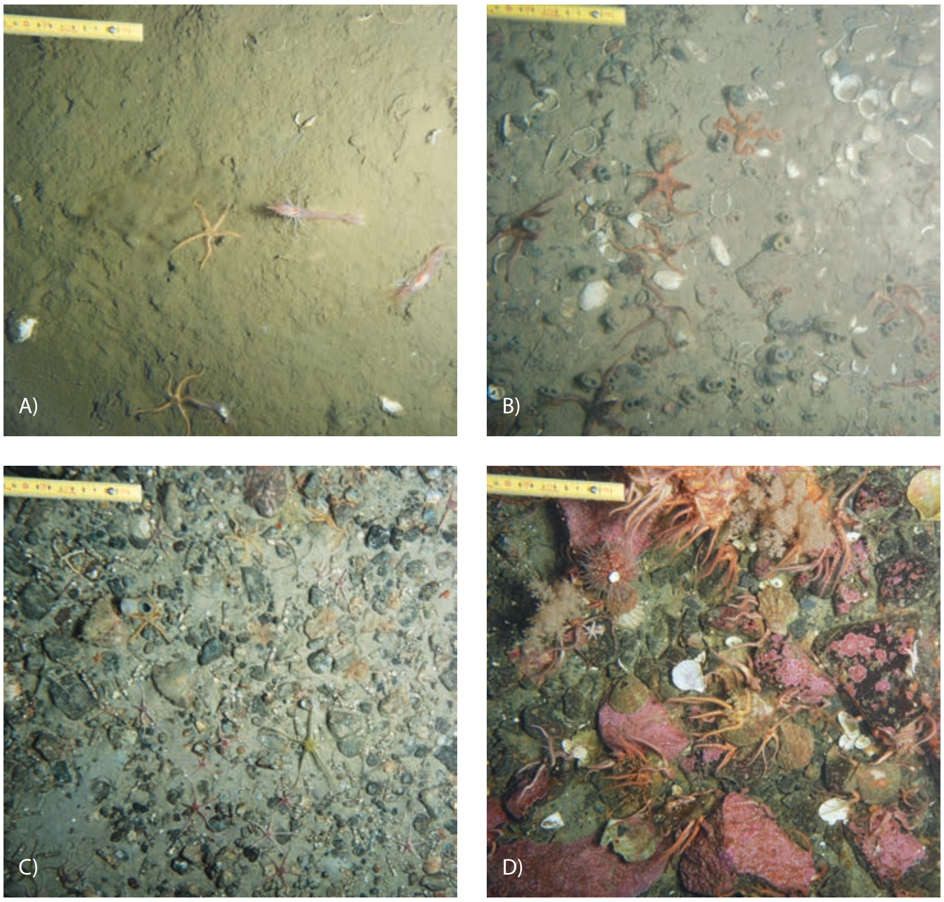

**Figure 8.5.** Photographs of the sea floor from eastern Baffin Bay in W Greenland, showing different benthic habitats. (A) soft mud, (B) soft sediment with shells and stones, (C) gravelly bottom and (D) boulder bottom (from Sejr *et al.* 2011).

Meiofauna in fjords has attained much less attention than macrofauna. The few published studies show that the glacial or glacio-fluvial inflows in inner fjord basins result in changes similar to those observed for macrozoobenthos, i.e. a decrease in diversity and standing stocks (Somerfield *et al.* 2006, Włodarska-Kowalczuk *et al.* 2007b, Grzelak & Kotwicki 2012).

Several species have a wide depth distribution, e.g. the annelids *Prionospio steenstrupi*, *Chaetozone setosa* (or *Chaetozone* complex) and *Maldane sarsi* that were among the dominating species on the Beaufort Sea shelf (Bilyard & Carey 1979) and the shelf and slope west of Svalbard (Włodarska -Kowalzcuk *et al.* 2004). Sejr *et al.* (2010) found that the total macrofaunal species richness in Godthaabsfjord and in an area offshore in W Greenland was in the upper range of values reported from the Canadian Arctic and the Norwegian shelf. The work of Curtis (1972) suggested a diverse polychaete fauna in Canadian Arctic fjords. Aitken & Fournier (1993) described the macrofauna inhabiting three fjords of eastern Baffin Island and compared it with earlier studies of Syvitski *et al.* (1989). Aitken & Fournier (1993) found that the macrobenthos communities in the fjords were comparable in composition to the fauna on the Baffin Island continental shelf and in E Greenland fjords, and that there was a consistent sequence of communities going from the head to the mouth of the fjords. Conspicuous species of the head community were the bivalve *Portlandia arctica*, followed by the polychaete *Onuphis conchylega*, and at the fjord mouth the maldanid polychaete *Asychis biceps*.

### Arctic shallows and littoral zone

In shallow coastal areas below the inter-tidal zone, with suitable benthic substrate and moderate ice scouring, the bottoms are covered by macro-algal forests, so-called kelp beds. These beds may support a diverse and productive benthic invertebrate fauna. In a study of kelp-associated fauna in the Hornsund fjord in W Svalbard, Włodarska-Kowalczuk *et al.* (2009) found an invertebrate species richness of 11.5 species per individual algal plant that was consistent among different algal species. Among 403 plant specimens, a total of 208 invertebrate species were found with the highest number of species found in the Bryozoa (70), Polychaeta (52) and Hydrozoa (37). The most common species were the bryozoans *Tricellaria ternata*, *Celleporella hyalina*, *Eucratea loricata*, *Cibrilina annulata* and *Crisia eburnea*; the gastropod *Margarites helicinus* and the barnacle *Balanus balanus*. Estimating the total number of species using an extrapolation method yielded 259 species, considered lower than for similar assemblages at lower latitudes. In a shallow sound (2-10 m) in W Greenland, dominated by soft bottom and partial ice cover during winter, Blicher *et al.* (2011) found macrozoobenthos in high abundance (> 7,000/m$^2$), with a total of 120 species at 15 stations. The most common taxa were the polychaetes *Cistenides granulata*, *Owenia fusiformis*, *Ampharete acutifrons*, species of *Pholoe* and *Polydora*, and the bivalves *Macoma calcarea*, *Mya neoovata* and *Crenella decussata*.

While the substrate of kelp beds as well as deeper (> 20 m) shelf bottoms may support a high diversity of invertebrates, the intertidal bottoms generally contain an impoverished fauna, likely due to ice scouring (Węsławski *et al.* 2011). In comparison, littoral zones without ice souring such as the non-Arctic Holandsfjord in northern Norway and Kachemak Bay in S Alaska have high species richness. In contrast, more ice scour at littoral zones like the Beaufort Sea shores or the Godhåbsfjord, W Greenland, yields richness up to two orders of magnitude lower than the sites in Norway and Alaska (Węsławski *et al.* 2011).

Also the intertidal benthic communities tend to move downward to upper subtidal with latitude, as clearly seen along the western coast of Novaya Zemlia (Zenkevich 1963). The same occurs along the Eurasian coast from west to the east. The reduction of tidal amplitude eastwards from the Barents Sea and severe ice conditions force macrobenthic species to avoid the uppermost meters of the shelf zone. However, this zone is severely under-sampled, as most studies in the Arctic shallows were done by research vessels with depth restrictions. Only a few studies describe the fauna and communities between 0 and 10 meters in the area from the SE Barents Sea to the Chukchi Sea. Using SCUBA equipment, such studies were done in the Baydara Gulf of the Kara Sea (Kucheruck *et al.* 1998), Franz Joseph Land, Novosibirsk Islands and Chauna Bay (Golikov 1990, 1994a, 1994b, 1994c, Golikov *et al.* 1994). Work in the eastern Arctic confirmed that the high Arctic intertidal almost lacks macrobenthos eastwards from the Barents Sea. Benthic communities, which are quite species rich close to the shore in the western Kara Sea, tend to shift to deeper water eastwards, where the upper depth limit of permanent macrofauna is reported to be at several meters, below the zone of ice scouring (Golikov *et al.* 1994). Although being devoid of macrofauna, the intertidal and upper subtidal zone is inhabited by meiofauna, which is rich in abundance (Sheremetevsky 1897) and assumedly also diverse. This may also be the case for macrofauna where the effects of ice conditions are relatively mild, even at very high latitudes (79° N at Svalbard), with an intertidal zone that can harbor over 40 macrofauna species that also contribute considerable biomass (e.g. Węsławski *et al.* 2011).

### Open shelf

About half of the Arctic Ocean area overlays shelf zones, i.e. areas at water depths down to 200-500 m. There have been great differences in investigation effort between the eastern and western Arctic. The wide open shelf of the Eurasian Arctic is covered much more densely by sampling points than the shelves of the North American Arctic. This could possibly be explained by differences in ice conditions, which has allowed exploration of most parts of Eurasian shelves without icebreakers. However, significant progress was achieved in exploration of the western Arctic during the last decades, and now the total sampling effort is more equal (Bluhm *et al.* 2011a and Fig. 1 therein).

In reviewing historical and recent benthic records, Cusson *et al.* (2007) found higher species richness in eastern than in central and western parts of the Canadian Arctic shelf. The total number of taxa of macrozoobenthos reached c. 1,000 in the Canadian Arctic Archipelago. Using the same data as Cusson *et al.* (2007), Witman *et al.* (2008) searched for general relationships between productivity and benthic species richness in the Canadian Arctic. They found that the shape of the relationships varied with community type, with negative linear relations restricted to sessile epifauna, while hump shaped relations occurred in Arctic macrobenthos (mixed epifauna, infauna). Furthermore, significant effects of chlorophyll *a* co-varied with the effects of salinity, suggesting that environmental stress as well as productivity influences diversity in the Canadian Arctic.

Conlan *et al.* (2008) studied spatial distribution of macrozoobenthos on the Canadian Beaufort shelf in relation to different habitats and reported a total of c. 500 taxa. These taxa occurred in varying densities in four different types of communities: (1) a community from the fast ice and flaw lead regions of the Beaufort shelf, dominated by the polychaete *Micronepthys minuta* and the bivalve *Portlandia arctica* and some amphipods, (2) a shelf slope community dominated by the polychaetes *Maldane sarsi*, *Lumbrineris impatiens* and *Tharyx* sp., a sipunculid and the bivalves *Bathyarca* sp. and *Yoldiella* sp., (3) a shallow-water community in an upwelling area dominated by the amphipods *Ampelisca macrocephala* and *Photis* sp., two species of ostracods and the polychaete *Barantolla Americana*, and (4) a community from the Cape Bathurst polynya, dominated by burrowing polychaetes such as *Maldane sarsi*, and the sediment-surface-feeding polychaetes *Terebellides stroemi*, *Melinna cristata* and *Tharyx* sp., together with the brittle star *Ophiocten sericeum*.

The large scale patterns in community distribution along the Eurasian coasts was summarized by Spiridonov *et al.* (2011), and it was shown that there was a shift from patchily distributed diverse communities in the western part of the area (Barents Sea) to more homogeneous distributions of main community types in the Siberian Arctic. The communities closer to the coast were dominated by bivalves (notably the genus *Tridonta,Macoma calcarea*, several nuculids, *Portlandia* species, *Astarte crenata*, *Yoldia hyperborea*, *Ciliatocardium ciliatum*) and were substituted seawards by ophiuroids (e.g. *Ophiocten sericeum*, *Ophiocantha bidentata* and *Ophiopleura borealis*) (map 2.4B in Spiridonov *et al.* 2011).

The 'Boreo-Arctic *Macoma* community' sampled by grab and described by Thorson (1957) was dominated by the bivalve species of the genera *Macoma* and *Astarte*. This is a common macrobenthic community of Arctic shelf sediments (Longhurst 2007). Of the shelf macrofauna reviewed by Piepenburg *et al.* (2011), the most widely distributed polychaetes were *Onuphis conchylega*, *Aglaophamus malmgreni*, *Eteone longa*, *Lumbrineris fragilis*, *Nicomache lumbricalis*, *Pholoe minuta* and *Scalibregma inflatum*. The most common molluscs were, in addition to the two above mentioned bivalve genera, *Musculus niger*, *Serripes groenlandicus* and *Yoldiella lenticula*. The most common crustaceans were the amphipods *Ampelisca eschrichti*, *Anonyx nugax*, *Arrhis phyllonyx*, *Byblis gaimardi* and *Haploops tubicola*, and the cumaceans *Diastylis* spp. and *Leucon nasica*. In echinoderms, the most common species were *Ophiocten sericeum*, *Ophiura robusta* and *Ophiacantha bidentata* (Piepenburg *et al.* 2011). All of these species are common also in boreal areas outside the Arctic.

The large standing stocks of widespread bivalves that dominate biomass in some shelf areas sustain the populations of gray whales *Eschrichtius robustus* and walrus *Odobenus rosmarus* (Longhurst 2007). For instance, in the *Macoma calcarea* community in the central Chukchi Sea, the greatest biomass of benthos was 4,232 g/m$^2$, with an average of 1,382 g/m$^2$ for the investigated areas (Sirenko & Gagaev 2007). Likewise, bivalves in the shallow coastal areas and banks off the Greenland coast provide important feeding items for walrus and the two eiders, common *Somateria mollissima borealis* and king eider *S. spectabilis* (Born *et al.* 2003, Boertmann *et al.* 2004, Blicher *et al.* 2011).

A study of the benthic fauna of the southern part of the Kara Sea (Jørgensen *et al.* 1999) reported nearly 500 taxa, consisting mainly of Crustacea (28%), Polychaeta (26.5%) and Mollusca (21.5%). There was a strong dominance of species with a Boreal-Arctic distribution (70.6%). However, there also was a clear increase in the proportion of Artic species going from marine to estuarine conditions and in a west to east direction, in agreement with the findings of Denisenko *et al.* (2003b). The most conspicuous species, proceeding from marine to estuarine conditions, were the polychaete *Spiochaetopterus typicus*, the bivalves *Tridonta borealis*, *Serripe*s *groenlandicus*, *Portlandia arctica* and, in the area with lowest salinity, the Arctic bivalve *Portlandia estuariorum* and the polychaete *Marenzelleria arctia*. The last of these has recently emmigrated into the Baltic Sea (Bastrop & Blank 2006). The megafauna and hyperfauna of the Kara Sea were not sampled at these locations, but if sampled they would most likely have resulted in a higher total number of taxa for the area. Similarly, Denisenko *et al.* (2003b) studying the macrozoobenthos of the Pechora Sea (SE Barents Sea) reported > 500 species consisting of Polychaeta, Mollusca, Crustacea, Echinodermata, Bryozoa and Cnidaria. Most species (69%) had a wide boreal-Arctic distribution, while only 15% were restricted to the Arctic.

Studies on macrofauna and productivity in the Barents Sea and on the influence of Arctic and Atlantic waters were conducted by Cochrane *et al.* (2009). While they showed a different faunal composition under the two water masses, they found no typical Arctic fauna under the Arctic water mass. Instead many species, many of them with a southerly boreal distribution, occurred under both water masses. These results led the authors to predict that a potential northern shift in the border of the Arctic water body would make the two water mass communities more similar in composition. Nearly 15 dominant species and taxa form about 90% of the biomass of macrozoobenthos in the Barents Sea. Conspicuous species are the bivalves *Tridonta borealis*, *Serripes groenlandicus*, *Macoma calcarea*, the polychaete *Spiochaetopterus typicus*, the sipunculoid *Golfingia margaritacea*, the sea star *Ctenodiscus crispatus* and several sponges (Denisenko 2004).

Sirenko *et al.* (1996) sampled the supra-benthic fauna, i.e. the fauna on the sediment and in near- bottom water in the Laptev Sea, from shelf depths down to the deep sea. They found 139 species in total, consisting of cnidarians, annelids, molluscs and arthropods, and species that are considered pelagic or benthic. Of these species 51 were recorded for the first time in the Laptev Sea area.

Compared with the shelf macrozoobenthos, the meiobenthos, including the protozoan Foraminifera, has received much less attention. Metazoan meiobenthos includes a wide range of higher taxa among about half of the known phyla (Giere 2009, Mokievsky 2009a). The most abundant and diverse metazoan meiofaunal taxa on the shelf are Nematoda, Harpacticoida and Turbellaria. There are more or less complete species lists for the White Sea area, where the small-sized biota represent the most significant component of newly described species. Among the 104 species new to science described from the vicinity of the White Sea Biological Station, 25 were free-living nematodes and 23 were crustaceans, mainly harpacticoid copepods (Tchesunov 2008).

The total species number of Arctic metazoan meiofauna represents c. 25% of the total number of known metazoan species (Mokievsky 2009a). In local Arctic sea faunas, this value varied from 6% to 20%, reflecting mostly differences in sampling effort rather than true differences in diversity. Very preliminary observations of overall meiobenthic diversity in the Russian Arctic seas are given in Spiridonov *et al.* (2011) (Fig. 8.6). Nematodes and harpacticoid copepods were the most diverse groups. The diversity of harpacticoid copepods was reviewed by Chertoprud *et al.* (2010).

Exept for the White and Barents Seas, the diversity of meiobenthos is likely underestimated in Arctic sub-areas. An almost overlooked meiofaunal group, likely due to inadequate sampling methods, is the free-living acoelomate flatworms (Turbellaria). Recent studies also show that this group plays an important role in sea-ice communities (Gradinger *et al.* 2010b). From what is known, the species diversity of turbellarians in the Arctic appears quite low, although the total number of species reported for the Barents Sea exceeds 100 (Sirenko 2001), or slightly less than half the number of nematode species in that area. Nearly the same figures were reported from ArcOD data, 134 species of benthic plathelminths compared with 403 species of benthic Aschelminths, which includes Nematoda (Tab. 8.1; Gradinger *et al.* 2010a). However, in the well studied areas outside the Arctic, the proportion of turbellarians is higher. For the North Sea, the list of species includes 735 species of nematodes, 515 species of harpacticoids (Heip *et al.* 1983) and 400 species of turbellarians (Martens & Schockaert

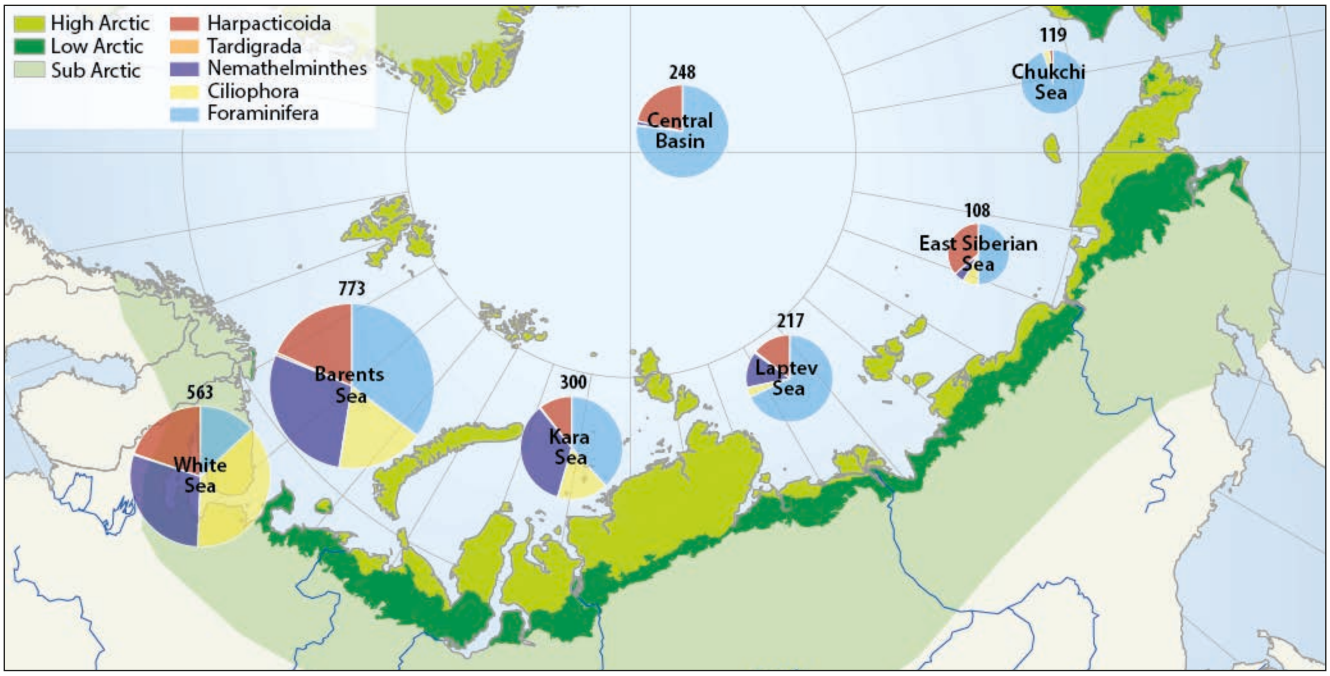

**Figure 8.6.** Map of the Russian Arctic showing the distribution of meiofauna diversity for different areas (from Spiridonov *et al.* 2011). Sizes of the cakes relates to total number of taxa are indicated above each cake.

1986). The German Wadden See, one of the best investigated areas in the world in terms of meiofauna, is home to 364 species of turbellarians, 333 of nematodes and and 119 of harpacticoids (Gerlach 2004). Therefore, at present it remains to be seen whether or not the relatively low proportion of turbellarians in the Arctic is related to poor knowledge or represents a true phenomenon.

The diversity of the less-studied meiofaunal taxa, such as Gastrotricha, Loricifera, Kinorhyncha and Tardigrada, is almost unknown from the eastern Arctic and Arctic deep-sea. While all these groups were reported from the Arctic (e.g. Mokievsky 1992, Soltwedel & Schewe 1998, Soltwedel *et al.* 2000, 2009b, Vanreusel *et al.* 2000), most were not identified to the species level.

### Deep-sea

The deep-sea invertebrate fauna is the least studied faunal component in the Arctic Ocean (Piepenburg 2005). The macrofauna was sampled on the continental margin down into the deep-sea (3,000 m) west of Svalbard by Włhodarska-Kowalzcuk *et al.* (2004). Contrary to the general parabolic bathymetric pattern of benthic diversity in the temperate North Atlantic outside the Arctic, they found a decreasing species richness with increasing water depth, and the diversity at depths lower than 1,000 m was much lower than in comparable temperate areas. They concluded that this was due to geographic isolation of the Greenland-Icelandic-Norwegian Seas from the Atlantic pool of species, rather than to differences in productivity, as the macrobenthic biomasses on the continental margin off Svalbard were comparable to those recorded at lower latitudes.

Kröncke (1994) studied macrozoobenthos in the area between Svalbard and the Makarov Basin, reporting low species abundance, biomass and species number (42 species from 30 sites and a total sampled area of 7.5 m$^2$, 500 µm mesh). The most common species was the amphipod *Jassa marmorata*. Four years later, using the same methodology, Kröncke (1998) described the macrofauna of the western Eurasian Arctic Ocean on a transect from the North Pole across the Amundsen Basin and Gakkel Ridge, towards the Morris Jesup Rise and the Yermak Plateau. The species richness found this time was higher, 108 taxa from 17 sites, and it was concluded that the findings contradicted the hypothesis of declining species richness with increasing latitude, with richness comparable to levels in Antarctic and even tropical regions. The most species rich groups in this study were Polychaeta and Crustacea, the latter represented by mainly Cumacea, Isopoda and Amphipoda. The macro- and megabenthic fauna in the Arctic Canada Basin was investigated by Bluhm *et al.* (2005). Based on samples sieved through a 250 µm mesh, they reported a total of 90 benthic invertebrate taxa from six sites at the 640-3,250 m depth interval, representing four different biogeographic affinities and at least three isopod species new to science. The identified species were dominated by cosmopolitan boreo-Arctic and boreo-Atlantic species. The former was exemplified by the bivalves *Cuspidaria glacialis* and *Dacrydium vitreum*, the amphipod *Aceroides latipes* and the polychaetes *Maldane sarsi*, *Terebellides stroemi* and *Lumbrineris fragilis*. The latter was characterized by the bivalves *Yoldiella frigida* and *Bathyarca frielei*. An example of the very small group of Arctic endemics was the bivalve *Nucula zophos*. A scaphopod, *Siphonodentalium lobatum*, was reported as the most common mollusc species in Arctic deep-sea basins (Bluhm *et al.* 2005).

The larger free-living nematodes in the deep-sea Canada Basin were studied by Sharma & Bluhm (2011). The study considered individuals larger than 250 µm, of a group that in benthic surveys is often categorized as meiofauna (≥ 32 µm to 1 mm). At the 640-3,848 m depth range they found 84 genera among 25 families, with total abundance varying from 0 to 6,800 ind./$m^2$. Dominant families were Comesomatidae and Oncholaimidae and dominant genera *Sabatieria* and *Viscosia*. Deubel (2000) studied macrofauna on the Lomonossov Ridge, northern Laptev Sea, at 500-4,170 m, finding 474 taxa from a sampled area of 20.5 $m^2$ using a 250 µm mesh.

In comparison with macrofauna, the deep sea meiofauna (< 0.5 mm) has received very little attention. For example, a study in the Fram Strait yielded 180 nematode genera (Fonseca *et al.* 2010). The number of putative species found in one locality at about 2,300 m in Fram Strait was 367 (Hasemann & Soltwedel 2011). The repeated survey on the Yermak Plateu (north of Spitsbergen, Svalbard, at the depths 700-1,200 m) gave the figure of 200 putative species distributed within 89 genera (Soltwedel *et al.* 2009b). Elsewhere, on a single transect in the central Arctic Ocean, more than 110 genera of nematodes were found (Vanreusel *et al.* 2000). Even less is known about other meiofaunal groups, which are represented in the Arctic deep-sea by a relatively long list of high taxa. For example, beside nematodes and harpacticoids, the Yermak Plateau also has polychaetes, ostracods, kinorhynchs, bivalves, gastropods, tanaidaceans and tardigrades (Soltwedel *et al.* 2000). The meiofauna of the area west of Svalbard was predominantly nematodes and harpacticoids, but also included polychaetes, gastrotrichs, kinorhynchs, tardigrades, rotifers and tantulocarids. Very few species from all these groups have yet been described from the Arctic. Even for nematodes, the number of known species is low if compared with the potential diversity in the deep sea (Miljutin *et al.* 2010). More detailed studies in eastern Arctic seas will surely increase the known figures for Arctic meiofauna.

Recently, in a circumpolar review, Bluhm *et al.* (2011b) assessed biodiversity of the benthic deep-sea fauna occurring deeper than the shelf break at 500 m. They reported 1,125 taxa from the deep-sea area bounded to the Atlantic by Fram Strait. Dominant species groups in decreasing order of species numbers were Arthropoda, Foraminifera, Annelida and Nematoda. The highest abundances, up to c. 10,000 ind/$m^2$, were generally found on the shelf slopes. Many of the deep-sea species (61%) also occurred on the shelf, such as the polychaete *Myriochele heeri*, the tanaid *Pseudotanais affinis* and the sea star *Pontaster tenuispinus*, suggesting a shelf origin of these species. Similarly, Bilyard & Carey (1979) reported maximum diversity and abundance of polychaetes at the outer shelf and upper continental slope in the western Beaufort Sea. Abundant species in this area were the widespread boreal polychaetes *Maldane sarsi*, *Heteromastus filiformis* and *Terbellides stroemi*. Other major findings in this review were that species composition of polychaetes indicated a strong influence from the Atlantic, that modern Pacific elements were lacking, and that there was no barrier effect of the mid-Arctic ridges. As in several other habitats and realms, the Arthropoda was the most species-rich phylum.

### The HAUSGARTEN case study

The recognition in the recent past that oceans are highly dynamic systems has led to new strategies in studying marine ecosystems, with the goals of achieving a more comprehensive understanding of marine processes and of developing predictions of potential system changes. Snapshot observations are no longer considered sufficient, as only long-term investigations allow the assessment of environmental factors that determine the dynamics, structure and complexity of marine communities. This is particularly obvious for the rapidly changing Arctic systems. Thus, in 1999 the German Alfred Wegener Institute for Polar and Marine Research (AWI) established the first and only Arctic deep-sea long-term observatory to detect and track the impact of large-scale environmental changes in the transition zone between the northern North Atlantic and the central Arctic Ocean (Soltwedel *et al.* 2005). The HAUSGARTEN observatory is located in Fram Strait, the only deep water connection between the central Arctic Ocean and the Nordic Seas, where exchange of intermediate and deep waters takes place. Hydrographic conditions in the area are characterized by the inflow of relatively warm and nutrient-rich Atlantic Water into the central Arctic Ocean (Rudels *et al.* 2000). Advection and the physical properties of these waters primarily control the climate of the Nordic seas and the entire Arctic Ocean (Karcher *et al.* 2011). Multidisciplinary research activities at HAUSGARTEN cover almost all compartments of the marine ecosystem, from the pelagic zone to the benthic realm, with the main emphasis on benthic processes.

The observatory currently comprises 17 sampling sites along a bathymetric transect (1,250-5,500 m water depth) and along a latitudinal transect of c. 150 km, following the 2,500 m isobath. The central HAUSGARTEN station, at 2,500 m, serves as an experimental area for unique biological short- and long-term experiments to determine the factors controlling biodiversity on the deep seafloor (Premke *et al.* 2006, Gallucci *et al.* 2008a, 2008b, Kanzog *et al.* 2009, Guilini *et al.* 2011). Work on the small benthic biota (size range: bacteria to meiofauna) focuses on *in situ* experimental work. Short-term study aspects include investigating the effects of sporadic food supplies, the reduction/prevention of food/energy supply, and the effects of physical disturbances. These experiments are intended to elucidate how the small benthic biotas interact with each other and with their changing environment. Benthic long-term studies at Hausgarten comprise biochemical analyses to estimate the input of phytodetrital matter and to assess activities and biomasses of the small sediment-inhabiting biota. Covering all size classes from bacteria to megafauna, a temporal assessment of the distribution patterns of benthic organisms is a major goal of these studies.

The metazoan meiobenthic studies at HAUSGARTEN between 2000 and 2004 revealed densities ranging on average from 149 to 3,409 ind./10 $cm^2$ (Hoste *et al.* 2007). Nematodes dominated at every depth and sampling year (85-99%), followed by harpacticoid copepods

(0-4.6%). Based on density of individuals, the bathymetric transect could be roughly subdivided into a shallow part between c. 1,000 and c. 2,000 m water depth, with equally high nematode and copepod densities (c. 2,000 nematodes and 50 copepods/10 cm$^2$), and a deeper part between c. 3,000 and c. 5,500 m, with clearly lower nematode and copepod densities (c. 600 nematodes and 11 copepods/10 cm$^2$).

Compared with deep-sea studies from the North Atlantic, the nematode community at HAUSGARTEN was characterized by very high species numbers, even though the number of genera was in the same order of magnitude (Hoste 2006). In the Arctic, there were relatively more rare genera and more species representing less than 1% of the overall nematode abundance. However, the overall nematode community structure at HAUSGARTEN was similar to other typical deep-sea communities, with dominant genera such as *Amphimonhystrella*, *Acantholaimus*, *Halalaimus* and members of the Desmoscolecidae and Monhysteridae. The nematode community composition changed gradually with water depth (Fig. 8.7). Differences were mainly due to variations in the relative abundance of genera rather than the presence/absence of genera. Some indicator species were found at most water depths, especially within the groups Monhysteridae, Xyalidae and Desmoscolecidae. Totaly, 640 morphotypes belonging to 152 genera and 33 families were recorded there with a prominent gradient in species richness: 432 putative species were found at 1,200 m depth, 361 at 2,500 m and 264 at 4,000 m (Hoste 2006).

Aside from water depth as the main factor accounting for differences in nematode communities, inter-annual variability in nematode community structure was apparent, with high relative abundances of *Dichromadora*, *Microliamus* and *Tricoma*. This was found to be related to high food availability (Hoste 2006).

Harpacticoid copepods, the second dominant group within the meiobenthos at HAUSGARTEN, comprised 89 species (Hoste 2006). Dominant families of copepod species numbers included the Ectinosomatidae (23.5%), Cletodidae (15.5%), Danielsseniidae (14.0%), Miraciidae (12.0%), Argestidae (7.5%), Ameiriidae (7.5%) and Huntamaniidae (5.0%). The female to male ratio was approximately 2.5:1. The copepod community comprised a wide range of body shapes, with members of each of the three ecotypes: endobenthic, epibenthic and interstitial. The bathymetric distribution of harpacticoid copepods could be divided into two depth ranges: 1,200-2,000 m and 2,500-5,000 m. according to the relative proportion of general body shapes or 'living forms': at the shallower part of the transect, the relative proportion of burrowing species was higher, whereas interstitial species, determined by body shape, were dominant at the deeper sites (2,500-5,000 m water depth). As with nematodes, harpacticoid diversity was higher at the upper part of the transect (Hoste 2006). Other meiobenthic groups found there were polychaetes, gastrotrichs, kinorhynchs, tardigrades, rotifers and tantulocarids. These groups were found in very low abundances, less than 2% of the total (Hoste *et al.* 2007).

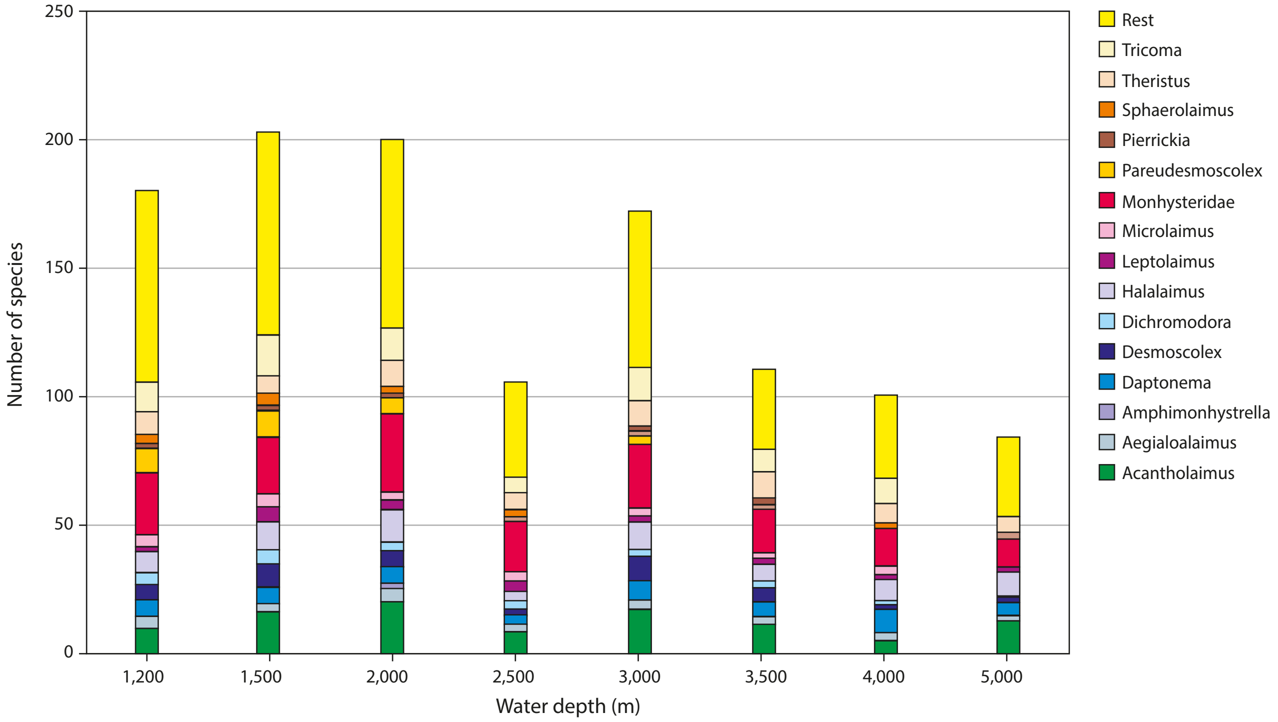

**Figure 8.7.** Stacked bar plot showing the number of nematode species for each dominant genus at different water depths along the bathymetric HAUSGARTEN transect (Hoste 2006).

Macrofauna in the HAUSGARTEN area was sampled twice during summer, for a bathymetric study along a depth gradient from 200 to 3,000 m in 2000 (Węsławski *et al.* 2003, Włodarska-Kowalczuk *et al.* 2004), and to study horizontal distribution patterns along an isobath at approximately 2,500 m in 2003 (Budaeva *et al.* 2008). Macrofaunal sample species richness decreased with water depth. There was, however, no clear bathymetric pattern in diversity measures; the classic increase of species richness and diversity at mid-slope depths was not observed. According to Włodarska-Kowalczuk *et al.* (2004), Shannon-Wiener diversity was the highest at 525 m ($H'_{(\log e)} = 3.54$) and lowest at 2,025 m depth ($H'_{(\log e)} = 1.46$). Species richness and diversity at the deep stations were much lower than in comparable studies from the temperate North Atlantic. Włodarska-Kowalczuk *et al.* (2004) related this finding to the geographic isolation of the Greenland-Icelandic-Norwegian Seas from the Atlantic pool of species.

Budaeva *et al.* (2008) sampled three sites along a 26 km transect along the 2,500 m isobath. Three box corers (0.25 $m^2$) were taken at each site, yielding a total of 3,714 specimens, belonging to 59 taxa. Total biomass ranged from 2.31 g ww/$m^2$ to 6.41 g ww/$m^2$. Dominant taxa of the macrofauna were the sponge *Tetractinomorpha* sp., the bristle worms *Myriochele heeri* and *Galathowenia fragilis*, the cumacean crustacean *Diastylis polaris*, the sipunculid *Sipunculus* sp., the snail *Mohnia mohni* and the bivalves *Bathyarca frielei* and *Tindaria derjugini*. Budaeva *et al.* (2008) discussed their findings in the context of results published by Włodarska-Kowalczuk *et al.* (2004) and suggested that the macrobenthos in the HAUSGARTEN region is organized at three spatial scales: communities that replace each other along the depth gradients, species assemblages that contribute to the heterogeneity within each vertical zone, and single-species patches that create variability at the local scale.

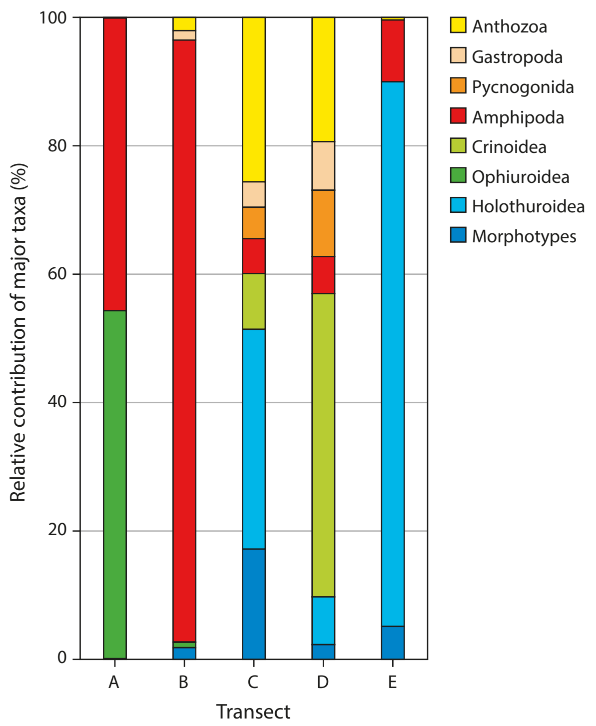

**Figure 8.8.** Taxonomic composition of the epi-/megafauna at the HAUSGARTEN observatory from photographic transects covering different water depth ranges (A: 1,313-1,316 m; B: 1,642-1,688 m; C: 2,432-2,629 m; D: 2,965-3,907 m; E: 5,333-5,404 m) (Soltwedel *et al.* 2009a). 'Morphotypes' denote unrecognised organisms.

Large-scale distribution patterns of epi/megafauna organisms were assessed using a towed photo/video system (Ocean Floor Observation System). As many megafaunal organisms from deep-sea environments are characterized by rare occurrence, it is advantageous that camera systems can survey transects at the scale of kilometers without causing disturbance or altering the habitat (Thistle 2003, Soltwedel *et al.* 2009a, Bergmann *et al.* 2011).

As elsewhere, megafaunal assemblages along the bathymetric transect of the HAUSGARTEN observatory are characterized by zonation, and the structure of benthic assemblages from different depths varies in terms of species composition, diversity and functional ecology (Soltwedel *et al.* 2009a). At HAUSGARTEN, megafaunal densities ranged between 11 and 38 ind./$m^2$, with highest densities at 1,650 m and lowest at 3,000 m depth. The number of taxa ranged from four at 5,500 m to 27 at 1,650 m water depth. The Shannon-Wiener diversity index ($H'_{(\log 2)}$), ranged from 0.34 at c. 1,700 m to 2.58 at c. 2,600 m.

The deposit-feeding boreo-Arctic brittle star, *Ophiocten cf. hastatu*, dominated the continental margins up to depths of c. 1,300m (Fig. 8.8), at mean densities of 17 ind./$m^2$. In contrast, at a nearby station, only some 300 m deeper, small amphipods dominated the fauna (37 ind./$m^2$). Deeper, at c. 2,500 m water depth, the deposit-feeding Arctic-boreal sea cucumber, *Kolga hyaline*, and suspension-feeding sea anemones accounted for the majority of megafaunal organisms, at densities of four and three ind./$m^2$, respectively. The suspension-feeding boreo-Arctic crinoid, *Bathycrinus carpenterii*, (5 ind./$m^2$) and sea anemones (2 ind./$m^2$) were the most abundant groups seen at c. 3,000 m water depth. The sea cucumber (*Elpidia heckeri*, 30 ind. / $m^2$) dominated the Molloy Hole. The zonation patterns appear to be controlled primarily by food availability (Soltwedel *et al.* 2009a).

### 8.2.4. Biogeography

Biogeography is generally understood as the study of broad-scale distribution patterns of species and their derivation in both a short- and long-term perspective. In recent time, this field forms an important component of the discipline macroecology together with ecology (Briggs 2007). Biogeography may help us to understand how some of the species diversity patterns we see today in the Arctic Ocean have been generated.

The Arctic invertebrate fauna on the seafloor is characterized by species with several different biogeographic affinities, with origins inside and outside the Arctic.

Considering the post Pliocene period, there are essentially four main groups with different affinities, although the groupings may vary somewhat among authors and taxonomic groups:

1. Widespread boreo-Arctic species found all over the Arctic and in sub-Arctic seas. There are, for instance, many representatives of this group among annelids.
2. Boreo-Arctic species of Atlantic origin. This is the largest group among echinoderms and the speciose crustaceans, accounting for c. 85% of the crustacean species in today's Arctic.
3. Boreo-Arctic species of Pacific origin. This is a smaller group in echinoderms restricted to the Chukchi Sea area (Sirenko 2001) and accounting for less than 10% of the crustaceans.
4. True Arctic species, including endemics only found in the Arctic. The number in this group is generally small but varies among taxonomic groups and accounts for instance for some 10% of the crustacean species and up to 30% of all bryozoan species.

The distribution patterns of species within these categories reflect the recent geological history of the Arctic but likely also reflect current dispersal barriers. In general, the true Arctic group is a minority, with relatively few endemic species. This is in contrast to the Antarctic which harbors many more endemics, attributed to the long history of geographic isolation by the Antarctic Circumpolar Current (e.g. Clarke *et al.* 2004, Hassold *et al.* 2009). The openness of the Arctic Ocean to the Pacific and the Atlantic Oceans during the last c. 4 million years probably has precluded extensive *in situ* evolution of species here.

### Historical redistributions

The origin of a species is to some extent also related to the time period being considered. When we look only at the post-Pliocene period, a major part of the fauna is related to that of the North Atlantic, but when including a longer time period, the picture changes. In the later part of the Pliocene, extensive transgressions of species between the Pacific Ocean and high latitudes of the Atlantic Ocean, via the Arctic Ocean, are thought to have taken place c. 3.5 million years ago, with the direction primarily from the Pacific to the Atlantic (Golikov & Scarlato 1989, Vermeij 1989, Briggs 2003, Vermeij & Roopnarine 2008). Consequently, many of the boreal species found in the northern Atlantic since the Pleistocene and now regressing towards the Pacific on the Eurasian side of the Arctic are possibly expatriated Pacific species that have evolved further to become secondary Atlantic species. This is for instance seen in the asteroid echinoderms (Mironov & Dilman 2010), where several Atlantic taxa have closely related congeners in the Pacific, such as the species pairs of *Pteraster obscurus – P. ornatus* (Asteroidea) and *Gorgonocephalus arcticus – G. eucnemis* (Ophiuroidea) (Smirnov 1994). The hypothetical schemes of these redistributions (Mironov & Dilman 2010), based on species distribution maps, are supported now by the first gene-geographical studies on Arctic marine invertebrates (Addison & Hart 2005, Nikula *et al.* 2007, Hardy *et al.* 2011, Carr *et al.* 2011). Since the Pliocene, some echinoderms endemic to the Arctic may also have evolved (Smirnov 1994), such as the echinoid *Pourtalesia jeffreysii*. The importance of this 'The Great Trans-Arctic Biotic Interchange' (Briggs 1995) may have been an 'enrichment' of the North Atlantic species pool, because as pointed out by Briggs (2007), there is little evidence from the marine realm that invasions have decreased native diversity, but have instead resulted in an overall increased diversity. This pool of species may be a great source of immigration into the Arctic Ocean through the Atlantic gateway in recent time.

### Historical extinctions

Later, in the Pleistocene Quarternary period, starting c. 2 million years ago, glaciation periods nearly eradicated the shelf fauna (Dunton 1992), e.g. via ice standing on the shelf sea floor in glacial periods. Moreover, during maximal glaciation, the sea level was c. 100 m lower than today (Hopkins 1973, Fairbanks 1989), and large emergent areas of the shelf were dry or not covered by ice (Chukchi, Beaufort and East Siberian Seas). During that time, the submersed ice-free parts in these areas may have acted as a refugium for some shelf species. If this was the case, the Beringian refugium was important both for marine and terrestrial species. The effects of these historical extinctions are likely seen in the bristle worms (Polychaeta), with littoral and shelf areas down to 300 m dominated by boreal-widespread species and a corresponding near absence of endemic species (Bilyard & Carey 1980). This, and relatively low species richness, was attributed to invasions in inter-glacial periods during the Quarternary (Bilyard & Carey 1980). The changing relative influence of the Pacific on the littoral fauna correlates well with distance from the Bering Strait, with highest proportion of Pacific species in the Chukchi Sea (Fig. 3 in Dunton 1992). The development of population genetic analyses will provide more opportunities to trace the species redistribution on a geological time scale and to evaluate cryptic species diversity in light of historical isolation (Carr *et al.* 2011).

### Present patterns

There are several different biogeographic schemes for the Arctic (Zenkevitch 1963, Larsen *et al.* 2003, Spalding *et al.* 2007, Zhirkov 2010), all of them dividing the Arctic Ocean into a deep-sea region with its own fauna and a number of shallow water (shelf) sub-divisions. One of the most prominent boundaries, separating the Arctic from the sub-Arctic, crosses the Barents Sea, from NW to SE (Fig. 8.9; Denisenko 1990). Although the exact positions of the boundaries may vary depending on taxonomic group, they broadly reflect the hydrological and climatic influence on the distribution of species with different biogeographic affinities. A second zoogeographical border in the Arctic is situated in the East Siberian and Chukchi Sea areas. However, the exact position of the border is still unclear (Mironov & Dilman 2010). There are also gaps in knowledge of species distributions in this region, many of which have eastern or western distribution limits. This applies to shallow-water and deep-water

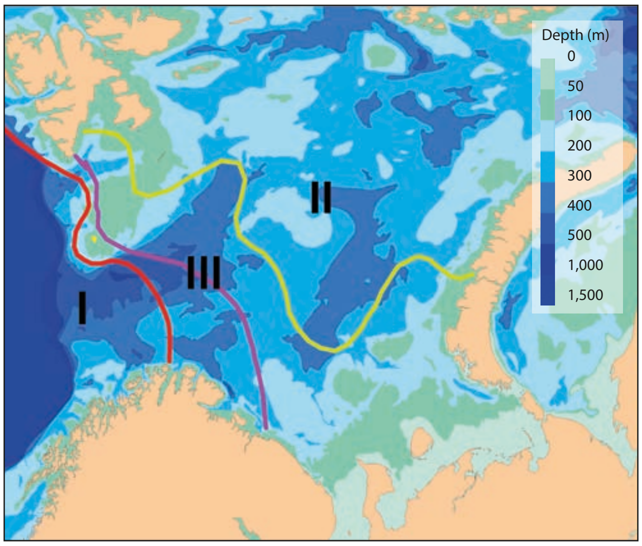

**Figure 8.9.** Biogeographic borders in the Barents Sea based on species distributions of bryozoans. Average position of the border with 50:50% of Atlantic boreal and Arctic species numbers is indicated by the purple line, and the red and yellow lines indicate the extreme positions of the border in cold and warm periods, respectively. Area III between them is the transitional zone between the Atlantic boreal and the Arctic regions. Thus, area I always has > 50% Atlantic boreal species, and area II always > 50% Arctic species (after Denisenko 1990).

species. The boundary in this region likely reflects the meeting of waters with Arctic and Pacific origin.

### Differences in affinity composition among regions

The Atlantic boreal influence is apparent in zoobenthic assemblages of the Barents Sea, a shelf sea at the entrance of the Atlantic, where boreo-Atlantic species dominate in areas influenced by Atlantic and Arctic water masses, and only few species can be characterized as truly Arctic (Cochrane *et al.* 2009). In the adjacent more easterly Kara Sea shelf, Jorgensen *et al.* (1999) and Denisenko *et al.* (2003a) reported c. 20% true Arctic species, c. 70% widely distributed boreal species, with the rest dominated by Atlantic boreal species and only few of Pacific boreal origin.

Biogeographical zonation in the Russian Arctic, recently reviewed by Spiridonov *et al.* (2011), is strongly influenced by freshwater outputs from the large Siberian rivers. The cold brackish shallow zone along the Russian Arctic coast harbors a number of relict species: the isopod *Saduria sibirica*, the bivalves *Cyrtodaria kurriana* and *Portlandia aestuariorum* and some others (Filatova 1957, Gurjanova 1970). Most of these species are not true endemics of the Arctic. During historical changes in their distributional ranges, many of the shallow water species found refuges in the Baltic Sea and North Pacific Ocean.

The deep sea areas (below 300 m) have a different long-term history than shallower areas, as Pliocene glaciations affected these habitats differently. The bathyal parts of the Arctic Ocean have likely not been affected by ice groundings during glacial periods and have a long history of relative isolation from other oceans, in particular from the Pacific due to the shallowness of the Bering Strait (70 m). As a result, the bathyal contains a more endemic fauna with few Pacific elements, as seen in the Polychaeta (Bilyard & Carey 1980) and several other groups (Vinogradova 1997). Examples of deep-sea endemism include sea cucumbers (Holothuroidea) of the genera *Elpidia* and *Kolga,* occurring with four other endemic species in the Arctic, at that time considered endemic (Rogacheva 2007). However, two of these species, *Elpidia glacialis* and *Kolga hyalina*, were later recorded at 2,700 m depth in the sub-Arctic Norwegian Sea (MAREANO 2009, Mortensen *et al.* 2009), indicating that they were not true Arctic endemics.

The differential effects of glaciation history on shelf and deep-sea areas are now also seen in the bathymetric distributions of species and differences in endemism between thes areas. There are probably more endemic species in the deep sea areas of the Arctic Ocean than on the shelf. While glaciation likely eradicated the fauna on large parts of the shelf, the deep-sea was not directly affected in this manner. For example, the Pacific boreo-Arctic echinoderms have a limited bathymetric range in the Arctic (often < 100 m), while the Atlantic boreo-Arctic species are mostly eurybathic. This is believed to be the result of substantial shelf glaciation on the Atlantic side that caused primarily eurybathic species to escape to great depths for survival, and later re-invade the shelves when conditions changed (Nesis 1983). In contrast, the Pacific side of the Arctic lacked significant shelf glaciation. As a consequence, only about two dozen echinoderm species occur deeper than 1,000 m in the Arctic Basin (Anisimova 1989).

### The latitudinal gradient

A strong spatial pattern in biogeography (macroecology) is the relationship between species richness and climate, and because climate changes with latitude, there is often a relationship between richness and latitude. Warm and wet areas often harbor more species than cold and dry areas (Currie *et al.* 2004). Broadscale richness patterns of several terrestrial and freshwater organism groups in the Arctic agree with this pattern, showing decreased richness with increasing latitude (see Fig. 2.1 in Payer *et al.*, Chapter 2). It is not clear, however, if richness of marine invertebrates follows this pattern.

Indeed, this general idea of lower diversity in the Arctic due to a harsh climate, but also in relation to the Antarctic, has recently been questioned regarding marine invertebrates (Kendall & Aschan 1993, Kendall 1996, Ellingsen & Gray 2002, Piepenburg 2005, Włodarska-Kowalczuk *et al.* 2007a). As more biodiversity investigations in the Arctic are accumulating, indications are that the Arctic harbors a higher diversity of invertebrate fauna than previously thought. The Arctic shelf fauna is similar in overall species richness to other shelf faunas, such as that of the Antarctic shelf (Piepenburg *et al.* 2011) or the Norwegian shelf (Ellingsen & Gray 2002), and intermediate on a global scale.

However, changes in diversity with latitude may differ depending on taxonomic groups and the geographic extent of the analysis conducted. The decline in diversity with increasing latitude, going from tropical to high Arctic conditions, obvious in the terrestrial realm, was seen in molluscs (Roy *et al.* 1998, Jablonski *et al.* 2000). In contrast, arthropods, by far the most species-rich group in the Arctic, showed high species richness in the Arctic compared with some adjacent non-Arctic areas (e.g. Archambault *et al.* 2010), and earlier studies of the speciose arthropod group Peracarida did not find a latitudinal gradient in species richness (Brandt 1997), nor was there a latitudinal gradient in nematode richness in the worlds oceans (Mokievsky & Azovsky 2002). An explanation of the relatively high species diversity in parts of the Arctic could, as described above, be the extensive immigration of species from the large species pools in the adjacent oceans, from the Pacific to a great extent in late Pliocene and from the Atlantic afterwards until recent time.

A conspicuous feature of Arctic marine invertebrate biodiversity in general, is the strong influence from faunas in adjacent sub-Arctic and boreal parts of the Atlantic and Pacific Oceans. To a large extent, the Arctic Ocean is populated by widespread amphi-boreal species together with a great proportion of species of post-Pliocene Atlantic origin and to a lesser extent of only recent Pacific origin or true Arctic species. Thus the Arctic Ocean is largely a sea of immigrants with only few endemic species. The dramatic geological history of the Arctic Ocean in conjunction with the low degree of isolation from adjacent oceans has probably precluded *in situ* evolution of species, and the species pool in the Arctic Ocean has been differentially affected by immigration through the two major marine gateways into the Arctic Ocean. Thus, the stronger Atlantic influence compared with the Pacific may have partly resulted from the closed Bering Strait prior to the opening 3.5 million years ago. During this same time, the much wider Atlantic gateway was open, allowing an influx of species into the Arctic.

#### Hotspots – or just species-rich areas

One recent popular conservation strategy, mainly based on terrestrial experience, is to protect as many unique or endemic species as possible, by protecting so-called biodiversity hotspot areas. Such areas should contain "exceptional concentrations of endemic species that are undergoing exceptional loss of habitat" (Myers *et al.* 2000). As seen above, there are relatively few endemic marine invertebrate species in the Arctic, based on our present state of knowledge. Therefore it is doubtful if hotspots, in terms of endemic marine invertebrates, exist at all in the Arctic. A major exception may be species within the ice realm, and particularly so the unique millennia-old ice shelves (see Michel, Chapter 14). Furthermore, there are areas in the Arctic that contain high numbers of both widespread and true Arctic species, which are very likely to undergo rapid habitat change due to climate warming. The most obvious area of this kind is the Barents Sea (including the Kara Sea) area. This area, with its distinct zoogeographical border, may be the region with the highest number of species within the Arctic (e.g. Gradinger *et al.* 2010a). Although this can partly be explained by relatively higher investigation efforts compared with other regions, the elevated richness is also seen to be due to high production and species enrichment from the Atlantic Ocean (Denisenko & Titov 2003, Cochrane *et al.* 2009, Węsławski *et al.* 2011).

Unlike the Barents Sea area, the East Siberian Sea does not show a particularly high species diversity. However, it is also the least studied of all Arctic shelves. Based on present-day knowledge, species richness is higher in the adjacent productive Chukchi Sea (Grebmeier & Barry 1991), at least for groups such as shelf macro- and megazoobenthos (Piepenburg *et al.* 2011) and bryozoans (Tab. 8.3). However, relatively high species diversity is also known on the outer shelf and slope of the Laptev Sea, investigated during recent decades (Bluhm *et al.* 2011b). Similar to the Barents Sea area, the Chukchi Sea region is enriched by species from the adjacent Pacific Ocean. The Labrador-Baffin Bay-W Greenland area, which is very much influenced by the Atlantic, also shows high species richness (Piepenburg *et al.* 2011). This leads to the conclusion that areas close to entrances of the two major gateways into the Arctic may be considered species rich because they are enriched from the large species pools in the adjacent Atlantic and Pacific Oceans. These areas correspond to the 'areas of advection' proposed by Węsławski *et al.* (2011). This means that many of these species here are not unique to the Arctic, but common further south.

Other hotspot-like areas may be polynyas, i.e. productive ice-free areas within the sea ice with rich pelagic life and strong pelagic-benthic coupling (e.g. Brandt 1995, Ambrose & Renaud 1995, see also Michel, Chapter 14). A high diversity of benthic peracarida crustaceans has been reported from such areas (Brandt 1995). It is not clear if Arctic endemics are also more speciose in such areas. Polynyas are certainly of conservation relevance because of high benthic biomass, often molluscs, supporting many bird/mammal stocks (see also Michel, Chapter 14).

## 8.3. TEMPORAL TRENDS

### 8.3.1. Observations of trends

To date only a few time series of biological parameters have been collected in the Arctic and only for a limited number of taxa and regions (e.g. Wassmann *et al.* 2011). Nonetheless, some show substantial change in both pelagic and benthic habitats, although examples are most common from the benthic realm. These changes include shifts in distribution ranges as well as levels of abundance and biomass. Most of the observed changes are near the Arctic margins rather than in the central Arctic. Some of these series did not show clear trends, while some temporal studies do show trends that can be explained by climate change, particularly by the borealization of Arctic marginal sea areas.

#### 8.3.1.1. Studies that did not show trends

Studies of macrobenthos in Onega Bay in the White Sea showed no major changes in dominant species between the 1950s and the 1990s (Solyanko *et al.* 2011a), and studies in the adjacent Gorlo Strait showed a similar result, i.e. no change in the biogeographic structure covering the period from 1920s to 2004. Also, there was no addition of North Atlantic species in the 2000s to those previously recorded in the area, leading to the conclusion that current climatic changes have not yet influenced the Gorlo Strait area (Solyanko *et al.* 2011b).

Berge *et al.* (2009) described changes in the community structure of decapods in Isfjord, Svalbard and found increases over the first half of the century for the spider crab *Hyas araneneus* and the hermit crab *Pagurus pubescens*, considered generalist species, while the specialist shrimps, *Lebbeus polaris* and *Spirontocaris spinus*, decreased in abundance. There was no change, however, in decapod species composition over the last 50 years.

Feder *et al.* (2005) studied the epibenthic fauna in the southeastern Chukchi Sea in 1976 and found that large crustaceans dominated abundance, while echinoderms, mainly composed of sea stars, dominated biomass. An investigation of the same area more than 20 years later (1998) did not show significant changes in biodiversity, while abundance and biomass had increased for the most dominant taxa such as the snow crab and the echinoderms *Ophiura sarsi* and *Stongylocentrotus droebachiensis*.

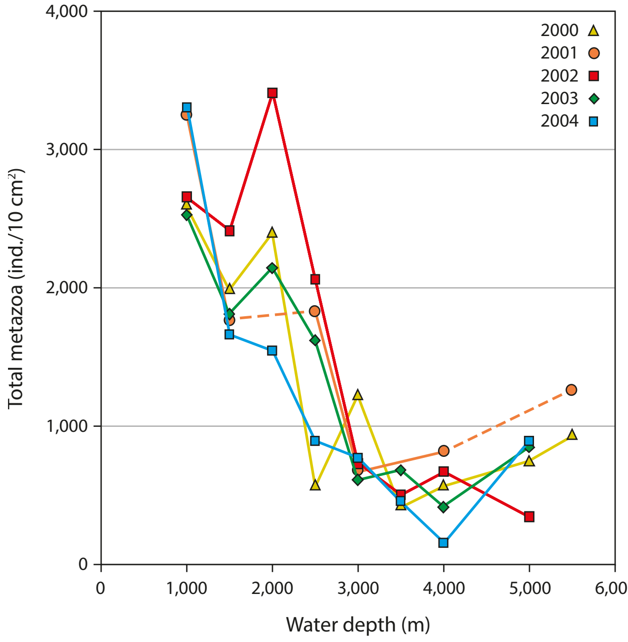

**Figure 8.10.** Metazoan meiofauna densities along the bathymetric HAUSGARTEN transect from 2000 to 2004 (redrawn from Hoste *et al.* 2007).

Renaud *et al.* (2007) reported high temporal stability of benthic community structure over decades in Van Mijenfjord, Svalbard, and the apparent absence of response to climate change was attributed to characteristics of semi-enclosed fjords counteracting the influence from the adjacent open sea.

No clear trends of change were found in abundance and composition of meiobenthos on the Yermak Plateau north of Svalbard during the ten year period 1997-2006 (Soltwedel *et al.* 2009b), or for meiofauna abundance from 2000 to 2004 in the eastern part of Fram Strait (Fig. 8.10; Hoste *et al.* 2007) .

#### 8.3.1.2. Studies showing trends where the causes may be other in addition to climate

The benthos survey in 1968-1970 (Antipova 1975) showed a large decline in total biomass almost throughout the Barents Sea compared with previous surveys in 1924-1935. A considerable alteration in the distribution of boreal and Arctic species was observed, and the decline in biomass was mainly at the expense of boreo-Arctic species. The decline in the benthos biomass was suggested to be related to climate changes (Fig. 8.11). However, intensive bottom trawling started early in the 20th century and might be the most compelling reason for biomass decline. Thus, while the distribution ranges of species could be affected by changes of water temperature, the total benthos biomass is likely mostly a consequence of disturbance caused by bottom gear (Denisenko & Titov 2003), an impact well established, for example, for the North or Irish Seas (Kaiser & Spencer 1996, Hill *et al.* 1999). While a single trawling event affects an area not exceeding several thousand square meters, the result of continuous trawling affects the entire ecosystem of the sea. Thus, small-scale impacts, repeated many times over a long period, result in changes affecting an entire marine basin (Mokievsky 2009b).

Blanchard *et al.* (2010) described temporal variability in macrobenthic communities over > 35 years (1971-2007) in an Alaskan glacial fjord on the southern border of the sub-Arctic, where they found a lack in long-term stability. Apart from a readjustment after a major earthquake in 1964, long-term climatic trends, in particular in the period 1989-2007, were seen as the major factors affecting stability of community structure.

#### 8.3.1.3. Studies showing trends likely due to climate change including borealization

Within the invertebrates, documented distribution shifts are more numerous in the benthic than pelagic realm, because benthos are easier to quantify due to their sessile habits, and the typically longer benthic life spans result in less seasonally modulated abundance and distribution that better integrate changes over longer time periods (e.g. Blacker 1957). Temporal studies are mainly available from areas close to the two major gateways into the Arctic, the Atlantic and the Pacific gateways.

**The Atlantic gateway**
In the deep Fram Strait, seafloor photographs taken at c. 2,500 m water depth in 2002 and 2004 indicated a striking decline in megafaunal densities and a decrease in trophic diversity (Bergmann *et al.* 2011). Inclusion of more recent footage from 2011, however, indicates a return to 2002 levels (M. Bergmann, unpubl. data). The rise of bottom water temperatures at HAUSGARTEN and the increased importance of Atlantic water masses in recent years could lead to severe changes in the production in the water column. The 'Atlantification' scenario, which is currently often suggested as the most likely outcome of global change in Fram Strait, may lead to retention of particles in the upper water column and less food reaching the seafloor, such that the benthic communities will be impoverished in the long run (Forest *et al.* 2010). Only continued observation will allow us to judge if the interannual changes witnessed are tied to climatic fluctuations such as the Arctic oscillation or are instead a consequence of the effects of global warming.

In the North Atlantic, a general warming of the ocean was observed in the 1920s and 1930s which resulted in a northward range expansion of several temperate fish species and benthic invertebrates, like the sea star *Asterias rubens*, the polychaete *Nereis virens* and the sea urchin *Echinus esculentus* along the coasts of Greenland and Iceland (Jensen 1939). In the Barents Sea, the warming resulted in a northward expansion of Atlantic species along the west coast of Svalbard (Drinkwater 2006). In the same area, several quantitative surveys (Denisenko 2001, Denisenko & Titov 2003) have also made it possible to evaluate the state of the benthos in the Barents Sea in specific climatic or historical periods. The benthos survey in 1924-1935 (see Zenkevitch 1963 for a review) was important as it probably represented the 'near-natural' state of that community before the increasing anthropogenic impacts on the Barents Sea, including impacts from intensive bottom trawling. The survey was made in a climatic period with temperatures close to long-term means (Fig. 8.11).

On a more local scale, decadal time series exists from several fjords. Glacial fjords are marine environments sensitive to natural and anthropogenic impacts – in particular the deep basin components with stratified salinity and restricted water exchange (e.g. Blanchard *et al.* 2010). Several studies have described temporal trends of invertebrates in such environments (Renaud *et al.* 2007, Blanchard *et al.* 2010). As reviewed by Węsławski *et al.* (2011), there are observations of different trends in macrofauna diversity in different parts of the Svalbard fjords – increasing trends of species richness at the mouth due to immigration with intruding Atlantic water and stable numbers in the inner parts, as in the Van Mijenfjord example.

Beuchel *et al.* (2006) studied the temporal variability of hard bottom macrobenthic diversity and composition on rocky banks of Kongsfjorden (Svalbard) over a period of 23 years (1980-2003). They reported a correlation between benthic diversity and the North Atlantic Oscillation (NAO) index (and related temperature of the West Svalbard Current), as well as a clear change in the composition of dominants that followed the shift of the NAO index from positive to negative mode. Similarly, in the Arctic rocky littoral zone at Svalbard, Węsławski *et al.* (2010) observed a change in diversity over 20 years with increasing temperatures. They reported a twofold increase in intertidal diversity, with an upward shift in algal occurrence on the coast. Sub-Arctic boreal species colonized new areas, while Arctic species retreated. The newcomers to the intertidal zone were present in 1988 in the subtidal zone. In the same fjord, Kedra *et al.* (2010) showed long-term changes in species composition in relation to Atlantic influence of soft sediment benthos. Most recently, a climate-driven regime shift was suggested to explain the abrupt changes in macroal-

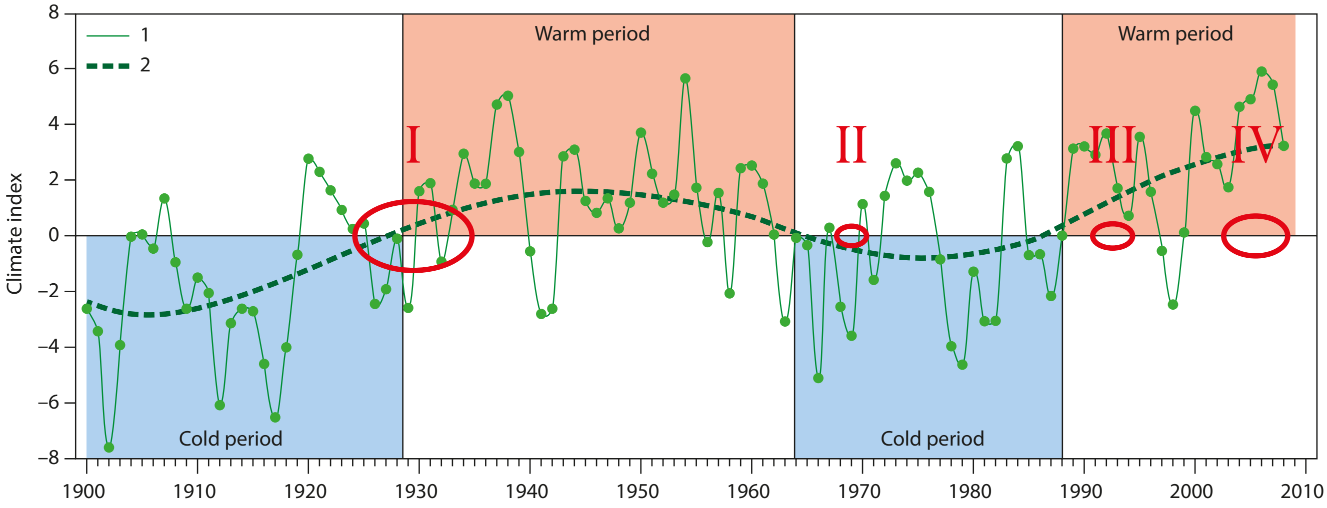

**Figure 8.11.** Interannual changes in the climatic index of the Barents Sea (1), with running mean curve (2), reflecting the cumulative variability of major indicators of climate (such as sea and air temperature and ice coverage), with warm periods marked in red and cold periods in blue). The periods of main quantitative benthos surveys are shown as red ellipses in the chart (modified from Anisimova *et al.* 2011).

gal cover in the rocky intertidal of two Svalbard fjords, one of them being Kongsfjorden (Kortsch *et al.* 2012). These changes occurred in the period 1995-2000 and had significant impacts on invertebrate abundances. The ecological processes thought to drive the observed regime shifts were suggested to be likely to promote the borealization of these Arctic marine communities in the coming years. Hence, a shift from long-lived, slow-growing Arctic benthic species to faster-growing temperate species on Svalbard reflects increasing water temperatures (e.g. Węsławski *et al.* 2010).

The main observed changes in crustacean diversity attributed to climate warming in the past decades are shifts in species distribution, with increasingly more boreal species advancing north with the West Svalbard Current and with Pacific waters into the Arctic basin (Węsławski *et al.* 2011). For the moment, this results in an increase in species count, as the species pool in lower latitudes is richer than in the Arctic. The fast shrinking multi-year pack ice cover that houses unique ice-associated species results in a diminished space for these species, which will consequently diminish their population size.

Climate change has also resulted in increased growth rates of mollusc species on the coast of NE Greenland (Sejr *et al.* 2009) and in species shifts of molluscs in Svalbard (Berge *et al.* 2005). Of five species of bivalves found in deposits of the Holocene Thermal Optimum in Svalbard and subsequently went extinct, the blue mussel *Mytilus edulis* was again recorded here in 2004 (Berge *et al.* 2005). This change agrees with Salvigsen *et al.* (1992), who predicted that in the course of climate warming, the populations dwelling at lower latitudes will recolonize theArctic coasts. The settlement of *Mytilus edulis*, which occurred in the outer part of the Isfjord, was possibly due to the elevated water temperatures and unusually high Atlantic water transport from the West Svalbard Current in 2002 (Berge *et al.* 2005).

**The Pacific gateway**

In the Bering and Chukchi Seas, data spanning several decades indicate that ocean warming has induced a shift in the species dominating biomass (Grebmeier 2012). Similarly, there have been northern range extensions in some epifaunal crabs, chitons and bivalves in the Chukchi Sea (Sirenko & Gagaev 2007). The change in distribution of female snow crab to the north in the Bering Sea (Orensantz *et al.* 2004) and a probable increase of that species in the Chukchi Sea (Bluhm *et al.* 2009) may also be related to climate change. However, observed trends in terms of benthic invertebrate biomass are not coherent and include (1) decreasing infaunal and/or amphipod biomass in the northern Bering Sea (Moore *et al.* 2003, Dunton *et al.* 2005, Grebmeier *et al.* 2006, Coyle *et al.* 2007), and (2) increased epifaunal biomass in the northern Bering and southern Chukchi Seas (Feder *et al.* 2005, Hamazaki *et al.* 2005, Bluhm *et al.* 2009). The example of biomass decrease could perhaps be interpreted in support of the prediction that the current benthos-favoring pelagic-benthic coupling will shift toward a pelagic-dominated system (e.g. Carroll & Carroll 2003, Grebmeier *et al.* 2006; see also Michel, Chapter 14). On a regional scale, biomass changes could also result from spatial community-wide shifts, specifically a northward displacement as documented in the Bering Sea (Mueter & Litzow 2008).

While changes in the ranges of species distribution appear primarily tied to water temperatures, changes in biomass, other than those related to harvests, result from a combination of shifts in energy flow or benthic-pelagic coupling and environmental conditions. For example, the increase in biomass of jellyfish in the Bering Sea throughout the 1990s was followed by a biomass collapse in 2000, with subsequent stabilization (Brodeur *et al.* 2008). These dynamics were linked to a number of factors, including ice cover, wind mixing, and sea surface temperatures, as well as prey availability, specifically juvenile Alaska pollock *Gadus chalcogrammus* and zooplankton.

## 8.3.2. Predictions

Like other organisms in the Arctic, marine invertebrates are likely affected by climate warming, and as described above some effects are already documented from the margins of the Arctic Ocean. However, major effects of warming are anticipated on the sympagic fauna which will lose its habitat as the ice disappears. We do not, however, expect major reductions of invertebrate species diversity due to global warming as large shelf areas in the Arctic Ocean area are already populated by species with more southerly origin, and because there are few endemic Arctic species. On the contrary, the Arctic faunal component with strong boreal influence may show increased diversity due to immigration of species adapted to warmer waters (e.g. Węsławski *et al.* 2011). From a long-term perspective there is concern that, due to the retreat of ice cover, we will see a new Pacific-Atlantic trans-Arctic interchange of species, as probably occurred 3.5 million years ago in the warm Pliocene period (Vermeij 1989). Vermeij & Roopnarine (2008) have made such predictions for present-day Arctic molluscs.

As a consequence of increased temperatures and increased advection, Węsławski *et al.* (2011) predicted a northward spreading of boreal species through the gateways to the Pacific and the Atlantic, thereby increasing diversity in the 'advective areas' on the Arctic side of the gateways.

Little is known about the time scale over which the immigration of species into the Arctic Ocean has taken place. Some immigration certainly took place immediately after termination of glaciation, but it is most likely that immigration, and local extinction inside the Arctic, is an ongoing process. In fact, the proportions of recently immigrated species from the Atlantic and Pacific at least qualitatively mirrors the current differences in water flows from the two oceans, with Atlantic flow many times that of flow from the Pacific (ACIA 2005). This indicates that, today, the potential for import of propagules to the Arctic would be far greater from the Atlantic than from the Pacific.

Furthermore, according to some authors (e.g. Denisenko 2007, Cochrane *et al.* 2009), due to less ice cover, production will increase in these areas, such as the Barents Sea, and consequently have the potential to support higher diversity. However, in other areas such as the Beaufort Sea, ice retreat will occur from shallow to deep sea areas and less production will reach the benthos there.

Whether increased production will result in increased species richness will depend on the productivity level in the hump-shaped relationship between productivity and richness (Witman *et al.* 2008). Some work has described increased benthic richness in productive areas (Brandt 1995 in a polynya, Carroll *et al.* 2008 under a polar front). There are, however, few studies supporting that such changes have taken place.

The temporal changes are multi-scale and include processes with different characteristic time scales from decades to thousands of years. Short-term fluctuations mostly affect species distribution ranges and abundances, while long-time changes are responsible for significant recombination in faunal composition. The time scale should be taken into account in any attempt to forecast future changes in Arctic biota.

Consequently, an important question is the extent to which the invasions of boreal and otherwise widespread species into the Arctic have affected native diversity. This is difficult to assess at this point, but species with Arctic and other origins to some extent do co-exist in the same local areas. Nevertheless, there is concern that human-induced invasions of alien species, such as the introduction of red king-crab in the Barents Sea (Sokolov & Miljutin 2008), could alter the composition of bottom communities (Frolova *et al.* 2003, Rzhavsky *et al.* 2004, Oug *et al.* 2011). The impact by the red king-crab would then be an impoverishment of the native fauna, because it consumes a wide spectrum of prey (Oug *et al.* 2011).

Another threat following climate change is the acidification of the sea with detrimental effects on species with calcareous skeletons or shells like molluscs. Comeau *et al.* (2012) predicted that, with the acidification expected in Arctic waters, populations of a key Arctic pelagic mollusc – the pteropod *Limacina helicina* – could be severely threatened due to hampering of the calcification processes (see also Michel, Chapter 14).

Thus, several studies refer to temperature rise resulting from climate change as the most important factor contributing to changes in biodiversity. However, change in temperature is not the only factor directly affecting marine invertebrate diversity in the Arctic Ocean. Different types of human activities, made increasingly possible by retreat in ice cover as consequence of climate change, have potentially important consequences for Arctic biodiversity. Some of them are not specific to the Arctic but are common for every type of marine systems of any latitude (Mokievsky 2009a). These activities include trawling of the bottom of the ice-free sea, other types of sediment disturbance such as from pipeline construction, dumping, development of port infrastructure, as well as pollution from various sources such as increased shipping and offshore oil and gas drilling. All of these could seriously affect Arctic invertebrate diversity at different geographic scales.

## 8.4. CONCLUSIONS AND RECOMMENDATIONS

### 8.4.1. Conclusions

The Arctic Ocean area hosts c. 5,000 species of marine invertebrates, which is a similar level as is found in the other polar environment, Antarctica, and is considered intermediate on a global scale. Arthropoda, mainly crustaceans, is the most speciose group and does not exhibit the decreasing richness with increasing latitude as found in Mollusca.

Although the Arctic contains great morphological heterogeneity and a vast number of environmental gradients, giving the opportunity for extensive niche adaptation, Arctic diversity seems largely a result of extinctions and dispersal events over the last c. 4 million years. Most species have origins from outside the Arctic, and overall there are few species endemic to the Arctic. The degree of endemism varies greatly among different taxonomic groups, where bryozoans for example seem to have a relatively high degree of endemism possibly partly due to their sessile habits and, maybe more importantly, poor dispersal ability.

The glaciation history of the two polar oceans seems fairly similar, but unlike the Antarctic which has a long history of geographic isolation, the Arctic has been, and is, open towards the two major oceans, the Pacific and the Atlantic, although the strength of the connections have varied over the last c. 4 million years. This is a likely explanation for the very low degree of endemism in the Arctic compared with the Antarctic. Today's biogeographic drivers of Arctic diversity are clearly seen in the distributions of origins in relation to the two major gateways into the Arctic, i.e. from the Atlantic and Pacific Oceans, respectively. On the continental shelves, the proportions of present-day Pacific and Atlantic species decrease with increasing distance from the Bering Strait and the NE Atlantic, respectively. Current inventories indicate that the Barents Sea has the highest species richness, being 'enriched' by boreal and sub-Arctic species. Today's Arctic deep-sea floor is most closely related to the present North Atlantic fauna, which in a geological time perspective contains a strong Pacific influence. The regional species richness is highest in Arctic regions close to the two gateways, the Chukchi

Sea for the Pacific and, even higher, the Barents Sea/Kara Sea for the Atlantic. These observations together with the distribution patterns of zoogeographical affinities indicate the importance of dispersal through the gateways into the Arctic Ocean.

While areas within the Arctic with high species richness have been identified, such as the Barents Sea, it is uncertain if there are real 'hotspots' of diversity, i.e. areas with high diversity of unique or endemic species in the Arctic. This is because many of these species may be abundant in waters to the south and thus not unique. The polynyas, ice-free areas within the area of sea ice, may be hotspots in terms of energy flow (Michel, Chapter 14), where benthic and pelagic invertebrates provide food for dense aggregations of birds and mammals.

There are already clear signs of global warming effects on invertebrates, for instance northward expansion of several boreal species. As would be predicted, this borealization has so far occurred in the margins of the Arctic Ocean, primarily at the two major gateways to the boreal parts of the Atlantic and Pacific. The rapidly melting sea ice means loss of habitat for sympagic fauna.

In addition to temperature rise, global change will acidify the oceans, and there is a great concern that this will negatively affect calciferous invertebrates like several benthic as well as pelagic molluscs. Experimental work shows that acidification hampers shell formation in wing snails.

## 8.4.2. Recommendations

It is recommended that conservation measures are targeted towards whole systems rather than individual species. Specifically, there are urgent needs to document and understand Arctic biodiversity patterns and processes to be able to prioritize conservation efforts.

**We need more inventories**

- This includes the need to know where the highest diversity occurs in the Arctic, particularly for endemic species, in order to conserve as many unique species as possible. Hence, there is a need for:
- Detailed surveys of diversity in hitherto understudied areas like the East Siberian Sea and the Canadian Arctic, together with deep-sea areas of the Central Arctic Basin and at the Arctic-Atlantic frontier. Studies are also needed in the shallow subtidal to 12 meters, which still is an understudied area.
- Increased sampling and taxonomic effort on poorly investigated groups, including several among the meiofauna.
- Establishing and continuing several observation sites for long-term monitoring of marine ecosystems in different parts of the Arctic proper to obtain a more holistic view of the changing Arctic. The existing biological stations together with marine protected areas could serve as a base for such long-term observations.
- A priority focus on consistent time series monitoring at sites in the species-rich Arctic areas close to the major gateways, as well as in some areas distant from the gateways. Given the likelihood of little time before more severe climate change effects will be manifested, this entails both the establishment of some new sites and the continuation of monitoring at existing sites such as the White Sea Biological Station, the Greenland Ecosystem Monitoring in Godthåbsfjorden in W Greenland and Young Sund in NE Greenland, and the HAUSGARTEN observatory west of Svalbard. The number of observatories in both deep and shallow waters has to be increased to include a wide spectrum of testing areas and communities. Repeated sampling should be conducted in the places of former studies, like those of Golikov (1990, 1994a, 1994b, 1994c) in the Laptev and West Siberian Seas. These studies provide a sufficient background to evaluate any changes in recent community structure and composition.

**We need research to understand maintenance of diversity so it is recommended:**

- To quantify immigration rates of boreal species into the Arctic and investigate the possible influence of global warming on these rates.
- To investigate whether or not immigration of boreal species 'enriches' native diversity, and whether immigrants have a negative influence on the native fauna.
- To further implement molecular taxonomy to discover the likely presence of sibling species and to reveal historical migration patterns. The most optimistic estimates predict a diversity of 'molecular operational taxonomic units' as much as three times the number of described morphological species, even in such well studied groups as the Polychaeta (Carr *et al*. 2011).
- To investigate how increased primary production, which may be one consequence of shrinking ice cover, affects species diversity both in the pelagic and the benthic systems. This could be performed in connection with polar fronts and productive polynyas.
- To investigate how climate change influences changes in biogeographic distributions, specifically the borealization process, habitat loss for sympagic fauna and the distribution of calciferous fauna.

**Based on present knowledge we recommend protection of the following areas:**

- Polynyas which are areas known to be important for maintaining seabird and mammal populations. These areas should be closed for fishing as well as petroleum extraction. The latter is necessary because it is virtually impossible to clean up oil in waters with broken ice.
- Large estuaries, which harbor several of the unique Arctic species.

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Purple saxifrage *Saxifraga oppositifolia* is a very common plant in poorly vegetated areas all over the high Arctic. It even grows on Kaffeklubben Island in N Greenland, at 83°40′ N, the most northerly plant locality in the world. It is one of the first plants to flower in spring and serves as the territorial flower of Nunavut in Canada. Zackenberg 2003. Photo: Erik Thomsen.

*Chapter 9*

# Plants

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## Contents

> » **Willows grow much faster now on the banks of Kolyma. As well in the summer pasture areas along the Arctic Ocean tundra willows are more plentiful and more now. On River Suharnaya the willow bushes are much bigger.**
>
> Reindeer herders of the Chukchi community of Nutendli, northeastern Sakha-Yakutia, Siberia; Mustonen 2007.

## SUMMARY

Based on published scientific literature, the diversity of plants in the Arctic is reviewed. The plants are divided into three main groups according to essential differences in anatomy, morphology and reproduction. These are vascular plants, bryophytes (mosses and liverworts) and algae (micro- and macroalgae). As a whole, these three plant groups have the ability to perform photosynthesis. As primary producers they play a key role in the environment, since photosynthesis provides resources for all other organisms. Vascular plants and bryophytes (together with the lichenized fungi, the lichens) are the main structural components of terrestrial vegetation and ecosystems, while algae are more abundant in fresh water and marine ecosystems.

Our knowledge of the taxonomic diversity of these three main groups is very uneven. Although serious knowledge gaps still exist, our understanding of vascular plant diversity in the Arctic was recently improved considerably by the publication of the *Annotated Checklist of the Panarctic Flora (PAF) Vascular plants* (Elven 2011), a result of many years of laborious research by taxonomists associated with the Panarctic Flora Project. The Arctic bryoflora is relatively well known, but a circumpolar Arctic checklist of mosses and liverworts has not yet been finalized. Knowledge of the circumpolar Arctic taxonomic diversity of algae is still rather fragmentary. Preliminary biodiversity assessments have been made for Arctic marine algae, but there has been no attempt yet to synthesize knowledge of the diversity of Arctic freshwater algae. Knowledge of the biodiversity of terrestrial algae in the Arctic is also very fragmentary.

The main difficulties in assessing biological diversity at subgeneric levels are the dissimilarities that exist in the taxonomic species concept and classification between the Arctic countries. Moreover, current species concepts from traditional morphological assessments are challenged by the latest molecular phylogenetic analyses, which sometimes conflict with traditional classification.

The vascular plant flora of the Arctic is relatively poor. Approximately 2,218 vascular plant species (including subspecies, apomictic aggregates and some collective species) are recognized. This is less than 1% of the known vascular plant species in the world (c. 0.85% based on an estimated total of 260,000 species; Raven *et al.* 2005). Arctic vascular plants belong to 430 genera and 91 families, almost all within the flowering plants (angiosperms). Gymnosperms are rare and species diversity per genus and family is low. Species-rich families with more than 100 species include Asteraceae (composite family), Poaceae (grass family), Cyperaceae (sedge family), Brassicaceae (mustard family), Rosaceae (rose family), Fabaceae (pea family), Ranunculaceae (buttercup family) and Caryophyllaceae (pink family). The genera *Carex* (sedge), *Salix* (willow), *Oxytropis* (oxytrope) and *Potentilla* (cinquefoil) are well represented, with each having more than 50 species. The majority of the Arctic species have a circumpolar distribution.

The Arctic territory is divided into 21 floristic provinces and five subzones. These strongly differ in species richness and composition. There is a pronounced increase in species numbers from the northernmost high Arctic subzone A (102 species) to the southernmost low Arctic subzone E (2,180 species). A comparison of species numbers per floristic province showed a range from approximately 200 species for the rather heavily glaciated and northern floristic province Ellesmere Land-N Greenland to more than 800 species for Beringian W Alaska.

Polyploidy[1] (allopolyploidy) levels are high in Arctic plants. Endemism is well developed. One hundred six species (and subspecies), or c. 5% of the Arctic vascular plant flora, are endemic to the Arctic. The genera *Papaver* (poppy), *Puccinellia* (salt marsh-grass, goose grass), *Oxytropis*, *Potentilla* and *Draba* (draba, whitlow-grass) are particularly rich in endemic species, and almost all endemic species are forbs and grasses, whereas there are no endemic woody species. Though the absolute number of Arctic endemic species increases from north to south, i.e. from the high Arctic to the low Arctic, the relative percentage of endemic species decreases.

The floras of the northern floristic provinces Ellesmere Land-N Greenland, Svalbard-Franz Joseph Land and Wrangel Island are relatively rich in Arctic endemic species. Ten Arctic endemic species are restricted to Wrangel Island and underline the hotspot character of this high Arctic island. Twenty Arctic endemic species are very rare, and as such are possibly threatened.

Borderline species are primarily non-Arctic species just reaching the southernmost extent of the Arctic (subzone E). Taxonomically this is a rather diverse group of 136 vascular plant species in 91 genera and 45 families.

Non-native species that occur as persisting stabilized introductions in the Arctic account for 5% of the flora (101 species). In addition there are 89 species native to the Arctic that also occur as stabilized introductions in other parts of the Arctic. In addition, more than 205 non-native species have been recorded in the Arctic only as casual introductions that do not persist. Non-native species mainly occur in and around settlements and towns, in particular in climatologically favorable parts of the Euro-Siberian Arctic.

No single, predominantly Arctic vascular plant species is known to have gone extinct due to human activities in the last 250 years. There are no species in the Arctic that are considered to be seriously invasive, but some are at risk of becoming so with increasing human traffic combined with climate change. The Arctic flora

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[1] Polyploidy: variations in chromosome number involving more than the diploid number of complete chromosome sets; allopolyploidy: polyploidy resulting from hybridization of species in which there was no effective pairing of the different sets of chromosomes preceding spontaneous doubling of the chromosome number.

is considered taxonomically, ecologically, biologically and genetically a coherent and distinctive complex of young and dynamic species that occupy a vast natural area characterized by a cold climate. The present Arctic vegetation shows climate change related changes such as greening, shrub expansion and floristical changes.

Local plants always played an essential role in the lives and cultures of Arctic indigenous peoples. The most useful plants have indigenous names, including not only vascular plants, but bryophytes and algae as well.

There are an estimated 900 species of Arctic bryophytes (mosses and liverworts). Distributional types are similar to those observed for vascular plants. Arctic endemism is known among bryophyte species, whereas many widely distributed species in the Arctic show considerable morphological plasticity representing subspecies, variants or forms. The bryoflora is in general rather uniform. Almost 80% of the species have a circumboreal distribution. In rather stable, moist to wet sites, bryophytes contribute substantially to vegetation biomass, and they contribute significantly to species richness of many vegetation types in other habitats. Very few vegetation types in the Arctic occur without bryophytes, and single shoots occur almost everywhere, in particular in the high Arctic. The ecosystem function of bryophytes is poorly studied, and the bryofloras of several Arctic regions are still incompletely known. The most species-rich families include Bryaceae (threadmoss family), Dicranaceae (forkmoss family), Amblystegiaceae (feathermoss family), Pottiaceae (tuftmoss family), Grimmiaceae (grimmia family), Sphagnaceae (bogmoss family), Hypnaceae (feathermoss family), Mniaceae (thyme-moss family), Brachytheciaceae (feathermoss family), Polytrichaceae (haircap family) and Splachnaceae (dung moss family), which collectively account for 70% of the total moss flora. *Bryum* (bryum moss), *Sphagnum* (bogmoss, peatmoss), *Pohlia* (nodding moss) and *Dicranum* (forkmoss) are among the most species-rich genera. Species-rich liverwort families include the leafy liverworts Scapaniaceae (earwort family), Jungermanniaceae (flapwort family), Gymnomitriaceae (frostwort family), Cephaloziaceae (pincerwort family) and Cephaloziellaceae (threadwort family), whereas *Scapania* (earthwort) and *Lophozia* (notchwort) are prominent genera. The use of bryophytes by indigenous peoples is very limited. There are no known threatened bryophyte species.

Algae are ubiquitous, ecologically important and constitute the first layer of marine and freshwater food webs. They occur either free floating in the upper water column (pelagic), associated with sea ice (sympagic), or attached to bottom substrates (benthic). Phaeophyta (brown algae) range in size from less than 2 µm to more than 100 m long in giant kelps. Pelagic algae, known as phytoplankton, and sea ice algae are autotrophic, single-celled eukaryotes ranging in size from 0.2 to 200 µm. Benthic algae mainly refer to marine macroalgae characteristic of coastal regions, but also include microalgae attached to various substrates along the seashore. Algae, including the autotrophic prokaryote cyanobacteria (blue-green algae), are classified into different groups or phyla, depending on the classification system used.

The following groups have been recognized in this review: (1) Archaeplastida, including Chlorophyta (green algae), Streptophyta, Glaucophyta, Rhodophyta (red algae), (2) Chromalveolata, with Cryptophyta, Haptophyta, Dinophyta, Stramenopiles (including Dictyochophyceae, Eustigmatophyceae, Pelagophyceae, Bacillariophyta (diatoms), Phaeophyceae (brown algae), Xanthophyceae, Chrysophyceae (yellow-green algae), Rhaphidophyceae), (3) Excavata (Euglenophyta), (4) Opisthokonta (Choanoflagellida), (5) Rhizaria (Chlorarachniophyta) and (6) Cyanophyceae (blue-green algae).

There is a conservative estimate of 4,000 algal species reported from the circumpolar Arctic, including both freshwater and marine habitats. The species diversity of microalgae and cyanobacteria for the Arctic is still largely unknown, especially in terrestrial and freshwater environments, but it is assumed to be much lower than in warmer regions of comparable size. In Arctic regions, marine diatoms are very diverse and abundant in annual sea ice, pelagic waters and benthic environments. Recent molecular studies reported a high diversity in the smallest-sized fraction of the phytoplankton in polar regions, frequently contributing to more than 50% of total phytoplankton biomass and production. In the western Canadian Arctic alone, 10,000 species of single-celled phytoplankton species were documented through molecular analyses, at least half of which are likely autotrophic. There are c. 200-215 seaweed (macroalgae) taxa in the Arctic, with endemism poorly developed. A major challenge facing biodiversity assessments will be matching morphology of a single-celled alga to a given gene sequence, which will require development of better sampling strategies and culture techniques for these small-sized microalgae.

## 9.1. INTRODUCTION

This plant chapter deals with the taxonomical biodiversity of organisms that are able to perform photosynthesis. They use light energy for conversion of carbon dioxide and water into chemical energy in the form of sugar and other organic substances under release of oxygen. Most of them are autotrophic, using carbon dioxide as their carbon source.

They include three main groups based on differences in anatomy, morphology, physiology and reproduction, and phylogenetic relationships.

The kingdom Plantae of the eukaryotic life domain comprises the green land plants. These are the vascular plants – Tracheophyta (Section 9.2) and the bryophytes – Bryophyta (Section 9.3). The vascular plants are subdivided into spore-producing plants (clubmosses – Lycopodiophyta and ferns – Pteridophyta) and seed-producing plants (Gymnospermae with uncovered seeds, Angiospermae with covered seeds). The bryophytes are divided into the hornworts (Anthocerophyta), liverworts (Hepatophyta) and mosses *sensu stricto* (Bryophyta) (Raven *et al.* 2005).

The autotrophic algae (Section 9.4) of the kingdom Protista comprise eukaryotic organisms which cannot be attributed to the kingdoms Fungi, Plantae or Animalia. The green algae (Chlorophyta) are ancestral to the algal Streptophyta and hence to the kingdom Plantae, the bryophytes – Bryophyta and vascular plants – Tracheophyta. Some other algae are both autotrophic and heterotrophic (Poulin *et al.* 2011).

The blue-green algae belong to the prokaryotic life domain Bacteria and are classified as Cyanobacteria (Raven *et al.* 2005).

As primary producers, all groups play a key role in the environment, since photosynthesis provides resources for all other organisms. Vascular plants and bryophytes (together with the lichenized fungi, the lichens; see Dahlberg & Bültmann, Chapter 10) are the main structural components of terrestrial vegetation and ecosystems, while algae are more abundant in freshwater and marine ecosystems.

The state of knowledge of Arctic vascular plants, bryophytes, and algae differs among countries, regions, and floristic provinces, and there remain many differences in taxonomic opinions among botanists on different continents. The data presented here should be viewed as a preliminary assessment.

Scientific names are used throughout the manuscript since there are no standardized common or vernacular names for plants, and many species (e.g. algae) lack common names altogether. For taxa with common names, these are provided in parentheses following the scientific names the first time a taxon is mentioned. These names are derived from several sources (among others Clapham *et al.* 1962, Böcher *et al.* 1968, Hultén 1968, Porsild & Cody 1980, Rønning 1996, Smith 2004 and Edwards 2012).

The total land surface of the Arctic is estimated at 7.11 million km$^2$, with an estimated 5 million km$^2$ covered by vegetation; the remainder is ice-covered (Walker *et al.* 2005). The Arctic territory has been and still is sparsely populated. While there was almost no impact by human populations on Arctic flora and vegetation prior to the 1960s, human impacts now pose an increasing threat in certain areas. Nevertheless, these impacts are minor compared with human impacts in the adjacent boreal zone.

## 9.2. VASCULAR PLANTS

The assessment presented here is largely based on the *Checklist of Panarctic Flora (PAF) Vascular Plants* compiled and edited by Reidar Elven and colleagues, who provided the first checklist and taxonomic assessment of all Arctic vascular plant species. The draft version from May 2007 was made available to us in March 2009 and is cited here as Elven (2007) and PAF. It is basically congruent with the more recent (and slightly updated) on-line version, the *Annotated Checklist of the Panarctic Flora (PAF) Vascular Plants* (Elven 2011). This first checklist covering all Arctic vascular plants is a working list that will continue to undergo modifications as new knowledge about species accumulates and taxonomic problems are resolved.

### 9.2.1. Taxonomic categories and species groups

The present assessment of Arctic vascular plant biodiversity uses the definitions of the Arctic area and the taxonomic concept presented in the PAF (Elven 2007). It includes 2,218 recognized species and subspecies, as well as several 'apomictic aggregates' (used for *Taraxacum,* dandelion and *Hieracium,* hawkweed) and a few 'collective' species (for convenience these will all be referred to as species here) (Appendix 9.1). In addition, some hybridogenous taxa that are reproductively isolated from their parents mostly by ploidy level are treated as species. More than 600 named entities (at the species level or below) are not accepted as distinct entities in the PAF, thus they are not considered here. The assessment of Arctic vascular plant diversity presented here should be regarded as preliminary; it is based largely on the PAF table of species distribution and frequency of occurrence within floristic provinces and subzones. The exact number of vascular plant species in the Arctic has not been settled mostly due to the difficulty of determining species boundaries in taxa that frequently hybridize and/or are primarily clonal, but also due to lack of knowledge and taxonomic expertise for some groups and due to the occurrence of cryptic species.

All species considered in this chapter occur somewhere in the Arctic territory – the definition used here approximates but is not completely congruent with its delineation on the Circumpolar Arctic Vegetation Map (CAVM) (compare Fig. 9.1 and 9.2; see also Section 2 in Meltofte *et al.*, Chapter 1). They are classified as native or non-native (Elven 2007). Native species include all those that are naturally established in areas within the Arctic. Native species include Arctic endemics which are restricted in their distribution to areas within the Arctic territory (floristic provinces and subzones A-E of the PAF), species that also occur outside the Arctic (typically Arctic-alpine species, which are also found in alpine areas of the neighboring non-Arctic regions to the south, subzone N of the PAF, which is defined as boreal and/or boreal-alpine), and 'borderline species' (mainly non-Arctic species just reaching the southernmost extent of the Arctic in subzone E). We also include non-native species with stabilized populations within the Arctic territory. Most of these species reached the Arctic as a result of human activities after approximately 1700 A.D.

We follow the taxonomic nomenclature as provided in the PAF. Numbers and calculations are based on all accepted 2,218 species. For our calculations of species richness for Arctic floristic provinces and subzones we do not include species with uncertain occurrence, which are indicated with "?" in these areas in the PAF. While the PAF made a concerted effort to reconcile the different taxonomic concepts across the Arctic, there remain some regional differences. How well a flora is known also varies among Arctic regions. Both problems likely affect the statistics presented here, in particular comparisons of species diversity across floristic provinces.

### 9.2.2. The Arctic territory and its subdivision

The delineation of the Arctic has been interpreted differently by various authors (Yurtsev 1994, Elvebakk *et al.* 1999, Nordal & Razzhivin 1999, CAVM Team 2003, Walker *et al.* 2005 and PAF). We follow the PAF delineation, which is largely derived from the Circumpolar Vegetation Map (CAVM Team 2003 and Walker *et al.* 2005). In areas with continental climate, the Arctic is considered to be the area north of treeline, just as in the CAVM. However, areas with extra-zonal occurrences of small pockets of trees in places with a distinct winter frost climate and mean July temperature above 10°C, such as small areas in the inland of S Greenland, are also included in the PAF. On the CAVM, this small area in S Greenland is excluded from the Arctic. Further, many areas with an oceanic climate in the North Pacific and North Atlantic are lacking trees, but have higher mean July temperatures and a less pronounced winter frost period. They are excluded from the Arctic in the CAVM, as are the vegetation belts of mountains in the neighboring boreal zone to the south. Thus we follow here the concept of including all of Greenland as belonging to the Arctic as proposed in PAF, and excluding those treeless areas in the North Pacific and North Atlantic regions that are included in the non-Arctic boreal zone.

The Arctic territory is roughly subdivided along two main axes in latitudinal subzones (Fig. 9.1) and longitudinal floristic provinces (Fig. 9.2). The latitudinal north-south axis mainly reflects the present climate gradient divided into five different subzones, which are separated according to climate and vegetation in the lowlands of each zone.

There is not consensus regarding a uniform nomenclature of the subzones, and in the following assessment we use the letters: A, B and C (for the high Arctic) and D and E (for the low Arctic) (CAVM Team 2003, Walker *et al.* 2005). However, subzone A might be appropriately named the Arctic herb subzone; B, the northern Arctic dwarf shrub subzone; C, the middle Arctic dwarf shrub subzone; D, the southern Arctic dwarf shrub subzone and E, the Arctic shrub subzone (Daniëls *et al.* 2000, CAVM Team 2003, Walker *et al.* 2005). The latitudinal extent of the subzones corresponds approximately with altitudinal vegetation belts in the

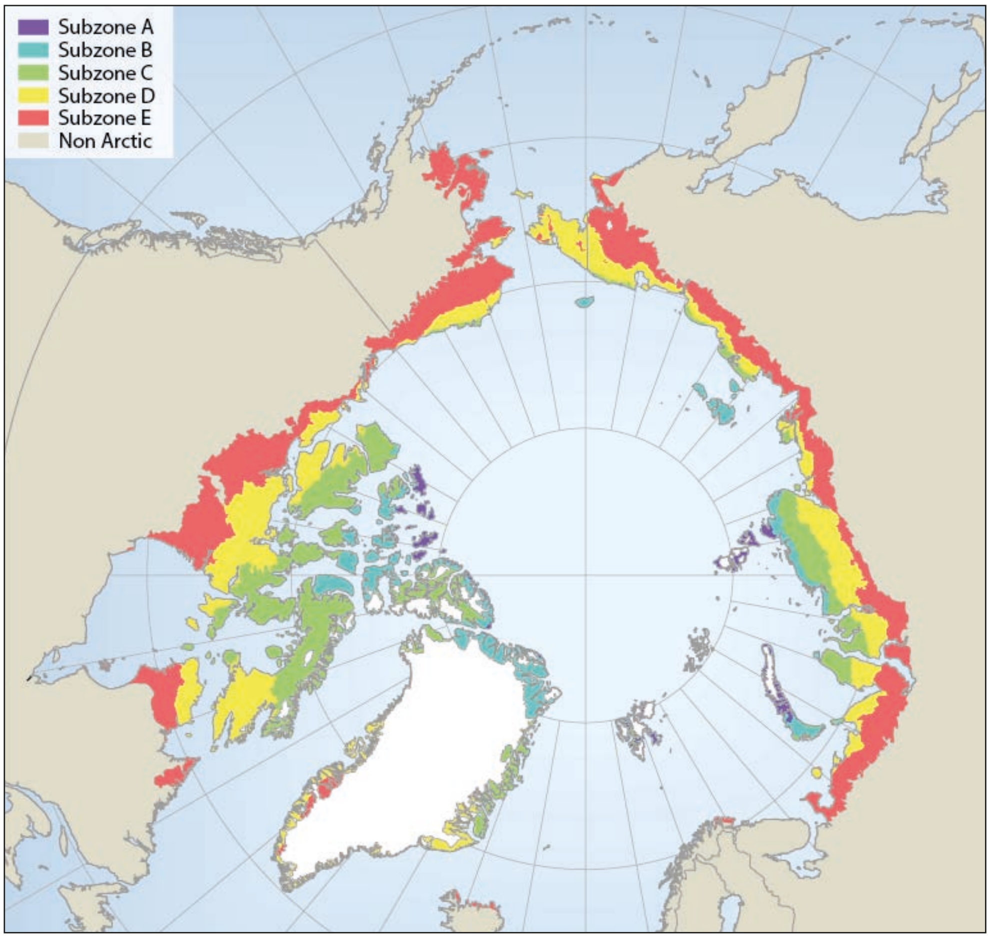


**Figure 9.1.** Bioclimatic subzones of the Arctic territory according to the Circumpolar Arctic Vegetation Map (CAVM Team 2003, Walker *et al.* 2005).

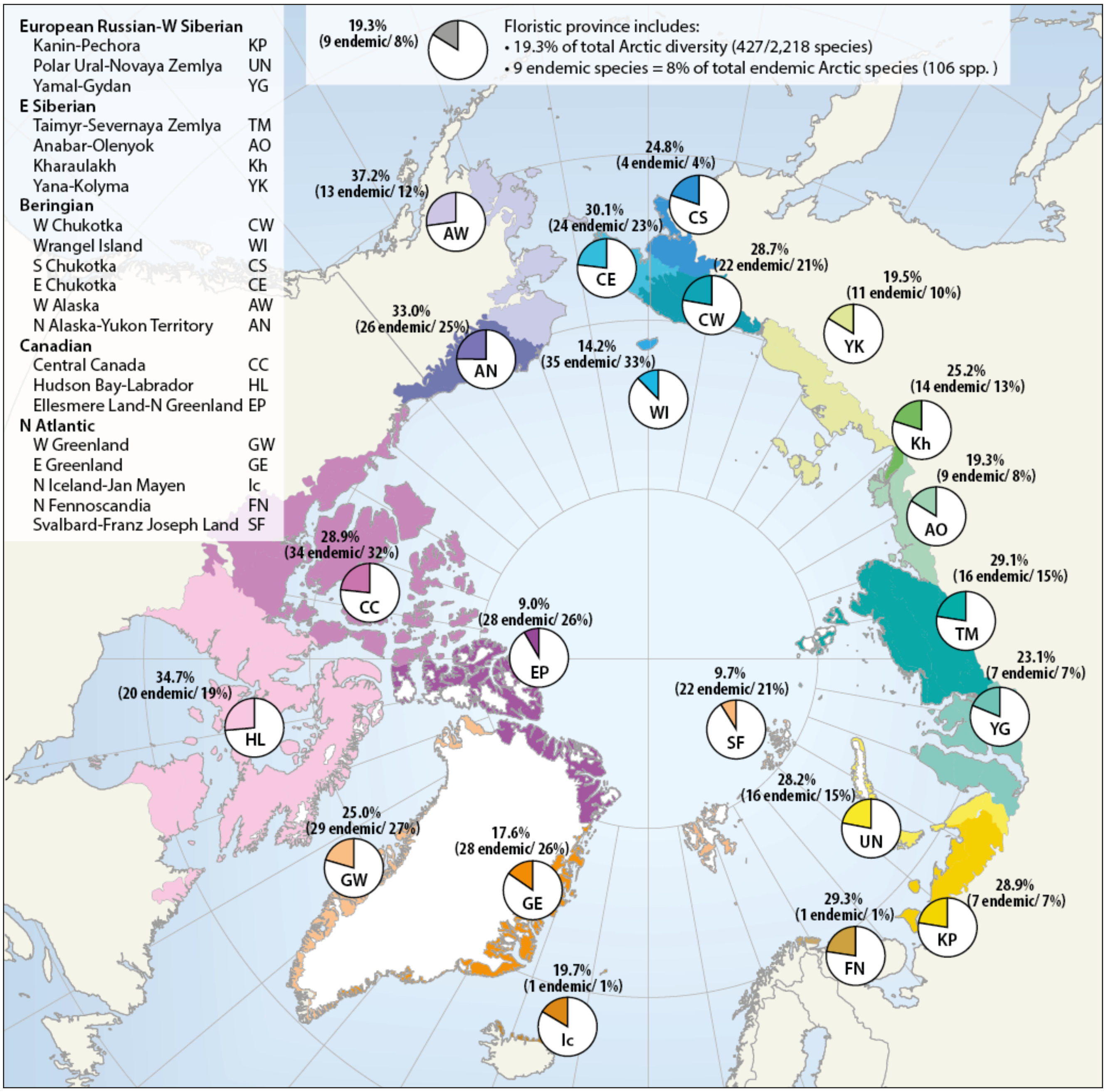


**Figure 9.2.** Map of species richness and endemicity of Arctic vascular plant floras in floristic provinces of the Arctic. Species richness of the floristic provinces is expressed as percentage of the total species richness of the Arctic (2,218 species), and species endemicity of the floristic provinces as rounded off percentage of the total number of Arctic endemic species (106). Floristic provinces and subzones according to Elven (2007).

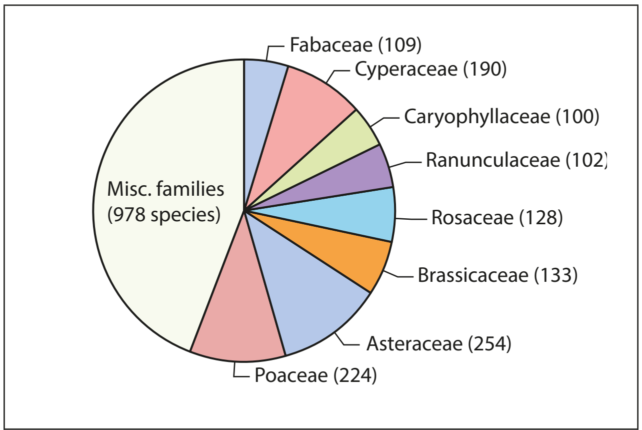
Arctic mountains. Accordingly, the lower mountain belt (named d) in subzone E corresponds with subzone D, the middle belt (named c) with subzone C, the upper belt (b) with subzone B, and the highest belt (a) with subzone A (Walker *et al.* 2005, Sieg *et al.* 2006).

The longitudinal east-west axis reflects different conditions in the past such as different plant chorological histories (i.e. history of spatial distributions) related to glaciations, land bridges and north-south-trending mountain ranges, resulting in the delineation of 21 floristic provinces (Fig. 9.2; Yurtsev 1994, PAF, see also CAVM Team 2003 and Walker *et al.* 2005).

### 9.2.3. The flora of the Arctic

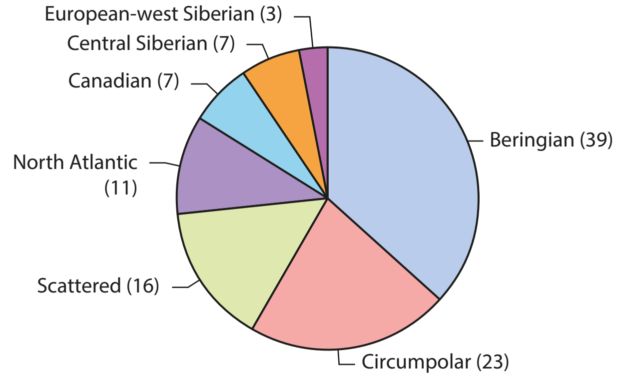
The vascular plant flora of the Arctic is relatively poor in species (see Fig. 1.1 in Meltofte *et al.*, Chapter 1). Our review suggests that 2,218 species occur in one or more subzones and floristic provinces of the entire Arctic territory. This is less than 1% of the estimated number of all vascular plant species of the world (Chapman 2009). The mean diversity of Arctic vascular plant flora is estimated to be 100-200 species per 10,000 km$^2$ (Barthlott *et al.* 1996).

**Figure 9.3.** Characteristics of the Arctic vascular plant flora.

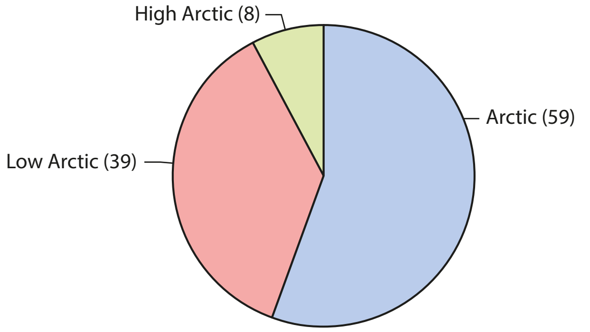


- Low diversity, species number less than 1% of the world flora
- 91 families, 430 genera, 2,218 species
- Few gymnosperms, angiosperms represent 96% of the flora
- Low species diversity per family, with 8 species-rich families accounting for > 50% of the flora (see above)
- Low species diversity per genus, with most species-rich genera *Carex* (152), *Salix* (72), *Oxytropis* (58), *Potentilla* (50), *Draba* (41), *Ranunculus* (40), *Papaver* (39), *Poa* (36), *Saxifraga* (35), *Artemisia* (33), *Puccinellia* (31), *Juncus* (30), *Pedicularis* (29), *Rumex* (28), *Astragalus* (28), *Silene* (24), *Erigeron* (24), *Luzula* (22) and *Eriophorum* (18)
- Around 5% endemic species, mainly Poaceae (24), Papaveraceae (15), Brassicaceae (15), Fabaceae (14) and Asteraceae (6), accounting for 70% of the endemic species flora
- Genera with relative high numbers of endemic species include *Papaver* (15), *Puccinellia* (13), *Oxytropis* (11), *Potentilla* (8) and *Draba* (8), accounting for 52% of the endemic species flora. Almost all are forbs or grasses, a few sedges, woody species absent
- Coherent with high percentage of circumpolar species
- High polyploidy (allopolyploidy) levels, in particular in the northern and longer glaciated areas
- Young with distinct phytogeographic history
- No strong influence by aliens
- Still native and with intact historical plant geography

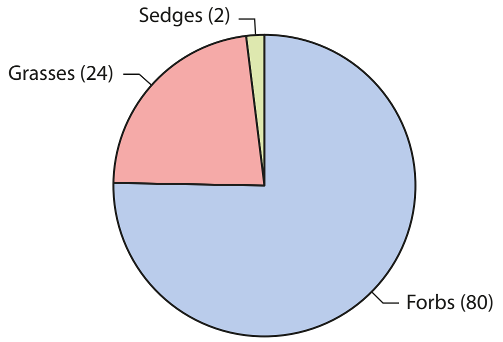
**Figure 9.4.** Distribution types and plant functional types of the 106 Arctic endemic vascular plant species.



Climatological distribution types



Plant functional types



### 9.2.3.1. Taxonomic structure

The 2,218 Arctic species included in the PAF (Appendix 9.1) are assigned to 430 genera in 91 families. The mean number of species per family is 24.4 and per genus 5.2; the mean number of genera per family is 4.7. Of the 2,218 recognized Arctic species, 106 are Arctic endemics (5%, Fig. 9.3 and 9.4, Appendix 9.2), 136 (6%) are 'borderline species' (Appendix 9.3), and 101 (4.8%) are introduced stabilized non-native species (Appendix 9.4).

Spore-bearing vascular plants play a very minor role in the Arctic vascular plant flora. They represent ferns and fern allies (Pteridophyta) and lycophytes (Lycopodiophyta) and comprise only 12 families with 21 genera and 72 species. They represent 13, 5 and 3%, respectively, of these taxonomic categories in the entire Arctic flora. Included here are the Lycopodiaceae (clubmosses, 14 species), Selaginaceae (spikemosses, 3), *Isoëtes* (quillworts, 3), *Equisetum* (horsetails, 12) and ferns (various families, 40). In contrast, seed-plants (Spermatophyta) are represented by 79 families, 409 genera and 2,146 species. They comprise gymnosperms (Gymnospermae, seed-plants with naked seeds not enclosed in an ovary) and flowering plants (angiosperms, Angiospermae, seed-plants with covered seeds enclosed in an ovary). The gymnosperms are represented in the Arctic flora by two families, five genera and 16 species representing 2, 1 and 1%, respectively, of these categories in the total flora. Gymnosperms are thus a minor contributor to the diversity of the Arctic flora (Fig. 9.3), a fact considered a prominent feature of the Arctic flora (Yurtsev 1994).

Flowering plants comprise 77 families, 404 genera and 2,130 species, representing 85, 94 and 96% respectively of the total flora. The basal angiosperms (including the magnoliids and Ceratophyllaceae, horn wort family) are very poorly represented with only two families (Nymphaeaceae, water lily family and Ceratophyllaceae, hornwort family), three genera and six species. The monocots (Monocotyledoneae) include 18 families, 102 genera and 566 species, representing 20, 24 and 26%, respectively, of these taxonomic categories in the flora. The eudicots (*sensu* Angiosperm Phylogeny Group 2009) are represented by 57 families with 299 genera and 1,558 species. They represent 63, 69 and 70%, respectively, of the diversity of these taxonomic categories in the entire flora. The most prominent families in terms of species numbers are the Asteraceae (composite family, 254 species), the Poaceae (grass family, 224), the Cyperaceae (sedge family, 190), the Brassicaceae (mustard family, 133), the Rosaceae (rose family, 128), the Fabaceae (pea family, 109), the Ranunculaceae (crowfoot or buttercup family, 102) and Caryophyllaceae (pink family, 100). With 1,240 of 2,218 species, these eight families represent 56% of the species of the entire Arctic flora (Fig. 9.3). Only 21 families (23% of 430) have more than 24 species, which is the mean species number per family. Sixty percent of the families have fewer than 10 species. The relatively low species diversity per family is considered another characteristic feature of the Arctic flora (Yurtsev 1994).

The most species-rich genera are *Carex* (sedge, with 152 species), *Salix* (willow, 72), *Oxytropis* (58), *Potentilla* (50), *Draba* (41), *Ranunculus* (crowfoot, buttercup, 40), *Papaver* (poppy, 39), *Poa* (bluegrass, meadow-grass, 36), *Saxifraga* (saxifrage, 35), *Artemisia* (wormwood, 33), *Puccinellia* (alkali grass, 31), *Juncus* (rush, 30), *Pedicularis* (lousewort, 29), *Rumex* (sorrel, dock, 28), *Astragalus* (milk vetch, 28), *Silene* (campion, 24), *Erigeron* (fleabane, 24), *Luzula,* (wood rush, 22) and *Eriophorum* (cotton grass, 18). Together they account for 38% of the total species diversity (Fig. 9.3). Overall species diversity of genera is rather low: 337 genera (78%) have 1-5 species. Only 93 genera (22%) have more species, accounting for 70% of the total species number. The relatively low species diversity per genus is considered another typical feature of the Arctic flora (Yurtsev 1994).

#### 9.2.3.2. Endemic species

The Arctic flora includes 106 species and subspecies endemic to the Arctic. Several of them are 'restricted range species', i.e. species with a distribution in an area of less than 50,000 km$^2$ (e.g. *Puccinellia svalbardensis* Svalbard alkali-grass). These 106 species account for about 5% of the entire flora (Appendix 9.2, Fig. 9.4). They mainly belong to Poaceae (24), Papaveraceae, the poppy family (15), Brassicaceae (15), Fabaceae (14) and Asteraceae (6), accounting for 70% of the entire endemic species flora. Genera with relatively high numbers of endemic species include *Papaver* (with 15 species), *Puccinellia* (13), *Oxytropis* (11), *Potentilla* (8) and *Draba* (8). Together these genera account for 52% of the endemic species flora. The genera *Poa* and *Braya* (braya, rose cress) each has four endemic species, and *Festuca* (fescue grass), *Ranunculus* and *Saxifraga* each has three endemic species in the Arctic. Almost all of these species are forbs (non-graminoid herbs) or grasses (Fig. 9.4). There are few sedges, and woody species are absent among Arctic endemics. The Beringian and circumpolar distribution types dominate (Fig. 9.4). The majority of species occur in both the low and high Arctic, with few restricted to the high Arctic (Fig. 9.4). The majority of endemic species show high polyploidy (allopolyploidy) levels; of the 75 species with known ploidy level, 31% are tetraploid and 45% are higher polyploids (Appendix 9.2). Polyploidy is a prominent feature of the entire Arctic flora, in particular in the northern and longer-glaciated North Atlantic region (e.g. Brochmann *et al.* 2004, Solstadt 2008).

#### 9.2.3.3. Borderline species

Borderline species (Appendix 9.3) are primarily non-Arctic species that just reach the southernmost extent of the Arctic (subzone E). This group of species is rather diverse, and includes 190 species representing 6% of all Arctic species, 91 genera and 45 families. Many 'borderline' species belong to the Asteraceae (16 species; 12%) or Cyperaceae (15 species; 11%). Hydrophytes and other species associated with wet habitats are frequent in this group. Seven aquatic genera (*Nymphaea,* water lily; *Nuphar,* pond lily; *Alisma*, water-plantain*; Sagittaria,* arrowhead; *Butomus,* flowering rush*; Scheuchzeria*, rannoch-rush; and *Potamogeton,* pondweed) account for 14 species (10%), with the genus *Potamogeton* represented by six species (4%). The borderline species group also includes some shrub and tree species of the genera *Salix*, *Alnus* (alder) and *Abies* (fir) that are common in boreal and temperate regions.

#### 9.2.3.4. Non-native species

Introduced non-native plants may be divided into two groups, stabilized introductions and casual introductions. Stabilized introductions are considered to be self-sustaining somewhere in the Arctic for at least one generation by generative or vegetative reproduction, whereas casual introductions are species that are present for short periods of time but do not persist (Elven 2007, 2011). One hundred and one non-native species (5% of the flora) are considered to be stabilized introductions in the Arctic (Appendix 9.4). In addition, there are 89 species (4%) that are native to one or more Arctic floristic provinces and subzones, but that are also found as non-native introduced species elsewhere in the Arctic. Of these 89 native species, 45 are found as stabilized introductions, 20 as casual introductions, and 24 as both stabilized and casual introductions in at least one floristic province or subzone. A total of 170 (8%) native and non-native species are considered as stabilized introductions somewhere in the Arctic. Including the native Arctic species also present as casual introductions in some parts of the Arctic increases this number to 190 species.

The group of non-native stabilized introductions is taxonomically diverse; however, Poaceae and Asteraceae account together for 33% of the stabilized introduced flora (Appendix 9.4). The most widespread non-native stabilized introduced species are *Lepidotheca suaveolens* (pineapple weed, stabilized introduction in 10 floristic provinces), *Plantago major* ssp. *major* (common plantain, stabilized in nine, casual in two) and *Trifolium pratense* (red clover, stabilized in eight). The native Arctic species that occur most widely as stabilized introductions include *Trifolium repens* (white clover, stabilized in 10, casual in one, native in two), *Puccinellia hauptiana* (european alkali grass, stabilized in nine, native in three), *Poa pratensis* ssp. *pratensis* (meadow-grass or Kentucky bluegrass, stabilized in eight, native in 11), *Stellaria media* (common chickweed, stabilized in eight, casual in one, native in five) and *Draba nemorosa* (woodland draba, stabilized in eight, native in three).

Elven (2011) lists an additional 205 non-native species that are known to occur in the Arctic only as casual introductions. As these species are not listed according to floristic regions in the main checklist, they are not included in the analyses presented here. They range from species reported only once to those that may appear regularly around settlements. The majority of these species are annual or biennial plants that are unable to reproduce in the Arctic. Others are perennials that are unable to survive the harsh Arctic climate. The number of casual introductions listed in PAF may be highly underestimated: a throughout review of casuals in Svalbard revealed about 100 species (I.G. Alsos & R. Elven, unpubl.) whereas PAF lists 53 species for this region.

Although there is little information about non-native invasive species in the Arctic, the majority of introduced species appear not to be invasive. Several native plants have become weedy in disturbed habitats, either in their native range or elsewhere in the Arctic, but are not considered to be a threat to the native vegetation. *Lupinus nootkatensis* (Nootka lupine), native to NW North America, was introduced as an ornamental in Greenland and has become a stabilized weedy species in SW Greenland, but is not considered to be seriously invasive since it is mostly restricted to disturbed sites (C. Bay and K. Høegn, pers. com. 2012). In Iceland it is a threat, including in the Arctic area of Iceland (Magnusson 2010). *Hordeum jubatum* (foxtail barley) is a troublesome native weed in the western Arctic of North America, but again is primarily restricted to disturbed sites and thus not considered a threat to native vegetation. Invasive species were not noticed in many areas in Greenland (F.J.A. Daniëls, unpubl.) and the Canadian Arctic (L.J. Gillespie, unpubl.). Daniëls & de Molenaar (2011) and Daniëls *et al.* (2011) did not observe such species in the tundra near the town of Ammassalik, SE Greenland during their fieldwork in the last 40 years, although in the town, a few casual non-invasive introductions were occasionally recorded. In Svalbard, the majority of introduced species have been considered as no risk, but recently several species were evaluated as low risk (watch list) and one as high risk (black list) of becoming invasive in Svalbard (Gederaas *et al.* 2012). *Anthriscus sylvestris* (cow parsley) was rather recently established (after 1988) (Liška & Soldán 2004), but the population is now large with fertile individuals about to 2 m high (Alsos *et al.* 2012b). Any spread of this species to bird cliffs would pose a threat both to the many redlisted species found there and to the birds as the foxes could hide during hunting. Although not currently a problem in the Arctic, invasive species are likely to increase in the Arctic due to the expanding visitation rates combined with climate warming. Each visitor to Svalbard transport on average a minimum of four seeds, many of them from species known to be invasive in other regions, and 26% of them are able to germinate under current Arctic climate (Ware *et al.* 2012).

#### 9.2.3.5. Origin and integrity of the Arctic flora

The present-day Arctic flora is of relatively recent origin (Murray 1995) and has been shaped through numerous large-scale climate changes resulting in cycles of fragmentation, range expansion and reunion of previously isolated populations (Stebbins 1984, 1985). During most of the Tertiary (65.2 million years ago) forests grew at high latitudes, e.g. in Canada and Greenland (McIver & Basinger 1999), and tundra did not appear until the late Pliocene when global temperatures dropped (Matthews & Ovenden 1990). Initially, tundra was distributed discontinuously, but became continuous by three million years ago (Matthews 1979). The early Quaternary flora was likely recruited from the Arcto-Tertiary forest and immigrants of ancestral stocks from temperate high mountain ranges in Asia and North America (Hultén 1937, Hedberg 1992, Murray 1995, Ickert-Bond *et al.* 2009). This floristic mixture has since repeatedly been re-arranged and re-mixed spatially by more than 20 cycles of glacials and interglacials during the Quaternary period (reviewed in Birks 2008; see also Payer *et al.*, Chapter 2).

During the last two decades, comparative molecular research on Arctic plant populations has contributed significantly to a better understanding of patterns and processes in the present Arctic flora (cf. Abbott *et al.* 2000, Abbott & Brochmann 2003, Abbott & Comes 2003, Brochmann *et al.* 2004, Alsos *et al.* 2005, 2007, Grundt *et al.* 2006, Solstadt 2008, Tkach *et al.* 2008, Consaul *et al.* 2010, Hoffmann *et al.* 2010, Westergaard *et al.* 2010, 2011a, 2011b, Hoffmann 2011). Abbott & Brochmann (2003) reviewed fossil, molecular and phytogeographical evidence for the existence of Beringia as a major glacial refugium for Arctic plants as previously proposed by Hultén (1937), and concluded that the evidence is excellent to support his proposal (e.g. for *Dryas integrifolia,* entire-leaf mountain avens and *Saxifraga oppositifolia*, purple saxifrage; Tremblay & Schoen 1999, Abbott *et al.* 2000).

Recently, molecular evidence supporting *in situ* glacial survival in the North Atlantic region has been reported for *Saxifraga rivularis* (brook saxifrage), *Arenaria humifusa* (low sandwort), *Sagina caespitosa* (tufted pearlwort) and *Carex rufina* (reddish sedge) (Westergaard *et al.* 2010, 2011a, 2011b). However, molecular evidence supports several long-distance dispersal events across great distances in North America, and between North America, Greenland and Europe, thus not corroborating Hultén's (1937) hypothesis that the North Atlantic was a strong barrier for plant dispersal in the Holocene.

The extreme Beringian/Atlantic disjunction in *Saxifraga rivularis* has evidently formed at least twice, with expansions out of Beringia to the Atlantic regions both before and after the last glaciation (Westergaard *et al.* 2010). A long-distance dispersal event of similar magnitude was also reported for the Beringian species *Arenaria longipedunculata* (long-stemmed sandwort), in which molecular and morphological data revealed a highly disjunct occurrence in W Greenland (Westergaard *et al.* 2011b). Postglacial, trans-Atlantic dispersal has been reported for an increasing number of Arctic and Arctic-alpine plant species, even for species lacking obvious morphological adaptations to long-distance dispersal (see Abbott & Brochmann 2003, Brochmann *et al.* 2004, Alsos *et al.* 2007, Westergaard *et al.* 2011a, 2011b). Although the Arctic flora has long been viewed as depauperate and species-poor, Grundt *et al.* (2006) showed how three circumpolar species of recent origin, *Draba fladnizensis* (white Arctic draba), *D. nivalis* (snow draba) and *D. subcapitata* (hemispherical draba), actually consist of many cryptic species separated by genetically based crossing barriers, but not morphologically and ecologically differentiated.

Frequency of polyploids is particularly high in the Arctic, and both frequency and ploidy level strongly increase northwards within the Arctic (Brochmann *et al.* 2004). A large number of species show high ploidy levels (mostly allopolyploids), particularly in northern areas and areas more recently glaciated such as the North Atlantic (Abbott & Brochmann 2003, Brochmann *et al.* 2004). A majority of plants are of hybrid origin, many of them between plants which themselves are, or were, of hybrid origin (reticulate evolution). Most of these hybrids have been stabilized via polyploidy. However, not all Arctic polyploids have been formed in the Arctic (Murray 1995). Successive cycles of divergent evolution among populations isolated in different glacial refugia, migration into deglaciated terrain, hybridization and polyploidy have built up increasingly intricate, high-ploidy complexes (Abbott & Brochmann 2003). Brochmann *et al.* (2004) found that for 'Arctic specialist taxa' (mainly Arctic and exclusively Arctic species with limited distribution) the frequency of polyploids appears much lower in Beringia, which was largely unglaciated during the last ice age, than in the heavily glaciated North Atlantic area. This was interpreted as an indication that polyploids are more successful in colonizing ice-free areas after deglaciation than diploids are. The evolutionary success of polyploids in the Arctic may be based on their fixed-heterozygous genomes, which may buffer against inbreeding and genetic drift through periods of dramatic climate change (Brochmann *et al.* 2004). Another aspect of the success of polyploids is their broader ecological amplitude and thus greater ability to cope with a changing climate and adapt to more diverse ecological niches than a diploid could (Brochmann *et al.* 2004).

Asexual reproduction commonly occurs in the Arctic flora and is demonstrated through apomictic seed production (e.g. dandelion *Taraxacum*; hawkweed *Hieracium*), pseudovivipary (e.g. viviparous alpine bluegrass *Poa alpina* ssp. *vivipara*), bulbils formation (e.g. nodding saxifrage *Saxifraga cernua,* leafy saxifrage *Micranthes foliolosa*) and vegetative spread through stolons and tillers (e.g. Bigelow's sedge *Carex bigelowii,* creeping alkaligrass *Puccinellia phryganodes,* spider saxifrage *Saxifraga platysepala*). However, sporadic sexual reproduction is still maintained, likely to avoid loss of genetic diversity. Seed banks are persistent and in several cases long-term viability and genetic differentiation among seeds could be demonstrated (summarized from Crawford 2008a; see also Section 2.3.5, Ims *et al.*, Chapter 7 and Cook, Chapter 17).

Annual herbs and trees are almost absent from the Arctic biome. The cold, dark and long winter and short summer with mean July temperature < 10 °C allow only very few annual species to complete their life-cycles within the year (e.g. Iceland purslane *Koenigia islandica* and the mastodon plant *Tephroseris palustris* var. *congesta*). Most species are perennial without specific Arctic life-history traits (Jónsdóttir 2011). Tall aerial plants such as trees (phanerophyte life-form) are absent due to harsh climatological conditions. The low hemicryptophyte life-form (half-earth plants, e.g. grasses, many forbs) strongly dominates the life-form spectrum, followed at a distance by representatives of the chamaephyte life-form (surface plants, e.g. dwarf shrubs) and geophytes (earth plants, e.g. orchids and several other forbs). All these survive harsh winter conditions near or in the soil, often under snow cover. Hence, compared with the other Earth biomes the Arctic flora is characterized by the absence of trees (phanerophytes), a few annual plants (therophytes) and the predominance of hemicryptophytes (forbs and graminoids) (cf. Polunin 1967). In terms of strategy types (Grime 2001), stress-tolerators (which are adapted to resist all conditions that restrict photosynthesis production) predominate, whereas ruderals, plants adapted to habitats where disturbance (destruction of biomass) frequently occurs, are almost absent.

Despite the slightly different concepts of the Arctic flora and territory used here, the results of our taxonomic examination of the Arctic vascular plant flora still support Yurtsev's (1994) view that the integrity of the Arctic flora is high, and therefore the Arctic deserves the status of its own floristic region. The identity of the Arctic vascular plant flora is based on several distinct features pertaining to taxonomic structure, distribution (e.g. endemism, circumpolar distribution), ecology and morphology (growth forms) and flora genesis and speciation (cf. Yurtsev 1994). There are relatively few species per genus and family in the Arctic, respectively five and 24 on average (Fig. 9.3). Several unique floristic characteristics support the Arctic flora: 60% of the families have less than 10 species, gymnosperms are poorly represented, percentage of endemism is relatively high (5%) and the percentage of non-native stabilized introduced species is relatively low (5%). The proportion of

**Table 9.1.** Summary of Arctic vascular plant species and distribution by Arctic flora province and subzone based on Elven (2007). Arctic floristic provinces, subzones (A-E), neighbouring boreal or boreal-alpine zone (N) and distribution derived from Elven (2007).

| **Floristic province** | | Number of stabilized introduced species | Casual introduced species | Rare species | Species with a scattered distribution | Borderline species | Frequent species | Present, abundance unknown | Present, abundance likely rare | Present, frequency likely scattered or sparse | Species for which presence is uncertain | Total species number without uncertain occurrencies | Mean species number per floristic province group |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **European Russian-W Siberian** | | | | | | | | | | | | | |
| Kanin-Pechora | **KP** | 52 | 18 | 239 | 165 | 14 | 151 | 3 | 0 | 0 | 22 | 642 | 593 |
| Polar Ural-Novaya Zemlya | **UN** | 32 | 8 | 209 | 228 | 5 | 137 | 6 | 0 | 0 | 24 | 625 | |
| Yamal-Gydan | **YG** | 16 | 4 | 238 | 129 | 23 | 96 | 7 | 0 | 0 | 29 | 513 | |
| **E Siberian** | | | | | | | | | | | | | |
| Taimyr-Severnaya Zemlya | **TM** | 23 | 16 | 310 | 121 | 35 | 136 | 4 | 0 | 0 | 38 | 645 | 516 |
| Anabar-Olenyok | **AO** | 1 | 0 | 200 | 144 | 14 | 67 | 2 | 0 | 1 | 37 | 429 | |
| Kharaulakh | **Kh** | 14 | 3 | 184 | 118 | 13 | 223 | 3 | 0 | 0 | 20 | 558 | |
| Yana-Kolyma | **YK** | 3 | 0 | 280 | 80 | 12 | 53 | 3 | 0 | 1 | 46 | 432 | |
| **Beringian** | | | | | | | | | | | | | |
| W Chukotka | **CW** | 8 | 4 | 219 | 151 | 2 | 238 | 14 | 0 | 0 | 28 | 636 | 621 |
| Wrangel Island | **WI** | 0 | 1 | 89 | 76 | 0 | 145 | 4 | 0 | 0 | 16 | 315 | |
| S Chukotka | **CS** | 7 | 2 | 236 | 146 | 9 | 136 | 13 | 0 | 0 | 33 | 549 | |
| E Chukotka | **CE** | 20 | 4 | 225 | 140 | 0 | 265 | 14 | 0 | 0 | 36 | 668 | |
| W Alaska | **AW** | 20 | 14 | 316 | 212 | 50 | 210 | 3 | 0 | 0 | 27 | 825 | |
| N Alaska-Yukon Territory | **AN** | 11 | 3 | 247 | 172 | 40 | 256 | 3 | 0 | 0 | 26 | 732 | |
| **Canadian** | | | | | | | | | | | | | |
| Central Canada | **CC** | 8 | 3 | 303 | 157 | 30 | 137 | 2 | 0 | 0 | 36 | 640 | 536 |
| Hudson Bay-Labrador | **HL** | 30 | 9 | 355 | 174 | 58 | 141 | 1 | 1 | 0 | 27 | 769 | |
| Ellesmere Land-N Greenland | **EP** | 0 | 0 | 77 | 46 | 0 | 76 | 0 | 0 | 0 | 5 | 199 | |
| **N Atlantic** | | | | | | | | | | | | | |
| W Greenland | **GW** | 50 | 26 | 144 | 174 | 0 | 159 | 1 | 0 | 0 | 18 | 554 | 449 |
| E Greenland | **GE** | 5 | 4 | 136 | 105 | 0 | 141 | 0 | 0 | 0 | 11 | 391 | |
| N Iceland-Jan Mayen | **Ic** | 52 | 2 | 80 | 74 | 17 | 211 | 0 | 0 | 0 | 16 | 436 | |
| N Fennoscandia | **FN** | 63 | 13 | 216 | 157 | 28 | 171 | 0 | 1 | 0 | 23 | 649 | |
| Svalbard-Franz Joseph Land | **SF** | 4 | 32 | 53 | 47 | 0 | 79 | 0 | 0 | 0 | 10 | 215 | |
| **Subzone** | | | | | | | | | | | | | |
| Arctic herb subzone | **A** | 0 | 0 | 41 | 23 | 0 | 38 | 0 | 0 | 0 | 11 | 102 | |
| N Arctic dwarf shrub subzone | **B** | 0 | 0 | 91 | 39 | 0 | 90 | 0 | 0 | 0 | 18 | 220 | |
| Middle Arctic dwarf shrub subzone | **C** | 3 | 27 | 204 | 85 | 0 | 188 | 0 | 0 | 0 | 91 | 507 | |
| S Arctic dwarf shrub subzone | **D** | 18 | 10 | 349 | 213 | 0 | 389 | 1 | 0 | 0 | 65 | 980 | |
| Arctic shrub subzone | **E** | 101 | 0 | 868 | 392 | 136 | 681 | 2 | 0 | 0 | 4 | 2,180 | |
| Non-Arctic-Boreal or Boreal-alpine | **N** | 34 | 0 | 195 | 563 | 0 | 1,304 | 1 | 0 | 0 | 13 | 2,097 | |

endemic species is very high considering the short period since the latest glaciation. The PAF analysis also shows that 14 species are found in all five latitudinal subzones and 21 floristic provinces around the Arctic, whereas many others have a distinctive circumpolar distribution, occurring in all geographical floristic province groups (Appendix 9.1). In addition, 76 Arctic non-endemic species, nearly 4% of all Arctic species, occur in all five subzones. Although not analyzed here, there is no reason to doubt that circumpolar species account for 35% to over 80% of the species in local floras (Yurtsev 1994).

The Arctic flora is young and has its own distinct natural phytogeographic history (Elven 2011). No single, predominantly Arctic vascular plant species is known to have gone extinct due to human activities in the last 250 years (Elven 2011), nor is the Arctic strongly influenced by invasive species. Unlike much of the rest of the world, the Arctic's native flora and plant communities are still intact (Elven 2011).

### 9.2.3.6. Species richness in Arctic subzones

The five Arctic subzones strongly differ in species richness and species composition. There is a pronounced increase in the number of vascular plant species from the northernmost subzone A (102 or 4.6% of known Arctic species) to the southernmost subzone E (2,180 or 98.2%; Tab. 9.1). The increase in species numbers from north to south (subzones A-E) in the Arctic is strongly correlated with the increase of the mean July temperature (e.g. Young 1971, Edlund & Alt 1989, Daniëls *et al.* 2000). Seventy-six Arctic species, all non-endemic, occur in all five subzones; fourteen of these species also occur in all floristic provinces (see Tab. 9.3) due to their very broad ecological and chorological amplitude. An interesting feature of subzone A is the absence of sedges (*Carex*) and woody plants (cf. Edlund & Alt 1989, Walker *et al.* 2011) and the high biodiversity on the sample plot scale of 25 m$^2$. In such plots up to 100 species can be found: vascular plants, bryophytes and lichens (cf. Vonlanthen 2008).

It is noteworthy that the number of Arctic endemic species also increases from north to south, i.e. from subzone A to subzone E, with 24 species present in subzone A, 34 in B, 66 in C, 76 in D and 71 in subzone E (Tab. 9.2, Appendix 9.2). However, the percentage of all species per subzone that are endemic is highest in subzone A (23.5%) and decreases from subzone B through E (15.4, 13, 7.8 and 3.3%, respectively). There is only one endemic species, *Saxifraga nathorstii* (Nathorst's saxifrage), restricted to a single subzone (subzone C) within the high Arctic, whereas 26 species are restricted to a single subzone in the low Arctic. Four species are confined to the low Arctic subzone D (*Oxytropis beringensis*, *O. kateninii*, *O. sverdrupii* and *Puccinellia banksiana,* Banks Island alkali-grass) and 22 species to subzone E (Appendix 9.2).

A group of eight high Arctic endemics with exclusive or main distribution in one, two or three of the high Arctic subzones (A, B and C) include *Puccinellia svalbardensis* (Svalbard saltmarsh grass), *P. gorodkovii*, *xPucciphippsia vacillans* (sterile hybrid between *Phippsia algida* and *Puccinellia vahliana*), *Saxifraga nathorstii*, *S. svalbardensis*, *Braya humilis* ssp. *ellesmerensis* (Ellesmere Island braya), *B. glabella* ssp. *prostrata* (prostrate braya) and *Draba arctica* ssp. *ostenfeldii* (Ostenfeld's braya). Thirty-nine endemic species are confined to the low Arctic subzones (D and E), and this group includes several species of the genus *Poa* and of the families Ranunculaceae, Fabaceae and Asteraceae. Fifty-nine Arctic endemic species occur both in the high Arctic and low Arctic. Common endemic species with wide distribution across the subzones include the grasses *Puccinellia angustata* (narrow alkali-grass) and *P. vahliana* (Vahl's alkaligrass) and the forbs *Potentilla hyparctica* ssp. *hyparctica* (Arctic cinquefoil), *Draba pauciflora* (few-flowered draba), *D. micropetala* (small-flowered draba), *D. simmonsii* (Simmons' draba), *D. oblongata* (Canada Arctic draba), *Cerastium arcticum* (Arctic chickweed), *Minuartia rossii* (Ross' stitchwort or cushioned sandwort), *Silene uralensis* ssp. *arctica* (polar campion) and *S. sorensensis* (Sorensen's campion).

The 136 borderline species are – not unexpectedly – all confined to subzone E, with their main distribution remaining outside the Arctic (Appendix 9.3).

As expected, the species considered stabilized introductions somewhere in the Arctic are mainly confined to the two southernmost subzones of the Arctic, with the majority confined to the warmest subzone (E). No introduced non-native species, either stabilized or casual, have been reported from high Arctic subzones A and B, whereas only one non-native species, *Barbarea vulgaris* (winter cress), has been reported as a stabilized introduction in subzone C (Appendix 9.4). In addition, two native Arctic species (*Sisyrinchium montanum*, blue-eyed grass, *Rumex acetosa* ssp. a*cetosa,* common sorrel) have been reported as stabilized introductions in subzone C. Hence, the number of stabilized introduced species decreases considerably from south to north with 101 in subzone E, 18 in D, three in C, and – as mentioned – none recorded from the high Arctic subzones A and B. In contrast, casual introduced species are more numerous in the high Arctic, and temporarily occur primarily in settlements and towns. Of the species that are native or stabilized in the Arctic, 27 have been reported as casual introductions from subzone C. Diversity of species that are only known as casual introductions in the Arctic is expected to be higher than that of stabilized introductions for all subzones, but distributional data have not yet been compiled.

### 9.2.3.7. Species richness in floristic provinces

A comparison of species numbers per floristic region showed a range from 199 species for the rather heavily glaciated and northern floristic province Ellesmere Land-N Greenland to 825 species for Beringian W Alaska (Tab. 9.1 and 9.2). The mean number for a floristic region is 543 species or 24.5% of the total number of species occurring in the Arctic.

Comparatively species rich are the provinces W Alaska (825; 37.2% of the total number of species occurring in the Arctic), Hudson-Labrador (769; 34.7%), N Alaska-Yukon (732, 33%), E Chukotka (668, 30.1%), Taimyr-Severnaya Zemlya (645; 29.1%) and Central Canada (640; 28.9%) (Tab. 9.1 and 9.2, Fig. 9.2). Provinces with a comparatively low species number, far below the mean value of 543 (24%) per floristic province, include E Greenland (391; 17.6%), the small Wrangel Island province (315; 14.2%), and the two high Arctic provinces Svalbard-Franz Joseph Land (215; 9.7%) and Ellesmere Land-N Greenland (199; 9%).

The mean species number for the three European Russian-W Siberian flora provinces is 593, for the four E Siberian flora provinces 516 and for the six Beringian

**Table 9.2.** Species numbers in floristic provinces and subzones. Islands indicated by •.
1 Subzone constitutes < 20% of floristic province, 2 20-50% and 3 > 50%.

| Floristic province | | Mean number of vascular plant species | Total number of vascular plant species | Percentage of number of species/ total species number (2,218) | Number of Arctic endemic species | Percentage Arctic endemics in flora of floristic province/subzone | Percentage of Arctic endemic species in total Arctic endemic flora (106) | Number of Arctic species confined to one floristic province/subzone | | Subzone | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | A | B | C | D | E |
| **European Russian-W Siberian** | | | | | | | | | | | | | | |
| Kanin-Pechora | **KP** | 593 | 642 | 28.9 | 7 | 1.1 | 6.6 | 0 | | | | | 2 | 3 |
| Polar Ural-Novaya Zemlya | **UN** | | 625 | 28.2 | 16 | 2.6 | 15.1 | 2 | | 1 | 2 | 2 | 2 | 2 |
| Yamal-Gydan | **YG** | | 513 | 23.1 | 7 | 1.4 | 6.6 | 0 | | | 2 | 2 | 2 | 2 |
| **E Siberian** | | | | | | | | | | | | | | |
| Taimyr-Severnaya Zemlya | **TM** | 516 | 645 | 29.1 | 16 | 2.5 | 15.1 | 4 | | 2 | 2 | 2 | 2 | 2 |
| Anabar-Olenyok | **AO** | | 429 | 19.3 | 9 | 2.1 | 8.5 | 0 | | | | 2 | 3 | 2 |
| Kharaulakh | **Kh** | | 558 | 25.2 | 14 | 2.5 | 13.2 | 2 | | | | | 1 | 3 |
| Yana-Kolyma | **YK** | | 432 | 19.5 | 11 | 2.5 | 10.4 | 0 | | | 2 | 2 | 2 | 1 |
| **Beringian** | | | | | | | | | | | | | | |
| W Chukotka | **CW** | 621 | 636 | 28.7 | 22 | 3.5 | 20.8 | 5 | | | | 2 | 3 | 2 |
| • Wrangel Island | **WI** | | 315 | 14.2 | 35 | 11.1 | 33 | 10 | | | | 3 | 1 | |
| S Chukotka | **CS** | | 549 | 24.8 | 4 | 0.7 | 3.8 | 0 | | | | | 2 | 3 |
| E Chukotka | **CE** | | 668 | 30.1 | 24 | 3.6 | 22.6 | 6 | | | | | 3 | 3 |
| W Alaska | **AW** | | 825 | 37.2 | 13 | 1.6 | 12.3 | 4 | | | | | 2 | 3 |
| N Alaska-Yukon Territory | **AN** | | 732 | 33 | 26 | 3.6 | 24.5 | 3 | | | | 1 | 2 | 3 |
| **Canadian** | | | | | | | | | | | | | | |
| Central Canada | **CC** | 536 | 640 | 28.9 | 34 | 5.3 | 32.1 | 2 | | 1 | 2 | 2 | 2 | 2 |
| Hudson Bay-Labrador | **HL** | | 769 | 34.7 | 20 | 2.6 | 18.9 | 0 | | | | 1 | 2 | 3 |
| • Ellesmere Land-N Greenland | **EP** | | 199 | 9 | 28 | 14.1 | 26.4 | 2 | | 2 | 2 | 2 | | |
| **N Atlantic** | | | | | | | | | | | | | | |
| • W Greenland | **GW** | 449 | 554 | 25 | 29 | 5.2 | 27.4 | 3 | | | 2 | 2 | 2 | 2 |
| • E Greenland | **GE** | | 391 | 17.6 | 28 | 7.2 | 26.4 | 1 | | | 2 | 2 | 2 | 2 |
| • N Iceland-Jan Mayen | **Ic** | | 436 | 19.7 | 1 | 0.2 | 0.9 | 0 | | | | 1 | | 3 |
| N Fennoscandia | **FN** | | 649 | 29.3 | 1 | 0.2 | 0.9 | 0 | | | | | | 3 |
| • Svalbard-Franz Joseph Land | **SF** | | 215 | 9.7 | 22 | 10.2 | 20.8 | 3 | | 2 | 2 | 2 | | |
| **Subzone** | | | | | | | | | | | | | | |
| Arctic herb subzone | **A** | | 102 | 4.6 | 24 | 23.5 | 22.6 | 0 | | | | | | |
| N Arctic dwarf shrub subzone | **B** | | 220 | 9.9 | 34 | 15.5 | 32.1 | 0 | | | | | | |
| Middle Arctic dwarf shrub subzone | **C** | | 507 | 22.9 | 66 | 13 | 62.3 | 1 | | | | | | |
| S Arctic dwarf shrub subzone | **D** | | 980 | 44.2 | 76 | 7.8 | 71.7 | 4 | | | | | | |
| Arctic shrub subzone | **E** | | 2,180 | 98.3 | 71 | 3.3 | 67 | 24 | | | | | | |
| Non-Arctic-Boreal or Boreal-alpine | **N** | | 2,097 | | | | | | | | | | | |

flora provinces 621. The three Canadian flora provinces have a mean of 536 species, whereas the five North Atlantic flora provinces have the lowest mean value at 449.

A comparison of mean species richness of the six Beringian floristic provinces with the 15 non-Beringian provinces shows that the Beringian floristic provinces have more species (mean 621) compared with a mean value of 524 for the non-Beringian provinces. One hundred and four species are both widespread in Beringia (i.e. found in at least three of the six provinces) and restricted to the Beringian region (i.e. the six Arctic Beringian floris-

**Table 9.3.** Fourteen species and subspecies distributed in all 21 floristic provinces and five subzones. Presence of indigenous/native species is indicated by a frequency value r = rare, s = scattered and f = frequent. Derived from Elven (2007).

| Floristic province | Species | *Bistorta vivipara* | *Cardamine pratensis* ssp. *angustifolia* | *Equisetum arvense* ssp. *alpestre* | *Equisetum variegatum* ssp. *variegatum* | *Juncus biglumis* | *Micranthes nivalis* | *Oxyria digyna* | *Phippsia algida* | *Poa pratensis* ssp. *alpigena* | *Ranunculus pygmaeus* | *Saxifraga cernua* | *Saxifraga cespitosa* ssp. *cespitosa* | *Saxifraga hirculus* | *Trisetum spicatum* ssp. *spicatum* | Number of rare species | Number of scattered species | Number of frequent species |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | | | | | **r** | **s** | **f** |
| **European Russian-W Siberian** | | | | | | | | | | | | | | | | | | |
| Kanin-Pechora | **KP** | f | f | f | s | f | s | s | r | f | f | f | s | s | f | 1 | 5 | 8 |
| Polar Ural-Novaya Zemlya | **UN** | f | f | f | f | f | f | f | f | f | f | f | f | f | f | 0 | 0 | 14 |
| Yamal-Gydan | **YG** | f | f | s | r | f | s | f | s | f | f | s | r | s | f | 2 | 5 | 7 |
| **E Siberian** | | | | | | | | | | | | | | | | | | |
| Taimyr-Severnaya Zemlya | **TM** | s | f | s | s | f | f | f | f | f | f | f | f | f | f | 0 | 3 | 11 |
| Anabar-Olenyok | **AO** | s | f | s | r | f | s | f | s | f | s | s | s | s | f | 1 | 8 | 5 |
| Kharaulakh | **Kh** | f | f | s | s | f | f | f | s | f | f | f | s | f | f | 0 | 4 | 10 |
| Yana-Kolyma | **YK** | s | f | r | r | f | f | f | f | f | f | s | s | f | r | 3 | 3 | 8 |
| **Beringian** | | | | | | | | | | | | | | | | | | |
| W Chukotka | **CW** | f | f | f | r | f | f | f | f | f | f | f | s | f | f | 1 | 1 | 12 |
| Wrangel Island | **WI** | f | f | f | f | f | f | f | f | f | f | f | f | f | f | 0 | 0 | 14 |
| S Chukotka | **CS** | s | r | f | f | s | f | r | f | f | s | f | r | f | f | 3 | 3 | 8 |
| E Chukotka | **CE** | f | f | f | f | f | f | f | f | f | f | f | s | f | f | 0 | 1 | 13 |
| W Alaska | **AW** | f | f | f | s | s | s | f | s | f | f | f | s | f | f | 0 | 5 | 9 |
| N Alaska-Yukon Territory | **AN** | f | f | s | f | f | s | f | f | f | f | f | f | f | f | 0 | 2 | 12 |
| **Canadian** | | | | | | | | | | | | | | | | | | |
| Central Canada | **CC** | f | f | s | f | f | f | f | f | s | f | f | f | f | f | 0 | 2 | 12 |
| Hudson Bay-Labrador | **HL** | f | f | f | f | f | f | f | f | f | f | f | f | f | f | 0 | 0 | 14 |
| Ellesmere Land-N Greenland | **EP** | f | s | s | f | f | f | f | f | r | s | f | f | f | f | 1 | 3 | 10 |
| **N Atlantic** | | | | | | | | | | | | | | | | | | |
| W Greenland | **GW** | f | f | f | f | f | f | f | f | f | f | f | f | r | f | 1 | 0 | 13 |
| E Greenland | **GE** | f | f | f | f | f | f | f | f | f | f | f | f | s | f | 0 | 1 | 13 |
| N Iceland-Jan Mayen | **Ic** | f | f | f | f | f | f | f | r | f | f | f | f | s | f | 1 | 1 | 12 |
| N Fennoscandia | **FN** | f | f | s | s | f | f | f | r | f | f | s | f | r | s | 2 | 4 | 8 |
| Svalbard-Franz Joseph Land | **SF** | f | f | f | f | f | f | f | f | f | f | f | f | f | f | 0 | 0 | 14 |
| **Subzone** | | | | | | | | | | | | | | | | | | |
| Arctic herb subzone | **A** | f | f | r | r | f | s | f | f | r | f | f | f | s | r | 4 | 2 | 8 |
| N Arctic dwarf shrub subzone | **B** | f | f | f | f | f | f | f | f | f | f | f | f | f | f | 0 | 0 | 14 |
| Middle Arctic dwarf shrub subzone | **C** | f | f | f | f | f | f | f | f | f | f | f | f | f | f | 0 | 0 | 14 |
| S Arctic dwarf shrub subzone | **D** | f | f | f | f | f | f | f | s | f | f | f | f | f | f | 0 | 1 | 13 |
| Arctic shrub subzone | **E** | f | f | r | f | f | f | f | r | f | f | f | f | f | f | 2 | 0 | 12 |
| Non-Arctic-Boreal or Boreal-alpine | **N** | f | s | r | f | s | f | f | r | f | s | f | f | f | f | 2 | 3 | 9 |

tic provinces plus adjacent Beringian areas to the south). These data clearly demonstrate the prominent position of Beringia in the Arctic flora when species richness is considered. However, in terms of species composition, this region also stands out with a much higher number of species either confined to or with their main distribution in the Beringian floristic provinces, such as *Selaginella sibirica* (Siberian spike-moss), *Carex podocarpa* (graceful mountain sedge), *Ranunculus grayi*, *Salix phlebophylla* (skeleton-leaved willow), *Oxytropis czukotica*, *Potentilla elegans* (elegant cinquefoil), *Phlox pumila*, *Douglasia ochotensis* (Arctic montane dwarf primrose) and *Tephroseris* *frigida* (Arctic groundsel). Most of the more common strictly Beringian species are confined to the low Arctic (subzones E and D), whereas almost 20% are known from the southernmost subzone C of the high Arctic, mostly from Wrangel Island.

Fourteen species are common to all 21 Arctic floristic provinces and all five Arctic subzones: *Cardamine pratense* ssp. *angustifolia* (cuckoo flower), *Micranthes nivalis* (snow saxifrage), *Saxifraga cernua* (nodding saxifrage), *S. cespitosa* ssp. *cespitosa* (tufted saxifrage), *S. hirculus* (yellow marsh saxifrage)*, Oxyria digyna* (mountain sorrel), *Bistorta vivipara* (alpine bistort), *Ranunculus pygmaeus* (pygmy buttercup), *Phippsia algida* (ice-grass or spiked snow-grass), *Poa pratensis* ssp. *alpigena* (northern meadow-grass), *Trisetum spicatum* ssp. *spicatum* (northern oat-grass), *Juncus biglumis* (two-flowered rush), *Equisetum arvense* ssp. *alpestre* (polar horsetail) and *E. variegatum* ssp. *variegatum* (variegated horsetail, Tab. 9.3). Several other species have a pronounced circumpolar distribution, e.g. *Hippuris vulgaris* (common mare's-tail), *Stellaria humifusa* (saltmarsh starwort), *Koenigia islandica* (Iceland purslane), *Ranunculus hyperboreus* ssp. *hyperboreus* (Arctic buttercup), *Carex rupestris* (rock sedge), *C. lachenalii* (Arctic hare's-foot sedge), *Cystopteris fragilis* (fragile fern) and *Luzula confusa* (northern wood-rush).

The number of Arctic endemic species per floristic province varies from only one (N Iceland-Jan Mayen and N Fennoscandia) to 35 (Wrangel Island) (Fig. 9.2, Tab. 9.2, Appendix 9.2). One-third of the 106 Arctic endemic species (33%) occur in the small Wrangel Island floristic province, and an almost equal number occur in the vast floristic province of Central Canada (34 species, 32%). Arctic endemic species are also well represented in the provinces of W Greenland (29, 27%), E Greenland (28, 26%), Ellesmere Land-N Greenland (28, 26%), N Alaska-Yukon (26, 25%) and E Chukotka (24, 23%). However, if the percentage of Arctic endemics in relation to the total flora of all the floristic provinces is considered, different conclusions are reached. The flora of the province Ellesmere Land-N Greenland consists now of 14% Arctic endemics, whereas the floras of the small provinces Wrangel Island and Svalbard-Franz Joseph Land consist of 11 and 10% Arctic endemic species, respectively, and Central Canada only 5% Arctic endemic species.

The paramount position of Wrangel Island is also shown by its 10 Arctic endemic species that are restricted to this island: *Poa hartzii* ssp. *wrangelica*, *Puccinellia wrightii* ssp. *colpodioides*, *Potentilla wrangelii*, *Papaver uschakovii*, *P. multiradiatum*, *P. chionophilum*, *P. nudicaulis* ssp. *insulare*, *Oxytropis uschakovii*, *O.uniflora* and *Packera hyperborealis* ssp. *wrangelica* (Tab. 9.2, Appendix 9.2). E Chukotka has six endemics (*Carex norvegica* ssp. *conicorostrata*, *Puccinellia beringensis*, *xPucciphippsia czuckzorum* (hybrid between *Phippsia algida* and *Puccinellia* probably *wrightii*), *Oxytropis beringensis*, *O. katenii* and *Cardamine sphenophylla*), W Chukotka has five of its own (*Smelowskia czukotica*, *Papaver anjuicum*, *P. hypsipetes, Oxytropis sverdrupii* and *Plantago canescens* ssp. *jurtzevii*), and four endemic species are confined to W Alaska (*Ranunculus glacialis* ssp. *alaskensis* (glacier buttercup), *Parrya nauraq*, *Primula anvilensis* (primrose) and *Douglasia beringensis*). The provinces N Iceland-Jan Mayen, N Fennoscandia, Kanin-Pechora, Yamal-Gydan, Anabar-Olenyok, Yana-Kolyma, S Chukotka and Hudson Bay-Labrador lack their own Arctic endemic species.

Borderline species are absent in the remote floristic provinces of Svalbard-Franz Joseph Land, Wrangel Island, Ellesmere Land-N Greenland and E Greenland. All of these provinces represent islands isolated from the mainland to the south, and are mainly entirely high Arctic (Tab. 9.2). They are also unknown from E Chukotka and W Greenland, whereas Hudson Bay-Labrador has the highest reported number of borderline species (44 species), followed by W Alaska (25) and Central Canada (19).

Numbers of stabilized introduced species are highest for the floristic provinces N Fennoscandia (63 species), Kanin-Pechora (52), W Greenland (50) and N Iceland-Jan Mayen (52), followed by Polar Ural-Novaya Zemlya (32), Hudson Bay-Labrador (30), Taimyr-Severnaya Zemlya (23) and W Alaska (20) (Tab. 9.1). Some parts of the Arctic, such as the floristic provinces Ellesmere Land-N Greenland and Wrangel Island, are noteworthy for the complete absence of stabilized introduced species. Such species have also not been reported for the province Anabar-Olenyok, whereas only a few species are reported for E Greenland (2), S Chukotka (5) and W Chukotka (6). Several non-native species (*Plantago major* (great plantain)*, Chenopodium album* (common lamb's-quarters)*, Thlaspi arvense* (field penny-cress), *Brassica rapa* ssp. *campestris* (turnip) and *Trifolium hybridum* (alsike clover)) are widespread in the Arctic, occurring in all five floristic province groups (see further Appendix 9.4).

Stabilized introductions can often be attributed to continuous human activities when they occur in and around settlements and towns, in particular in climatologically favorable parts of the Euro-Siberian Arctic. In Iceland and N Fennoscandia, stabilized introductions strongly dominate in old cultural landscapes. In S and W Greenland, extensive small-scale agriculture using fields, hay meadows and pastures was introduced by Norse settlers more than 1,000 years ago, and nowadays agriculture, sheep breeding and forestry are common practices there (cf. Pedersen 1972, Fredskild 1988). The group of stabilized introductions is taxonomically very heterogeneous, as expected. They mainly include common species of synanthropic European vegetation (Appendix 9.4). Species of ruderal and arable weed vegetation include *Descurainia sophia* (tansy-mustard), *Thlaspi arvense* (penny-cress)*, Capsella bursa-pastoris* (shepard's-purse) and *Lamium purpureum* (purple dead-nettle). The grasses *Elytrigia repens* (couch), *Anthoxanthum odoratum* (sweet-vernal grass), *Lolium perenne* (rye-grass), *Poa pratensis* ssp. *angustifolia* (narrow-leaved meadow-grass), *P. supina* (supine bluegrass)*, Dactylis glomerata* (cock's foot), *Phleum pratense* (timothy) and *Alopecurus geniculatus* (marsh-foxtail), and the forbs *Trifolium pratense* (red clover), *Primula elatior* (oxlip) and *Veronica chamaedrys* (germander apeedwell) are indicators for nutrient-rich mesic and wet grasslands (Mucina 1997, Jarolímek & Šibík 2008).

### 9.2.3.8. Hotspots

Seen from large-scale perspectives such as subzones and floristic provinces, the taxonomic diversity of vascular plants in the Arctic is low in comparison with the vascular plant flora of non-Arctic biomes (Barthlott *et al.* 1996; see Fig. 1.1 in Meltofte *et al.*, Chapter 1). The same often applies for regional Arctic floras. However, there are several areas of enhanced taxonomic diversity in the Arctic due to strong abiotic factors, such as a heterogeneous climate. These areas of enhanced taxonomic diversity are often associated with dramatic topography, such as mountainous areas, and have been referred to as 'Arctic hotspots' (Elvebakk 2005) or polar oases (Crawford 2008a). They are extrazonal, locally warm areas with biodiversity elements not found in their surroundings. In Arctic hotspot complexes, topographic complexity leads to high climatic diversity and correspondingly higher biodiversity in flora and vegetation (Elvebakk 2005).

Four such hotspot complexes are found in Svalbard, where several thermophilous, low Arctic or southern species occur locally in high Arctic environments (Elvebakk 2005). Hotspots in high Arctic Canada include the Fosheim Peninsula on west-central Ellesmere Island (e.g. Hot Water Creek; Edlund *et al.* 1989) and Lake Hazen (Crawford 2008a) in the northernmost part of Ellesmere Island with a rich thermophilous vascular flora of 117 species (this is about 57% of the total flora of the Ellesmere Land-N Greenland floristic province (see Section 9.2.3.7), in the world's northernmost extension of high Arctic subzone C. Other hotspots in Canada include the Minto Inlet area of NE Victoria Island, where scattered tall willow riparian thickets with a diverse understory occur in *Carex* dwarf shrub tundra (Edlund 1983). Hotspots in Greenland are among others the continental inland of W Greenland around Søndre Strømfjord/Kangerlussuaq (Böcher 1954, Sieg *et al.* 2006) (subzone E of the low Arctic) with south-facing slopes of boreal-low Arctic steppe vegetation (*Saxifrago-Calamagrostietea purpurascentis*; Drees & Daniëls 2009) and the inland of S Greenland (Feilberg 1984) with Qinguadalen (Fredskild & Odum 1990) as a core area of the sub-Arctic forest enclave in low Arctic Greenland. The central part of Beringian Wrangel Island is certainly the most pronounced hotspot complex of the Russian Arctic (Kholod 2007). Due to the small-scale climatic and biotic diversity, the Arctic hotspot complexes are strongly recommended as Arctic field laboratories for climate change-related research (see Elvebakk 2005 and see Section 9.2.7).

## 9.2.4. Traditional use of vascular plants

Local fauna and flora have always played an essential role in the life and culture of the indigenous peoples of the Arctic (e.g. Robbé 1994, Ainana & Zagrebin 1997, Garibaldi 1999, Jones 2010). Traditionally, many plant species were collected for consumption of flowers, berries, stems, leaves or roots, and for other uses. Preservation for later consumption followed traditional customs. The use of plants as food by Inupiat and use as medicines by indigenous peoples in Alaska are described in Garibaldi (1999) and Jones (2010). Plant use by Chukotkan indigenous peoples is reviewed in Ainana & Zagrebin (1997). Traditional uses of plants by Arctic peoples in Canada are summarized in Aiken *et al.* (2007). Recent publications synthesize the knowledge of elders on the traditional use of plants by Gwich'in in sub-Arctic western Canada (Andre & Fehr 2000), by Inuit on Baffin Island (Ootoova *et al.* 2001), and by Inuvialuit in the western Canadian Arctic (Inuvialuit elders with Bandringa 2010).

Traditional use of plants in low Arctic SE Greenland is described by Robbé (1994), who studied the life and culture of Inuit hunters and their families in the small settlement Tiniteqilaq, Ammassalik district, in the 1960s. The uses of plants are varied in Greenland, as they are elsewhere in the Arctic, and include the use as vegetables in particular *Angelica archangelica* (garden angelica; stem), *Rhodiola rosea* (stone crop; flower, leaf, root), *Oxyria digyna* (mountain sorrel; leaf, root), *Taraxacum croceum* (leaf) and *Bistorta vivipara* (alpine bistort; root). The berries of other species such as the dwarf shrubs *Empetrum nigrum* ssp. *hermaphroditum* (black crowberry) and *Vaccinium uliginosum* ssp. *microphyllum* (polar bilberry) were eaten fresh or preserved for consumption. *Salix glauca* ssp. *callicarpaea* (grayleaf willow), *Betula nana* (dwarf birch) and *Juniperus communis* ssp. *nana* (common mountain juniper) were used as firewood or to make tools, while *Thymus praecox* (wild thyme) was used as a substitute for tobacco. Grasses and sedges, in particular *Poa alpina* (alpine meadow-grass), *Carex* spp. and some others, were used as insulation between the two sole layers in double-skinned seal skin boots (kamiks). Many useful plants have Greenlandic names (e.g. Osterman 1938, Böcher *et al.* 1966, Robbé 1994, Foersom *et al.* 1982).

## 9.2.5. Rare and threatened Arctic endemic species

### 9.2.5.1. Rare Arctic endemic species

Among the 106 Arctic endemic species, 69 species show a very restricted distribution within the Arctic territory, occurring in only one or two of the 21 floristic provinces. Forty-seven species are only known from one province (Appendix 9.2), and 28 of these are known only from one of the six Beringian provinces. The small island province Wrangel Island harbors 10 of its own endemics, E Chukotka has six and W Chukotka has five such endemics, whereas S Chukotka has none. Of the Beringian North American provinces, W Alaska has four own endemics as compared with only three in N Alaska (*Poa hartzii* ssp. *alaskana, Papaver "murrayii"* and *Potentilla* aff. *pensylvanica*). Among the Canadian provinces, Central Canada has two of its own endemic species (*Papaver* sp. "Banks" and *Braya thorild-wulfii* ssp. *glabrata*, smooth Greenland braya). Ellesmere Land-N Greenland has two local endemics (*Braya humilis* ssp. *ellesmerensis,* Ellesmere braya and *B. glabella* ssp. *prostrata,* prostrate braya), whereas Hudson Bay-Labrador lacks its own endemic species (see also Tab. 9.2).

Among the North Atlantic floristic provinces, W Greenland has three of its own rare endemics (*Sisyrinchium groenlandicum*, *Puccinellia porsildii* and *P. groenlandica*), whereas E Greenland has only one single endemic of its own: *Saxifraga nathorstii*. N Iceland-Jan Mayen and N Fennoscandia are lacking their own Arctic endemics altogether, whereas Svalbard-Franz Joseph Land is known to harbor (at least) three local endemics: *Puccinellia svalbardensis* (Svalbard alkali-grass), *Saxifraga svalbardensis* (Svalbard saxifrage) and *Potentilla insularis*. Of the three European Russian-W Siberian floristic provinces, only Polar Ural-Novaya Zemlya has two endemic species (*Astralagus gorodkovii* and *A. igoshinae*), while Kanin-Pechora and the Yamal-Gydan province are lacking their own endemic species. Similarly, two of the four E Siberian flora provinces (Anabar-Olenyok and Yana-Kolyma) lack their own endemics, whereas the Taimyr-Severnaya Zemlya province has four endemics (*Puccinellia gorodkovii*, *Oxytropis tichomirovii*, *O. middendorffii* ssp. *schmidtii* and *Draba taimyrensis*), and two endemics are restricted to the Kharaulakh province (*Oxytropis sordida* ssp. *arctolensensis* and *Papaver leucotrichum*).

Twenty rare (r) Arctic endemic species are restricted to only one floristic province and only one Arctic subzone (Tab. 9.4, Appendix 9.2) and almost all occur in the low Arctic (subzones D and E). An exception is *Saxifraga nathorstii*, which is found in subzone C of the high Arctic in the E Greenland floristic province.

### 9.2.5.2. Threatened Arctic species

Currently, we have no evidence that any Arctic plant species has become extinct in the last 250 years (Elven 2011). Nevertheless, all species with very low abundance and a restricted distribution might be considered potentially threatened in the context of future climate change. Such species may meet the guidelines of IUCN (2008) for threatened status when climate warming is considered a threat, however exact information on distribution, population number and size is often lacking. Other IUCN assessment criteria, such as information on population trends, are almost completely lacking for Arctic vascular plants.

In the Atlas of Rare Endemic Vascular Plants of the Arctic (Talbot *et al.* 1999), 69 taxa were identified as rare, although a different species concept from that in PAF was used. Moreover, 12 'micro-species' (agamospecies) of *Taraxacum* were included by Talbot *et al.* (1999) as well as several species of sub-Arctic or boreal territories such as the treeless Aleutian Islands. Considering these differences, we present in Tab. 9.4 a reduced list of 20 potentially threatened rare Arctic endemic species that occur in only one floristic province and one Arctic subzone based on our own evaluations from the PAF.

**Table 9.4.** The 20 Arctic endemic species and subspecies known only from one Arctic floristic province and one subzone as rare (r), and as such potentially threatened. Species ordered by family; their status in Talbot *et al.* (1999) is also indicated where included: VU = vulnerable; DD = data deficient; LR = lower risk; nt = near threatened.

| Species | | Status |
|---|---|---|
| Brassicaceae | *Parrya nauraq* | |
| | *Smelowskia czukotica* | VU |
| Cyperaceae | *Carex norvegica* ssp. *coniorostrata* | |
| Fabaceae | *Astralagus gorodkovii* | VU |
| | *Astralagus igoshinae* | DD |
| | *Oxytropis beringensis* | LR (nt) |
| | *Oxytropis katenii* | DD |
| | *Oxytropis middendorfii* ssp. *schmidtii* | |
| | *Oxytropis sordida* ssp. *arctolenensis* | LR (nt) |
| | *Oxytropis sverdrupii* | LR (nt) |
| Iridaceae | *Sisyrinchium groenlandicum* | LR (nt) |
| Papaveraceae | *Papaver anjuicum* | |
| | *Papaver hypsipetes* | |
| | *Papaver leucotrichum* | LR (nt) |
| Plantaginaceae | *Plantago canescens* var. *jurtzevii* | |
| Poaceae | *Poa hartzii* ssp. *alaskana* | LR (nt) |
| | *Puccinellia beringensis* | |
| Primulaceae | *Douglasia beringensis* | VU |
| Ranunculaceae | *Ranunculus glacialis* ssp. *alaskensis* | VU |
| Saxifragaceae | *Saxifraga nathorstii* | |

While threats to the endemic Arctic species are generally poorly known, they might increase because the Arctic is at the forefront of experiencing the effects of climate change, and other more direct human impacts are also increasing (ACIA 2005).

A new project on Red-listing of Arctic vascular plant species was recently initiated and should be finalized during 2014 (CAFF Flora Group). Only the species level is considered in the project, because of uncertainties about the status of many subspecies. For the same reason, *Taraxacum* and *Hieracium* micro-species are excluded from consideration, as they are poorly known in many cases and have extremely narrow distributions. The Red List for Arctic vascular plants will include mainly rare endemic species because of lack of good monitoring data. So far, a candidate list of 164 species is under discussion. For those species, all known data will be collected and evaluated following IUCN criteria (IUCN 2008). If considered threatened, they will be assigned an IUCN status of Critically Endangered, Endangered or Vulnerable. It is likely that only very few Arctic vascular plants will be considered threatened according to these criteria. It is critical to note that in the near absence of any population trend data on Arctic plants, critical evaluation of these taxa is very difficult. Trends on declining population size or number of individuals have so far not been detected and, if they do exist, would likely be too low to meet the IUCN criteria. The current status and trends of Arctic plants is based on much fragmentary information, and many assumptions have to be made in order to make informed decisions on the status of Red-listed species. For now, the best available information is the number of sites recorded in herbaria based on specimen collections or field observations. One needs to consider that the absence of a taxon in a distributional map is not necessarily a reflection of the situation in nature, but might represent a knowledge gap. For example, in the recent Red List reassessment of vascular plant species in Svalbard (which has a relatively well-known flora), the status of 28 species changed, but the majority of these changes was due to increased knowledge as a result of recent fieldwork (K.B. Westergaard, pers. com.).

Genetic diversity, in addition to species diversity, is also an important consideration when assessing the threatened status of a species. For example, the loss of genetic diversity is greatest if small genera are lost; given that mean species diversity within a genus is low in the Arctic, this may be an important consideration. While rare Arctic endemics are of obvious conservation concern, Arctic populations of species with an Arctic-alpine distribution should also be considered. Such species often have a very fragmented distribution with isolated populations likely not cross-breeding; thus, giving greater weight to these isolated genetically distinct Arctic populations may be appropriate (Väre *et al.* 2003). Also, climate change induced loss of habitat may cause considerable loss of genetic diversity within species, which may reduce the species ability to adapt to a changing climate (Alsos *et al.* 2012a)

## 9.2.6. Trends and monitoring efforts

Elders of the Kolymskaya village reported in 2006 that willows are moving to tundra and to river banks. They said:

> » *It tells of the changes which are under way. You should graze cows and horses, not reindeer on these spots. All of the tundra is covered with willows and bushes. It grows very fast now. We do not know how we can herd reindeer in the middle of these changes.*
>
> (Mustonen 2007).

Most vascular plants in the Arctic are long-lived to very long-lived, and many of them may have the genetic potential to spread into novel niches or persist in a changing climate. There are few threats that will affect the entire Arctic today or in the near future, but climate change certainly will (ACIA 2005). It is hard to predict what direct effects climate change will have on Arctic plant species. Many of them have already experienced pronounced climatic changes in post-glacial times. Climate change could affect the vegetation in several ways, and this too is hard to predict (Euskirchen *et al.* 2009). Northern plants are expected to loose 36-43% of their current distribution under the A2 climate change scenario and 26-43% under the B2 scenario (Alsos *et al.* 2012). It is reasonable to predict that in many cases borderline species and many others with southern distributions will increasingly move into the Arctic. Daniëls & de Molenaar (2011) observed a tendency of sub-arctification of the vascular plant flora near Ammassalik, SE Greenland, during the last 100 years. Other studies across the Arctic have shown decadal and multidecadal changes in species composition of plant communities (e.g. Callaghan *et al.* 2011a, 2011b, Daniëls *et al.* 2011, Henry *et al.* 2012, Kapfer *et al.* 2012, Schmidt *et al.* 2012). In general, these changes are minor in dry habitats, however more pronounced in moist and wet sites, such as snow beds, mires, fens and shallow ponds. This is likely explained by substrate drying due to earlier snow melt along with strong warming in summer. Shrub expansion in the Arctic is reported in several publications (see summary by Klein *et al.* 2008 and Ims & Ehrich, Chapter 12). A recent study by Henry *et al.* (2012) showed that increased shrub cover all over the Canadian Arctic was supported by results from experimental warming. The fate of cold climate plants in a warmer world has been amply addressed and summarized by for example Callaghan (2005) and Crawford (2008a, 2008b). Possible changes in the composition of the vascular plant flora are difficult to predict. However the heterogeneity of Arctic habitats together with genotypical and phenotypical variability of Arctic plants will certainly result in the evolution of adaptations that may benefit from higher temperatures and longer growing seasons (Crawford 2008b). Callaghan (2005) suggests that Arctic biodiversity is likely resistant to variations in climate, but perhaps not to competition that will come from southern species expanding their ranges to the north. Crawford (2008b, p. 224) expects that "botanists in the future may look forward to relaxed exploration of a diverse and plentiful flora as far as north as land exists."

While the CAFF Circumpolar Biodiversity Monitoring Program (CBMP) is promoting active engagement of local communities in monitoring programs (Gofman 2010) and has initiated a Terrestrial Expert Group, the formation of formal networks dealing with plants in the Arctic as a whole has been rather slow. There are a few regional initiatives that are working towards providing baseline information on plant biodiversity in the Arctic. The most advanced of these initiatives is a detailed monitoring plan in Svalbard to document population trends in selected rare plant species, a monitoring effort initiated by the Norwegian Polar Institute.

Monitoring programs have been established in two areas of Svalbard. A program in Colesdalen is focusing specifically on population trends in five rare vascular plant species (Arnesen *et al.* 2012), while the program in Endalen is focusing on monitoring vegetation and possible effects of climate change and pollution on floristic composition (Aarrestad *et al.* 2010). In 2008-09, monitoring of population trends in five vascular plants, of which four are regionally Red-listed, was initiated in Colesdalen: the annual herb *Euphrasia wettsteinii* (EN), the perennial herb *Campanula rotundifolia* ssp. *gieseckiana* (common harebell) (EN), and the dwarf shrubs *Vaccinium uliginosum* spp. *microphyllum* (CR), *Empetrum nigrum* ssp. *hermaphroditum* and *Betula nana* ssp. *tundrarum* (EN) (Alsos 2011). Occurring on warm south-facing slopes with favourable climate, these species are at their climatic limit in Svalbard and are expected to be sensitive to climate change. Action plans are currently being prepared for the four Red-listed species (Alsos & Arnesen 2009). With their local distributions very well documented, monitoring is focusing on population dynamics and development, and includes monitoring of local climate and physical conditions at the habitats.

In Alaska, the U.S. National Park Service's Arctic Parks Network has initiated inventory and monitoring in remote regions to describe current biodiversity, and to give land managers and other agencies the information needed to make more informed decisions about protecting potentially rare and endangered species (Parker 2006, Racine *et al.* 2006). Similarly, the U.S. Bureau of Land Management is actively monitoring rare plants in Alaska (Carroll *et al.* 2003, Cortés-Burns *et al.* 2009). The University of Alaska Fairbanks, which administers the Toolik Lake Field Station, has several Long-Term Ecological Research sites in the northern foothills of the Brooks Range. Cortés-Burns *et al.* (2009) reviewed information on 31 rare vascular plants of Alaska's North Slope Region, including population number and location, but no information on population size is given. In response to the increasing threat of the establishment and spread of non-native plant species (see Lassuy & Lewis, Chapter 16), the U.S. Forest Service has developed a ranking system to help identify problematic non-native plants and to prioritize control efforts in Alaska (Carlson *et al.* 2008).

While there are numerous programs focused on monitoring vegetation change as a result of climate change in Arctic Canada and a few in Greenland, there are almost none focused specifically on monitoring populations of rare or threatened species. One example is the extensive monitoring at Zackenberg, NE Greenland, which has taken place over the last 18 years (e.g. Bay 2006, Meltofte *et al.* 2008). The Government of the Northwest Territories in Canada initiated the NWT General Status Ranking Program in 1999 to collect information on wild species as a tool for setting conservation priorities. Information is assembled in an on-line database, the NWT Species Monitoring Infobase, and reports on the general status ranks are published every five years. The ranks of all vascular plant species were first published in 2006 using the following categories: 'May Be at Risk', 'Sensitive', 'Secure', 'Alien' or 'Undetermined' (Working Group on General Status of NWT Species 2006). The 2011 report documented 89 changes in ranks of vascular plant species, all due to new information, taxonomic change or a more rigorous assessment of threats, rather than a real change in status (Working Group on General Status of NWT Species 2011).

The necessity of establishing an International Arctic Vegetation Database for circumpolar biodiversity studies was recently articulated by Walker & Raynolds (2011) and Walker *et al.* (2013). Plants, mainly vascular plants and bryophytes, and lichens are the main structural components of the plant communities in the terrestrial Arctic landscapes. The floristic composition of these communities reflects the present day local habitat conditions and the geographical position of the plant communities. Thus, the distribution of plant communities shed light on environmental conditions, and they can be regarded as early warning systems for environmental change. However, circumpolar knowledge of plant community types and their classification is still rather poorly developed (cf. Walker *et al.* 1994, Daniëls *et al.* 2005), and a circumpolar floristic classification system is still lacking. There is thus a strong need to bring together all existing plot-based vegetation analyses in an International Arctic Vegetation Database along with intensifying the exploration of vegetation in poorly studied and unstudied areas. In particular, floristical vegetation plot analyses are very scarce from the climatologically most extreme, ecologically unique and likely most sensitive and vulnerable part of the Arctic, its northernmost Subzone A (cf. Walker *et al.* 2012). Hence, storage of plot-based vegetation analyses in an International Arctic Vegetation Database is fundamental for circumpolar biodiversity studies, monitoring and predictive modeling efforts (Walker & Raynolds 2011, Walker *et al.* 2013).

### 9.2.7. Conclusions and recommendations

There is a great need for intensifying biodiversity research on Arctic flora with emphasis on molecular phylogenetic taxonomy, vegetation classification, monitoring and modeling. Coordination and cooperation between researchers must be improved. Baseline information on the distribution of Arctic plant species, including population number and size, is essential for accurately determining species status. Given the almost complete lack of population trend data for Arctic plant species, monitoring programs should be established in order to gather trend data. The conservation status of Arctic plant species can only be objectively assessed once information becomes available on the population status and trends of individual species and their plant community types. Due to their small-scale climatic and biotic diversity, Arctic hotspot complexes are strongly recommended as Arctic field laboratories for climate change-related research (see Elvebakk 2005) and for consideration as protected areas. In particular, monitoring of species ranges along altitudinal gradients in Arctic mountains is strongly recommended. Here we might expect above all species response to climate warming due to the relatively steep climate gradient (e.g. Elvebakk 2005, Schwarzenbach 2006, Pauli *et al.* 2007, Jedrzejek *et al.* 2012, 2013).

## 9.3. BRYOPHYTES

Bryophytes comprise three monophyletic groups: mosses (Bryophyta; Bryopsida), liverworts (Hepatophyta; Hepaticopsida) and hornworts (Anthocerotophyta;

Antherocerotopsida) (Raven *et al.* 2005). The liverworts are generally considered the oldest group of aquatic-terrestrial plants, derived from algal (charophycean) ancestors in the Ordovician (Graham & Gray 2001). Earth's oldest fossil record of bryophytes is the liverwort *Metzgeriothallus sharonae,* dating from the Middle Devonian (Givetian) in eastern New York, USA (Hernick *et al.* 2008). Our current understanding of the phylogeny of bryophytes and other land plants was reviewed by Groth & Knoop (2005). Their phylogenetic analysis of molecular sequences from the mitochondrial genome provided evidence for the status of liverworts as the basal group of extant land plants and hornworts as sister to the tracheophytes (Gradstein & Heinrichs 2005).

Bryophytes strongly differ from vascular plants in life cycle, structure and physiology. Both have a diplohaplont life cycle characterized by the fact that meiosis (reduction of chromosome pairs to one copy) occurs before syngamy. However in bryophytes meiosis does not occur immediately before syngamy as in vascular plants. The haploid (n) gametophyte is the dominant stage (or phase) in all bryophyte groups, whereas in vascular plants it is the diploid (2n) sporophytic generation. The gametophyte is formed after germination of uniform haploid spores (homoiospory) produced by meiosis in the sporophyte, which is attached to the gametophyte. Germinated spores each produce a protonema that develops into a mature individual. These can be thallose or with leafy stems with different growth forms. In male sex organs many spermatozoids are produced, whereas only one egg cell is formed in female sex organs. Bryophytes can be monoecious, with gametophores possessing both male and female sex organs on the same plant; or dioecious, with gametophores that bear male and female sex organs on separate plants. Transport of spermatozoids to the egg cells is only possible in water. After fertilization, the sporophyte develops and remains connected with the gametophyte. Asexual propagation is common and contributes to short-distance dispersal, whereas spores, which can be long-lived, also contribute to long-distance dispersal. Chromosome numbers in liverworts and hornworts are generally low and stable (9 and 5, respectively) but polyploidy including allopolyploidy is present especially in the Arctic (Schuster & Damsholt 1974, Vilnet *et al.* 2010). In mosses, higher chromosome numbers occur, and autopolyploidy (polyploidy arising from chromosomes of the same source through spontaneous doubling of chromosome number) is not uncommon (Schofield 1985, During 1992, Damsholt 2002, Raven *et al.* 2005, Glime 2007).

Bryophytes have a rather simple morphology, anatomy and physiology. The gametophyte is either thallose (in liverworts and hornworts) or with leafy stem (liverworts and mosses) and may be attached to the substrate by rhizoids. True roots, stems and leaves are not developed. Lignin synthesis for support of vertical growth is absent. Most bryophytes are not able to regulate uptake and release of water, gases and minerals. Contrary to almost all vascular plants, bryophytes are poikilohydric, thus physiologically inactive when dry (Schofield 1985). Low stature and a poikilohydric nature make them mainly dependent upon conditions of the uppermost soil, substrate surface and adjoining atmosphere. As a result, bryophytes are weaker competitors than vascular plants. However they seem well adapted to their "limited mode of life, but also liberated, being able to grow where vascular plants cannot" (Proctor 2000a, 2000b).

Bryophyte biodiversity on a worldwide scale in terms of species number is rather low compared with that of the vascular plants. Nowadays c. 16,000 bryophyte species are known worldwide; c. 6,000 liverworts, c. 100 hornworts and c. 9,900 mosses (Raven *et al.* 2005). This is only c. 6% of the c. 260,000 vascular plant species (Raven *et al.* 2005).

As a group, bryophytes have a cosmopolitan distribution (Herzog 1926, Shaw *et al.* 2005). They become dominant where vascular plants meet less optimal growth conditions. They can cope with harsh and special environmental conditions and show various growth forms (Birse & Gimingham 1957) and life strategies (During 1979, 1992) (see also Schofield 1972 and Longton 1982, 1988).

### 9.3.1. Bryophytes in the Arctic

Bryophyte vegetation in the Arctic is mainly dominated by turf and mat growth forms (Schofield 1972). Short turfs are loose or more frequently compact colonies, < 1-2 cm tall, formed by sparingly branched acrocarpous mosses with main shoots parallel and erect. The branches are erect and of indeterminate growth, such as in e.g. the moss genera *Pottia* and *Bryum* and some liverworts e.g. *Tetralophozia setiformis* (monster pawwort), *Lophozia personii* (chalk notchwort) and species of the genera *Gymnomitrion* (frostwort) and *Scapania* (earwort). Tall turfs are > 2 cm tall, and are divided into turfs of acrocarpous mosses with erect branches such as in e.g. *Dicranum* (forkmoss) and *Polytrichum* (haircap moss) and turfs of pleurocarpous mosses with divergent branches forming more frequently loose colonies such as in e.g. *Orthothecium chryseon* (golden autumn moss), *Drepanocladus* (hookmoss) and *Sphagnum* (bogmoss). Mats are formed by leafy liverworts, e.g. the genus *Cephalozia* (pincerwort), *Ptilidium ciliare* (ciliated fringewort), *Marsupella arctica* (Arctic rustwort), *Cephaloziella* (threadwort) and *Lophozia* (notchwort), or mosses (e.g. *Racomitrium,* fring-moss) with determinate branching of prostrate or ascending interweaving shoots in compact colonies. In turfs, mats and carpets many species of bryophytes are usually intermingled, so in small patches of c. 3-5 $m^2$ up to 15-20 species can be found. Open turfs and thread growth form (single shoots on lichens and on bare soil) are characteristic for many bryophytes in the high Arctic, especially on exposed sites. In cracks in patches of bare soil in spotted tundras, on bare soil between boulders, in cracks between polygons, and on wet bare soil on solifluction slopes, single thalli of liverworts such as e.g. *Athalamia, Sauteria* as well as *Scapania gymnostomophyla* (narrowlobed earwort), *S. cuspiduligera* (untidy earwort), *Leiocolea heterocolpos* var. *harpantoides* (ragged notchwort) and many more occur. Their small size (often less than 1 mm broad and several mm long) allow many species to persist in microhabitats.

There is little known about life strategy types of bryophytes in Arctic. This topic is discussed in only a few publications (Mogensen 1987, 2001). The life strategy types perennial stayer, colonist and fugitive are most conspicuous in the Arctic as was shown for Greenland by Mogensen (1987, 2001), however shuttle species occur as well. Perennials stayers occur in relatively constant or regularly, moderately fluctuating environments. They have a long, variable life span, a low sexual and asexual reproduction effort and small spores (< 20 µm), and can be divided into competitive and stress-tolerant perennial stayers (During 1992). Their growth form is mainly tall turf (e.g. *Dicranum*) and rough mats (*Calliergon,* spear moss*, Drepanocladus* and *Sphagnum*). Colonists have a short lifespan (< 5 years), a high asexual and sexual reproductive effort and very persistent, small spores (< 20 µm). Their growth form is predominantly short turf (e.g. *Pohlia,* nodding moss*, Andreaea,* rockmoss and *Amphidium*, yokemoss) and smooth mat (e.g. *Cephaloziella, Anthelia,* silverwort and *Cephalozia*). Fugitives are ephemeral or annual with a high sexual reproductive effort, frequent sporophyte development and with small spores (< 20 µm). The spores are very persistent and can be long-lived. The gametophyte has an open turf growth form. They are widespread and mainly occur in small-scale unstable and disturbed habitats (e.g. *Funaria,* cord-moss, *Desmatodon*, screwmoss, *Pottia,* tuftmoss and *Stegonia*, screwmoss). Species of the dung moss family Splachnaceae (e.g. *Splachnum vasculosum,* rugged collar-moss and *Tetraplodon pallidus*, cruet-moss) have a shuttle strategy. They grow on temporary organic substrates such as the dung of musk oxen, reindeer, Arctic hares and lemmings. They have a short turf growth form, a pauci-pluriennial life span and their sexual reproductive effort is high. They frequently produce sporophytes and clumps of spores are distributed by insects.

In small ponds and lakes, mires, bogs, spring areas, along melt water creeks and snow beds (Fig. 9.5), and amid dwarf shrub heaths and rocks, mosses and liverworts are locally abundant and dominant, constituting plant communities of their own (cf. Holmen 1955, Brassard 1971a, 1971b, Steere 1976, Longton 1982, 1988, Frisvoll & Elvebakk 1996, Dierßen 2001, Dierssen &

**Figure 9.5.** Moss-rich snow bed near Cape Isachsen, Ellef Ringnes Island, Canada (Arctic subzone A). The vegetation is dominated by the mosses *Bryum cryophilum* (red), *Aulacomnium turgidum* (mountain groove moss) and *Orthothecium chryseon*. Photo: Fred J.A. Daniëls, July 2005.

Dierssen 2005). Beyond that, bryophytes often contribute strongly to the species richness of many other tundra vegetation types (cf. Hadač 1989, Möller 2000, Sieg *et al.* 2006, Kholod 2007, Walker *et al.* 2011, Jedrzejek *et al.* 2012). Very few vegetation types in the Arctic occur without bryophytes. Single shoots occur almost everywhere, in particular in the high Arctic. On a fine scale (up to a few square kilometers), species diversity of bryophytes (and lichens) is higher than that of vascular plants. The bryophyte flora of Svalbard counts c. 388 species whereas less than 200 species of vascular plants are recorded for this archipelago. Nevertheless, the overall species number of bryophytes in the Arctic is distinctly lower than that of vascular plants (c. 2,218) (this chapter), while the small group of hornworts (worldwide c. 100 species) is absent. In general species number of bryophytes decreases from the taiga zone to the Arctic but the contribution of bryophytes in plant diversity increases. Particularly in the Murmansk Province situated in the sub-Arctic the ratio of bryophyte species to vascular plants species (including adventive species) is c. 1:2, whereas in Svalbard this ratio is c. 2:1 (N.A. Konstantinova, unpubl.). Diversity of bryophytes in the Arctic (c. 900 species) is 2.5 times lower than the diversity of vascular plants, whereas the world species number of bryophytes (16,000 species) is c. 16 times lower than that of vascular plants (c. 260,000 species).

The use of bryophytes by indigenous peoples of the Arctic is little known and probably very minor. In SE Greenland, three bryophyte species were reported to be commonly used, although not for consumption: *Polytrichum* species as lighter of oil lamps, *Sanionia uncinata* (sickle-leaved hookmoss) as wick in oil lamps and *Racomitrium lanuginosum* (wooly fringemoss) as sponge and cleaning tissue (Robbé 1994). Some bryophytes have Greenlandic names: *Dicranum fuscescens* (dusky forkmoss, issuatsiaat illaagutaasat), *Marchantia alpestris* (mountain livergreen, issuatsiaat sialussiutillit), *Hylocomium splendens* (glittering woodmoss, issuatsiaaat qaleriiaattut), *Racomitrium lanuginosum* (issuatsiaat qasertut), *Sanionia uncinata* (issuatsiaat kukiusallit) and *Sphagnum girgensohnii* (Girgensohn's bog-moss, issuatsiaat iparaq) (Foersom *et al.* 1982).

## 9.3.2. Arctic bryofloristic studies

Steere (1954, 1971) reviewed the main results of Arctic bryology research up to the 1950s and 1970s, respectively. The latter publication is an important reference work comprising more than 150 titles of taxonomic and floristic studies. One year later, Schofield (1972) published a thorough review of the main results of bryological research in Arctic and boreal North America and Greenland.

The monographs of the moss floras of the Queen Elizabeth Islands in high Arctic Canada (Brassard 1971a, 1971b) and of Arctic Alaska (Steere 1978), the liverwort floras of Arctic Alaska (Steere & Inoue 1978), of W Greenland (Schuster & Damsholt 1974) and S Greenland (Schuster 1988), the three volumes of the Illustrated Moss Flora of Arctic North America (Long 1985, Crum 1986, Murray 1987), and the moss checklist of Canada (Ireland *et al.* 1987) are other key contributions to the Arctic bryoflora.

Longton (1988) mentioned species numbers for several Arctic regions stating that assessment of the size, geographical affinity and history of the Arctic bryofloras is still hampered by inadequate distribution data and taxonomic uncertainty. Particularly in boreal and Arctic mosses and liverworts, taxonomic problems are considerable due to their reactions to unfavorable or extreme environmental conditions (e.g. Schuster & Damsholt 1974, Steere 1979, Schuster 1988). Steere (1979) stated "The genus *Bryum* in the high Arctic will remain an almost impenetrable mystery." The taxonomic problems are of biological/physiological and bryogeographical nature. In polar deserts with high alkalinity and little precipitation many species occur as dwarf forms. Liverworts of the genera *Lophozia* and *Scapania* show considerable plasticity, which may explain the lack of consistency in taxonomic approach particularly in the families Lophoziaceae, Scapaniaceae and Jungermanniaceae (e.g. Schuster & Damsholt 1974, Damsholt 2002, Konstantinova & Vilnet 2009, Konstantinova *et al.* 2009, Söderström *et al.* 2010, Vilnet *et al.* 2010; see also Appendix 9.5). Thus, in Russia *Scapania* is by far the most species-rich liverwort genus (with 29 species), whereas *Lophozia* is split into a number of separate genera and has only eight species. In Greenland and Alaska, *Lophozia* is the most species-rich genus (with 35 and 31 species, respectively), whereas *Scapania* has 24 and 20 species, respectively. These differences are mainly due to different taxonomic concepts of these genera and their families (Tab. 9.6, Appendix 9.5). There is also a considerable variation in the moss genera *Drepanocladus*, *Calliergon* (spearmoss) and *Brachythecium* (feathermoss) (Hedenäs 1992). Other problems are associated with the lack of knowledge in many areas influencing the results of biodiversity studies on genus and family level (Afonina & Czernyadjeva 1995, 1996).

Other important floristic publications in the last three decades include checklists (e.g. Frisvoll & Elvebakk 1996, Afonina 2004) and regional and local monographs (e.g. Lewinsky 1977, Schuster 1988, Afonina *et al.* 2005, Belkina & Likhachev 2008, Konstantinova & Savchenko 2008, Damsholt 2010). Molecular phylogenetic studies of Arctic bryophytes are becoming more common, and the results of such studies will certainly influence taxonomic concepts and classification systems in the future, and consequently the assessment and interpretation of diversity and origin of the Arctic bryoflora (e.g. Konstantinova & Vilnet 2009, Konstantinova *et al.* 2009, Söderström *et al.* 2010, Vilnet *et al.* 2010).

## 9.3.3. Regional surveys of Arctic bryodiversity

The present assessment of species richness in different regions of the Arctic is derived from heterogeneous sources that differ in age (from 2010 back to 1978)

| **Moss region**<br>Census | **Russia**<br>1995/6 | **Svalbard**<br>1996 | **Greenland**<br>2003 | **Canada**<br>1987 | **Alaska**<br>1978 |
|---|---|---|---|---|---|
| Number of moss species | 530 | 288 | 497 | 343 | 408 |
| Number of genera | 154 | 103 | 133 | 103 | 136 |
| Number of families | 43 |  | 22 | 30 | 38 |
| Number of species in genus |  |  |  |  |  |
| *Bryum* | 39 | 18 | 42 | 25 | 26 |
| *Sphagnum* | 36 | 13 | 24 | 18 | 30 |
| *Pohlia* | 20 | 11 | 18 | 14 | 11 |
| *Dicranum* | 16 | 10 | 13 | 12 | 12 |
| *Hypnum* | 11 | 4 | 12 | 11 | 14 |
| *Encalypta* | 10 | 8 | 10 | 9 | 12 |
| *Drepanocladus* | 4 | 1 | 15 | 12 | 15 |
| *Grimmia* | 15 | 8 | 14 | 10 | 6 |
| *Brachythecium* | 20 | 6 | 19 | 9 | 8 |
| *Schistidium* | 8 | 12 | 15 | 6 | 7 |
| *Splachnum* | 5 | 5 | 5 | 5 | 5 |
| Percentage of moss flora | 32 | 22 | 36 | 30 | 29 |
| Number of species in family |  |  |  |  |  |
| Bryaceae | 65 | 33 | 64 | 44 | 45 |
| Dicranaceae | 53 | 31 | 48 | 35 | 37 |
| Amblystegiaceae | 46 | 19 | 50 | 40 | 46 |
| Pottiaceae | 43 | 14 | 33 | 31 | 44 |
| Grimmiaceae | 35 | 27 | 43 | 23 | 17 |
| Sphagnaceae | 36 | 13 | 24 | 18 | 30 |
| Hypnaceae | 34 | 10 | 25 | 19 | 23 |
| Mniaceae | 28 | 13 | 22 | 17 | 15 |
| Brachytheciaceae | 27 | 9 | 23 | 12 | 13 |
| Polytrichaceae | 20 | 13 | 15 | 15 | 15 |
| Splachnaceae | 18 | 9 | 14 | 10 | 17 |
| Percentage of Arctic moss flora | 77 | 62 | 73 | 77 | 74 |
| Number of liverwort species | 201 | 85 | 173 | 78 | 135 |
| Total number of bryophyte species | 731 | 373 | 670 | 421 | 543 |

**Table 9.5.** Species numbers of species-rich moss genera and families in the Arctic. Numbers highlighted in coloured fields are used in calculating the percentage of the total moss flora. Listed are *Splachnum*, genera with at least 10 species and families with at least nine species.

and species concepts, classification and nomenclature. These sources also pertain to regions of unequal size and intensity of research. Primarily, sources for this assessment include the following: for Arctic Russia, Afonina & Czernyadjeva (1995, 1996) (mosses) and Konstantinova *et al.* (2009) (liverworts); for Svalbard, Frisvoll & Elvebakk (1996) (mosses and liverworts); for Greenland, Goldberg (2003) (mosses) and Damsholt (2010) (liverworts); for the Canadian Arctic Archipelago, Ireland *et al.* (1987) (mosses); and for Alaska, Steere (1978) (mosses) and Steere & Inoue (1978) with later additions of Potemkin (1995) (liverworts).

In the absence of a detailed circumpolar checklist of bryophytes of the Arctic, the present comparative analysis and evaluation of these sources allow a global picture of the variation of the Arctic bryoflora.

The area covered by these publications is not completely compatible with the Arctic territory of the CAVM (Walker *et al.* 2005). The very small Arctic part of northern Iceland and the Norwegian continent are not covered, whereas for Canada only the Arctic Archipelago and the eastern Arctic are included. Transition areas between taiga and tundra in Russia and Alaska are probably partly included.

Only species are considered; infraspecies categories are not considered here. Because of the absence of a checklist of bryophytes of the Arctic, the nomenclature of species and genera follows the literature used in the regional checklists. Liverworts are primarily assigned to families according to Damsholt (2002), otherwise to Konstantinova *et al.* (2009) and Steere & Inoue (1978). Moss genera were primarily assigned to families according to Brotherus (1923), otherwise to Afonina & Czernyadjeva (1995, 1996).

The time limitations of preparing the present assessment did not allow inclusion of all new scattered literature

| **Liverwort region**<br>Census | **Russia**<br>2009 | **Svalbard**<br>1996 | **Greenland**<br>2010 | **Canada**<br>1947 | **Alaska**<br>1978 |
|---|---|---|---|---|---|
| Number of liverwort species | 201 | 85 | 173 | 78 | 135 |
| Number of genera | 73 | 34 | 50 | 28 | 49 |
| Number of families | 29 | 15 | 22 |  | 30 |
| Number of species in genus |  |  |  |  |  |
| *Scapania* | 29 | 16 | 24 |  | 20 |
| *Lophozia* | 8 | 16 | 35 |  | 31 |
| *Jungermannia* | 5 | 4 | 9 |  | 4 |
| *Cephalozia* | 9 | 4 | 5 |  | 5 |
| *Cephaloziella* | 11 | 2 | 12 |  | 4 |
| *Marsupella* | 8 | 2 | 10 |  | 2 |
| *Leiocolea* | 6 |  |  |  |  |
| *Lophoziopsis* | 7 |  |  |  |  |
| *Orthocaulis* | 5 |  |  |  |  |
| *Nardia* | 5 | 1 | 4 |  | 2 |
| *Barbilophozia* | 4 | 5 |  |  | 3 |
| *Gymnomitrion* | 4 | 3 | 5 |  | 2 |
| *Tritomaria* | 3 | 4 | 5 |  | 4 |
| *Anastrophyllum* | 1 | 1 | 4 |  | 6 |
| Percentage of liverwort flora | 46 | 44 | 61 |  | 46 |
| Number of species in family |  |  |  |  |  |
| Scapaniaceae | 32 | 18 | 28 |  | 24 |
| Jungermanniaceae | 77 | 36 | 64 |  | 52 |
| Gymnomitriaceae | 14 | 6 | 18 |  | 4 |
| Cephaloziaceae | 13 | 7 | 11 |  | 8 |
| Cephaloziellaceae | 11 | 2 | 12 |  | 4 |
| Percentage of liverwort flora | 73 | 64 | 77 |  | 56 |
| Number of moss species | 530 | 288 | 497 | 343 | 408 |
| Total number of bryophyte species | 731 | 373 | 670 | 421 | 543 |

**Table 9.6.** Species numbers of species-rich liverwort genera and families in the Arctic. Numbers highlighted in coloured fields are used in calculating the percentage of the total liverwort flora. Listed are liverwort genera with at least 10 species and families with at least 9.

of recent years, such as e.g. on three *Sphagnum* species new to the bryoflora of Greenland (Flatberg 2007). The same applies for some recent molecular-based studies on phylogeny and systematics of the liverwort families Lophoziaceae, Scapaniaceae, Gymnomitriaceae and Jungermanniaceae (e.g. Söderström *et al.* 2010, Vilnet *et al.* 2010), which resulted into rearrangements of taxa.

### 9.3.3.1. Russia

About 731 bryophyte species are known from Arctic Russia including 530 moss species and 201 liverwort species (Tab. 9.5, 9.6, 9.7). In the Russian Arctic, the 530 moss species include 154 genera in 43 families (Afonina & Czernyadjeva 1995; Tab. 2 in Afonina & Czernyadjeva 1996) (Tab. 9.5). Prominent families (with more than 10 genera) include Pottiaceae and Dicranaceae (each 16) and Amblystegiaceae and Hypnaceae (feather moss family; each 14). Mniaceae (thyme moss family), Bryaceae and Polytrichaceae have seven genera each, and Brachytheciaceae and Grimmiaceae each have six (Tab. 1 in Afonina & Czernadjeva 1996). Species diversity is highest in Bryaceae (65 species), followed by Dicranaceae (forkmoss family; 53), Amblystegiaceae (feather-moss family; 46), Pottiaceae (43), the monotypic Sphagnaceae (36), Grimmiaceae (35), Hypnaceae (34) and Mniaceae (28), Brachytheciaceae (27), Polytrichaceae (20) and Splachnaceae (18). These families provide 77% of the species of the moss flora. Species diversity is highest in the genus *Bryum* (Bryaceae; 39 species) and *Sphagnum* (Sphagnaceae; 36), followed by *Pohlia* (Bryaceae; 20), *Brachythecium* (Brachytheciaceae; 20), *Dicranum* (Dicranaceae; 16), *Grimmia* (Grimmiaceae; 15) and *Encalypta* (extinguisher moss, Encalyptaceae, extinguisher moss family; 10). These genera account for 32% of the species of the total Russian Arctic moss flora (Tab. 9.5).

Two hundred and one species of liverworts in 73 genera and 33 families are reported from the Russian Arctic (Konstantinova *et al.* 2009) (Tab. 9.6, Appendix 9.5), and are here assigned to 29 families. Species diversity is highest in Jungermanniaceae (*sensu* Damsholt 2002; 77 species) and Scapaniaceae (32) followed by Gymnomitriaceae (14), Cephaloziaceae (13) and Cephaloziellaceae (11) (Tab. 9.6). Together they make up 73% of the total Russian liverwort flora. Species diversity is highest in the genus *Scapania* (Scapaniaceae; 29 species), followed by *Cephaloziella* (Cephaloziellaceae; 11), *Cephalo-*

*zia* (Cephaloziaceae; 9), the rustwort genus *Marsupella* (Gymnomitriaceae; 8) and the genus *Lophozia* (Jungermanniaceae; 8). *Lophoziopsis* has seven species, *Leiocolea* six and *Jungermannia*, *Orthocaulis* and *Nardia* (flapwort) five each. These latter five genera are all classified here as Jungermanniaceae. These genera comprise 46% of the liverwort flora in the Russian Arctic. However, molecular-based studies on phylogeny and systematics of the Lophoziaceae, Scapaniaceae, Gymnomitriaceae and Jungermanniaceae (e.g. Söderström *et al.* 2010, Vilnet *et al.* 2010) have resulted in considerable rearrangements of families and genera. Thus, quite different classification concepts are certain to be considered in the future.

#### 9.3.3.2. Svalbard

The small high Arctic island archipelago of Svalbard has been relatively well investigated. About 373 bryophyte species are known from here (Tab. 9.5 and 9.6). Frisvoll & Elvebakk (1996) accepted 288 moss species in 103 genera for Svalbard. Genera with 10 or more species include *Bryum* (18 species), *Sphagnum* (13), *Schistidium* (12), *Pohlia* (11) and *Dicranum* (10), collectively contributing to 22% of the total moss flora of Svalbard. Species-rich families include Bryaceae (with 33 species), Dicranaceae (31), Grimmiaceae (27), Amblystegiaceae (19), Pottiaceae (14), Sphagnaceae, Mniaceae and Polytrichaceae each with 13 species, Hypnaceae (10) and Brachytheciaceae and Splachnaceae with nine species each, collectively making up 62% of the Svalbard moss flora (Tab. 9.5).

The 85 liverwort species belong to 34 genera assigned here to 15 families (Tab. 9.6, Appendix 9.6). Jungermanniaceae shows by far the highest species diversity (36 species), followed by Scapaniaceae (18). These two families collectively account for 64% of the liverwort flora of Svalbard. Species numbers are highest in *Lophozia* (including *Lophoziopsis, Leiocolea sensu* Konstantinova *et al.* 2009) and *Scapania* (16 each), followed by *Barbilophozia* (pawwort, 5, including *Orthocaulis*). Recently, 14 species were added to the bryoflora of the archipelago (Konstantinova & Savchenko 2006, 2008a, 2008b, 2012, Borovichev 2010).

#### 9.3.3.3. Greenland

Around 670 bryophyte species are known from Greenland (Tab. 9.5 and 9.6). Mogensen (2001) mentioned 478 moss species (incl. 31 species of S*phagnum* and seven of *Andreaea*) from Greenland (cf. also Mogensen 1987, Jensen 2003). However Lange (1984) and Crum (1986) accepted 23 species of *Sphagnum.* Goldberg (2003) listed 497 moss species in 133 genera collected from Greenland and housed at the Museum Botanicum Hauniense (Copenhagen). This is the only 'checklist' currently available. Species-rich genera include *Bryum* (42 species), *Sphagnum* (24), *Brachythecium* (19), *Pohlia* (18), *Drepanocladus* and *Schistidium* (15 each), *Grimmia* (14), *Dicranum* (13), *Hypnum* (12) and *Encalypta* (10) (Tab. 9.5). Together, they comprise 36% of the total number of moss species in Greenland (Tab. 9.5). The species number of *Sphagnum* is not up to date, since Flatberg (2007) found three new species in Greenland, *Sphagnum concinnatum*, *S. tundrae* and *S. olafii.* They are not considered in the present calculations (see Section 9.3.3). The most species-rich families are Bryaceae (64 species), Amblystegiaceae (50), Dicranaceae (48), Grimmiaceae (43), Pottiaceae (33), Hypnaceae (25), Brachytheciaceae and Sphagnaceae (24 each), Mniaceae (22), Polytrichaceae (15) and Splachnaceae (14). Together they account for 73% of the total moss flora of Greenland (Tab. 9.5).

The estimated number of liverwort species is 135 (Mogensen (1987, 2001). A recent unpublished checklist of the hepatics of Greenland by Damsholt (2010) comprises 173 species in 50 genera, assigned here to 22 families (Damsholt 2002) (Appendix 9.7). Genus diversity is highest in Jungermanniaceae (10 genera), followed by Gymnomitriaceae and Cephaloziaceae (5 each) and Aneuraceae, Aytoniaceae, Cleveaceae and Scapaniaceae (three each). Together they account for 61% of the species diversity of the liverwort flora of Greenland. Species diversity is highest in Jungermanniaceae (64 species), followed by Scapaniaceae (28), Gymnomitriaceae (18), Cephaloziellaceae (12) and Cephaloziaceae (11), together accounting for c. 77% of the species diversity of the entire liverwort flora of Greenland (Tab. 9.6).

#### 9.3.3.4. Canada

At least 421 bryophyte species occur in Arctic Canada (Tab. 9.5 and 9.6). Steere (1947) provided a first thorough account of the moss flora of the eastern Canadian Arctic, including 304 species. Brassard (1971a) produced an impressive bryogeographical monograph of the moss flora of the high Arctic Queen Elizabeth Islands, NWT. and Nunavut, comprising 233 moss species. The checklist of the mosses of Canada (Ireland *et al.* 1987) accepts 343 species in 103 genera in 30 families for the Arctic archipelago (Appendix 9.8), which represents c. 35% of the total Canadian moss flora (965 species). High generic diversity is found in Pottiaceae (14 genera), Dicranaceae (13) and Amblystegiaceae (9), whereas Polytrichaceae, Splachnaceae, Bryaceae, Mniaceae and Hypnaceae each have five genera. Species diversity is highest in the genera *Bryum* (25 species), followed by *Sphagnum* (18), *Pohlia* (14), *Drepanocladus* and *Dicranum* (12 each), *Hypnum* (11) *and Grimmia* (10) accounting for 30% of the moss flora, and in the families Bryaceae (44 species), Amblystegiaceae (40), Dicranaceae (35), Pottiaceae (31) and Grimmiaceae (23), followed by Hypnaceae (19), Sphagnaceae (18), Mniaceae (17), Polytrichaceae (15), Brachytheciaceae (12) and Splachnaceae (10). These families account for 77% of the total Canadian Arctic moss flora (Tab. 9.5).

The liverwort flora is likely less well known. The most comprehensive work to date is that by Polunin (1947) referring to 72 species in 28 genera from the Canadian eastern Arctic. Since then, many local studies have been published (e.g. Steere & Scotter 1979, Scotter & Vitt 1992, Maass *et al.* 1994). In Schuster's (1966-1992) comprehensive six-volume hepatic flora of North America, new data on the eastern Canadian Arctic are accumulated; however, there is no published reference work specifically for Canadian Arctic liverworts.

#### 9.3.3.5. Alaska

Approximately 543 bryophyte species are known from Alaska (Tab. 9.5 and 9.6), including 408 moss species north of the Arctic Circle (Steere 1978) (Tab. 9.5). They are referred to 136 genera and 38 families. The 11 most species-rich families are Amblystegiaceae (46 species), Bryaceae (45), Pottiaceae (44), Dicranaceae (37), Sphagnaceae (30) and Hypnaceae (23), Grimmiaceae and Splachnaceae (17 each), Polytrichaceae and Mniaceae (15 each) and Brachytheciaceae (13). Together they account for 74% of the total species diversity of this part of Alaska. The most species-rich genus is *Sphagnum* (with 30 species, Sphagnaceae), followed by *Bryum* (26, Bryaceae), *Drepanocladus* (15, Amblystegiaceae), *Hypnum* (12, Hypnaceae), *Dicranum* (12, Dicranaceae), *Encalypta* (11, Encalyptaceae) and *Pohlia* (11, Bryaceae). They contribute 29% of the total moss flora of this part of Alaska.

The liverwort flora of Arctic Alaska comprises at least 135 species in 49 genera and 30 families (Steere & Inoue 1978) (Tab. 9.6). The Lophoziaceae (with 43 species) and Scapaniaceae (24) are the most species-rich families, followed by Jungermanniaceae (9), Cephaloziaceae (8) and Calypogeiaceae (5). The genera *Lophozia* and *Scapania* are by far the most species-rich (31 and 20 species, respectively), followed by *Cephalozia* (5 species), and *Cephaloziella* and *Diplophyllum* (earwort) (4 each). Assigning the genera and species to families according to Damsholt (2002), Jungermanniaceae and Scapaniaceae are by far the most species-rich families (52 and 24 species, respectively), accounting for 56% of the total liverwort biodiversity of Arctic Alaska (Tab. 9.6).

### 9.3.4. Taxonomic structure of the Arctic bryoflora

Based on previous bryofloristic surveys (Section 9.3.3 and Tab. 9.5 and 9.6), the estimation of 850 species by Matveyeva & Chernov (2000) cited in Callaghan (2005) and several recent new records, we estimate the total species number of the Arctic bryophyte flora to be c. 900. Arctic Russia is the most species rich (720 species), followed by Greenland (670), Arctic Alaska (543), the Canadian Arctic Archipelago (543) and the Svalbard archipelago (373).

Species number of the mosses varies from 288 (Svalbard) to 530 (Arctic Russia). Prominent moss families in all five regions include Bryaceae, Dicranaceae, Pottiaceae and Amblystegiaceae, Sphagnaceae and, to a lesser degree Grimmiaceae and Hypnaceae. Species numbers of the ecologically specialized peat moss family Sphagnaceae are distinctly lower in Svalbard, the Canadian Arctic Archipelago and Greenland (13, 18 and 24, respectively) than in Arctic Alaska and Russia (30 and 36, respectively). The latter regions are contiguous to or belong to the northern boreal mainland of the large North American and Eurasian continents (cf. Afonina 2004), where conditions for peat formation are more favorable than in the high Arctic. The ecologically specialized dung moss family Splachnaceae is widely distributed in all five regions, with five genera and 9-18 species. Throughout the Arctic territory, the genera *Bryum*, *Pohlia*, *Sphagnum*, *Dicranum*, *Drepanocladus*, *Brachythecium*, *Schistidium* and *Grimmia* are well represented with many species.

Species diversity is distinctly lower for liverworts than for mosses (78-201 liverwort species per region versus 288-530 moss species, Tab. 9.5 and 9.6). The most prominent liverwort families with many species in the Arctic include Jungermanniaceae and Scapaniaceae, followed at far distance by Gymnomitriaceae, Cephaloziaceae and Cephaloziellaceae, while *Scapania* and *Lophozia* are the most prominent genera with many species.

In Arctic Russia, 65% of the moss families and 95% of the moss genera have fewer than 10 species, whereas 79% of the genera have fewer than five species (Tab. 1 and 2 in Afonina & Czernyadjeva 1996). For the liverwort families these values are 83, 97 and 85%, respectively (derived from Tab. 9.6).

Comparable percentages occur in the other Arctic regions showing that, as in vascular plants, high species diversity is restricted to a relative small group of genera and families. This is a typical feature of Arctic floras (Yurtsev 1994).

### 9.3.5. Large scale variation of species richness

Bryophyte floras show variation in longitudinal and latitudinal distribution related to climate and habitat variation, different glaciations and migration histories (e.g. Brassard 1971a, 1974, Schofield 1972, Steere 1976, 1979, Afonina & Czernyadjeva 1996). However, a detailed survey of this variation as has been provided for vascular plants does not exist at present for bryophytes.

#### 9.3.5.1. Longitudinal variation

The longitudinal phytogeographical variation of the moss flora is exemplified here for Arctic Russia (Tab. 9.7). The Russian Arctic is divided from west to east into three phytogeographical sectors with a total of 15 regions: the European-W Siberian (EWS) sector with five regions, Franz Joseph Land (ZF), Kanin-Pechora (KP), Polar Ural (PU), Novaya Zemlya and Yamal-Gydan (YG); the E Siberian (ES) sector with six regions, Taimyr (TA), Severnaya Zemlya (SZ), Anabar-Olenik (AO), Kharaulakh (KH), Yana-Kolyma (YK) and Novosibirskiye Islands (NS); and the Chukotka (C) sector with four regions, Continental Chukotka (CC), Wrangel Island (WI), S Chukotka (SC) and Beringian Chukotka (BC) (Tab. 9.7).

Afonina & Czernyadjeva (1996) pointed out that real, existing diversity of the Russian Arctic moss flora de-

**Table 9.7.** Numbers of moss species in sectors and regions of the Russian Arctic after Afonina & Czernadjeva (1996).

| Sector and region | Number of species | Restricted to sector | Number of species | Restricted to region |
|---|---|---|---|---|
| **European-W Siberian (EWS)** | 395 | 39 | | |
| Franz Joseph Land (ZF) | | | 113 | |
| Kanin-Pechora (KP) | | | 255 | 3 |
| Polar Ural (PU) | | | 339 | 13 |
| Novaya Zemlya (NZ) | | | 203 | 4 |
| Yamal-Gydan (JG) | | | 252 | 3 |
| **E Siberian (ES)** | 385 | 27 | | |
| Taimyr (TA) | | | 309 | 8 |
| Severnaya Zemlya (SZ) | | | 99 | |
| Anabar-Olenik (AO) | | | 192 | 4 |
| Kharaulakh (KH) | | | 282 | 6 |
| Yana-Kolyma (YK) | | | 248 | 6 |
| Novosibirskiye Islands (NS) | | | 174 | 2 |
| **Chukotka (C)** | 429 | 54 | | |
| Continental Chukotka (CC) | | | 171 | 1 |
| Wrangel Island (WI) | | | 241 | 5 |
| S Chukotka (SC) | | | 326 | 9 |
| Beringian Chukotka (BC) | | | 396 | 19 |

pends mainly on the knowledge of the regional floras, the geographical position of the region and variation in relief and diversity of habitats.

There are 395 species in the EWS sector, including 39 specific species (‘regional endemics’, so far only known in the Russian Arctic from this sector). There are 385 recorded species from the ES sector including 27 specific species, and 429 species from the C sector including 54 specific moss species. Species numbers are distinctly different among regions. Species numbers of Severnaya Zemlya (SZ) and Franz Joseph Land (ZF) are relatively low (99 and 113, respectively), whereas Polar Ural (PU) and Beringian Chukotka (BC) are rich in species (339 and 396, respectively). The Beringian Chukotka region is the most diverse with 396 species, including 19 species only known in Russia from here. The high species richness (429 species) of the Chukotka (C) sector (see also Afonina 2004) and the presence of a high number of species (54) not yet documented elsewhere in Russia may be explained by geographical (variable mountain relief, extensive areas of Paleozoic carbonate rocks) and historical (the existence in the past of the Bering Land Bridge) factors. Some species are very rare and have not yet been found elsewhere in Russia such as *Funaria polaris*, *Seligeria oelandica*, *Heterocladium procurrens*, *Orthotrichum pellucidum*, *Racomitrium afoninae* and *Schistidium cryptocarpum*. Other species are rare with disjunct E Asian and North American distributions, e.g. *Trachycistus ussuriensis*, *Bryoxiphium norvegicum* and *Leptopterigynandrum austro-alpinum*. Thus the paramount position of Beringian Chukotka (and of Wrangel Island, which belongs to Beringia as well), is not only expressed in its vascular plant flora (Section 9.2), but also in its highly diverse and distinct moss flora (see also Afonina 2004).

Mountain moss floras appear richer than Arctic plain floras, as demonstrated by comparing the regions Polar Ural (339 species) and Yamal-Gydan (252 species). The richer flora of Polar Ural is certainly related to the higher diversity of local climate and habitats.

Around 12% of all moss species of Arctic Russia are common and widely distributed, and are often locally dominant in the vegetation all over the Russian Arctic (derived from Afonina & Czernyadjeva 1995). They include many mainly circumboreal/Arctic-alpine species (e.g. black rock-moss *Andreaea rupestris*, *Aulacomnium turgidum, Brachythecium turgidum* (turgid brachythecium moss), *Bryoerythrophyllum recurvirostrum* (red beard-moss), *Bryum cyclophyllum* (round-leaved bryum), *Campylium stellatum* (bog star-moss), *Cinclidium arcticum* (Arctic cupola-moss), *Conostomum tetragonum* (helmet-moss), *Dicranum spadiceum*, *Ditrichum flexicaule* (slender-stemmed hair moss), *Encalypta rhaptocarpa* (ribbed extinguisher-moss), *Hylocomium splendens* (glittering woodmoss), *Limprichtia revolvens*, *Meesia triquetra* (three-ranked hump-moss), *Oncophorus wahlenbergii* (Wahlenberg’s spur-moss), *Paludella squarrosa* (tufted fen-moss), *Pohlia cruda* (opal thread-moss), *Polytrichastrum alpinum* (alpine haircap), *Polytrichum piliferum* (bristly haircap), *Racomitrium lanuginosum*, *Sanionia uncinata*, *Sphagnum teres* (rigid bogmoss), *S. warnstorfii* (Warnstorf’s bogmoss), *Syntrichia ruralis* (a screw-moss), *Tetraplodon mnioides* (slender cruet-moss), *Tomenthypnum nitens* (woolly feather-moss or golden silk moss) and *Warnstorfia exannulata* (ringless hook-moss). Most of these species occur in plant communities of the circumpolar classes *Scheuchzerio-Caricetea* (mires and rich fens), *Carici-Kobresietea* (graminoid and prostrate dwarf shrub vegetation on non-acidic substrates) and snow beds (*Salicetea herbaceae*) (cf. Sieg *et al.* 2006). Around 32% of the moss species have a sporadic distribution, occurring in a majority of the regions. A large number of species, c. 40%, are considered rare, known from only a few regions, although this may partly be due to poor knowledge of some difficult taxonomic groups. About 16% of the species are so far known only from one locality in the Russian Arctic.

### 9.3.5.2. Latitudinal variation

High Arctic areas have fewer species than low Arctic areas, as exemplified by comparing the numbers of moss species of the non-Beringian E Siberian high Arctic Novosibirsky Islands (NS) with that in the adjacent low Arctic Yana-Kolyma (YK) region in Arctic Russia (174 and 248 species, respectively) (Afonina & Czernyadjeva 1996) (Tab. 9.7). The Polar Ural (PU) in the low Arctic has 339 species, whereas Novaya Zemlya (NZ) in the high Arctic, which belongs to the same Euro-Siberian (EWS) sector, has only 203 species. In the Chukotka (C) sector, Wrangel Island (WI) has 241 species, whereas Beringian Chukotka (BC) to the south has 396. Species richness of the Russian Arctic Islands is relatively low.

These islands are isolated from mainland Russia and situated at high latitudes, mostly in the high Arctic.

Other examples of latitudinal variation are found in Greenland, where 134 moss species were documented in Peary Land, N Greenland (Holmen 1960) versus nearly 500 species for all of Greenland (Goldberg 2003). Mogensen (1987) showed that c. 58% of the Greenlandic moss flora consists of species with a southern distribution in Greenland, 18% are widely distributed and 24% are northern species.

The northern local floras in high Arctic Ellesmere Island have fewer species as compared with floras on the southern part of the island. The moss flora of the Lake Hazen area, northern Ellesmere Island, comprises c. 45 species (Powell 1967), whereas 84 moss species are reported from the Alexandra Fiord lowlands in the middle of Ellesmere Island (Maass *et al.* 1996).

The same trend is seen in liverwort floras, where diversity decreases with increasing latitude. The liverwort flora of S Greenland includes 139 species (Schuster 1988), that of W Greenland (66° N-72° N) 136 species (Schuster & Damsholt 1974), whereas northern floras seem to have fewer species, e.g. Peary Land, N Greenland with 25 species (Arnell 1960), Svalbard with 85 (Frisvoll & Elvebakk 1996), the eastern Canadian Arctic with 72 (Polunin 1947) and northern Ellesmere Island with 43 (Schuster 1959). However all these figures should be considered with caution, since the state of knowledge of the liverwort flora from these areas varies greatly.

## 9.3.6. Origin of Arctic bryofloras and distribution types

So far, assumptions on the origin of Arctic bryofloras are generally based on the analysis of distribution patterns (e.g. Schuster & Damsholt 1974, Schuster 1988), environmental and geographical conditions, glaciation histories and refugia, degree of taxonomic isolation of species (Brassard 1971a, 1974) and (sub)fossil records (e.g. Mogensen 1984, Hedenäs 1994). However, ongoing and future phylogenetic and phylogeographic studies certainly will add new insights and conclusions to this field.

Apart from several cosmopolitan mosses such as *Bryum argenteum* (woolly silver moss) and *Ceratodon purpureus* (redshank), and liverworts such as *Aneura pinguis* (greasewort) and *Cephalozia bicuspidata* (two-horned pincerwort) together with some small groups of ecologically or geographically disjunct species, three general distribution types are of special interest in a broader, circumpolar Arctic perspective: circumboreal species, Arctic species and amphi-Beringian species (cf. Schofield 1972, Steere 1976, 1979).

The circumboreal species are widely distributed in temperate, boreal and Arctic climates of the Northern Hemisphere. Most (c. 75-80%) of the bryoflora of Arctic Alaska belongs to this group, and this percentage might hold for the entire Arctic. Most of the species considered sporadic (S), common (C) and widespread (W) in Arctic Russia (Afonina & Czernyadjeva 1995, 1996, Afonina 2004) (see Section 9.3.5.1.) belong to this distribution type. Most of these species are believed to have expanded their distribution by colonizing the devegetated and deglaciated areas in the circumpolar North after the Pleistocene glaciations (Crum 1966, Steere 1976, 1978, 1979).

Arctic (including Arctic-alpine) species comprise around 15% of the North American bryoflora (cf. Brassard 1971a, 1974, Steere 1979). Possible explanations for the presence of these bryophyte species in the high Arctic Canadian Queen Elizabeth Islands were thoroughly addressed by Brassard (1971a). In a later publication, the possible evolution of these Arctic bryophyte taxa was plausibly explained by taking into account their degree of taxonomic isolation and a possible area change as a Tertiary taxon, a newly evolved Quaternary taxon or a recent taxon (Brassard 1974). *Arnellia fennica, Bryobrittonia pellucida* (Fig. 11 in Afonina 2004), *Aplodon wormskjoldii*, *Philocrya aspera* (Fig. 4 in Afonina 2004) might represent old species already present in the Arctic before the Quaternary. Regarding *Arctoa anderssonii*, *Cyrtomnium hymenophylloides*, *C. hymenophyllum*, *Psilopium cavifolium* (Fig. 2 in Schofield 1972), *Seligeria polaris* and *Voitia hyperborea* (Fig. 9 in Afonina 2004), it is assumed that these Arctic species might have evolved before or during the Quaternary (cf. also Mogensen 1984). *Aulacomnium acuminatum*, *Cinclidium latifolium*, *C. arcticum*, *Timmia comata*, *Tritomaria heterophylla*, *Bryum wrightii*, *Didymodon leucostomus*, *D. johansenii*, *Fissidens arcticus*, *Funaria polaris* (Fig. 8 in Afonina 2004), *Hygrohypnum polare*, *Hygrolejeunea polaris*, *Oligotrichum falcatum* (Fig. 6 in Afonina 2004), *Scapania simmonsii* and *Trichostomum cuspidatissimum* (Fig.1 in Schofield 1972) may be pre-Quaternary taxa or ones that evolved during the Quaternary. Two other groups totalling c. 24 species (Tab. 3 in Brassard 1974, see also Schofield 1972) and including *Barbula icmadophila*, *Campylium arcticum*, *Ceratodon heterophyllus*, *Distichium hagenii*, *Mnium blyttii*, *Rhizomnium andrewsianum*, *Seligeria pusilla*, *Tortella arctica*, *Bryum arcticum*, *B. calophyllum*, *B. cryophilum*, *Drepanocladus badius*, *D. brevifolius* (Fig. 3 in Schofield 1972) and *D. lycopodioides* together with *Lophozia* species such as *L. hyperarctica*, *L. pellucida* and *L. quadriloba* likely represent young taxa that presumably evolved during the early or late Pleistocene (Brassard 1974). Other taxa mainly restricted to the Arctic proper with a circumpolar distribution include *Cnestrum glaucescens* (Fig. 27 in Afonina 2004), *Timmia sibirica* (Fig. 34 in Afonina 2004), *Plagiothecium berggrenianum* (Fig. 39 in Afonina 2004), *Schistidium cryptocarpum* (Fig. 18 in Afonina 2004), *Sphagnum arcticum* (Fig. 2 in Afonina 2004) and *Encalypta brevipes* (Fig. 12 in Afonina 2004).

The smaller Arctic amphi-Beringian moss flora includes *Drepanocladus latinervis*, *Pohlia beringiensis* (Fig. 30 in Afonina 2004), *Rhizomnium gracile* (Fig. 31 in Afonina 2004), *Schistidium andreaeopsis*, *Bryoxiphium norvegicum*, *Grimmia pilifera*, *Herzogiella adscendens*, *Pseudotaxiphyllum* *elegans*, *Didymodon subandreaeoides*, *Leptopterigynandrum austro-alpinum* (Afonina & Czernadjeva 1996, Fig. 37 in Afonina 2004) and *Racomitrium afoninae* (Fig. 15 in Afonina 2004). Their distribution pattern is explained by the existence of an ice-free land bridge between northeastern Asia and northwestern North America during the last glaciations (Afonina 2004). These species are likely fragments of a Tertiary bryoflora (Steere 1969).

Bryophytes have in general a wider distribution (reproduction by light spores and vegetative reproduction) than vascular plants, and as a result endemism is much lower in this group.

Endemism of Arctic bryophytes is apparently much higher on the infra-species level (N.A. Konstantinova, unpubl.).

Endemism in liverworts was considered high in northern Ellesmere Island and Greenland, maybe as the result of refugia during the last Wisconsin Glaciation (cf. Schuster 1959, Holmen 1960, Brassard 1971a). However, most of these species were later recorded in many Arctic regions and must therefore now be considered pan-Arctic 'endemics'.

Nevertheless, a large number of liverworts are restricted to the Arctic and adjacent mountain ridges of the sub-Arctic. Such species are defined in Russian geobotanical literature as 'meta-Arctic' species.

According to Konstantinova (2000) 44 liverwort species have a predominantly Arctic distribution. Most of these are poorly known and were described mainly from Ellesmere Island and Greenland (Schuster 1969-1992, 1988, Schuster & Damsholt 1974). During the last decades, many species regarded as endemics of Ellesmere Island or Greenland were found in several other regions of the Arctic and sub-Arctic, particularly in Svalbard, Russia and Alaska (e.g. *Anastrophyllum sphenoloboides*, *Cephaloziella polystratosa*, *Lophoziopsis* (*Lophozia*) *pellucida* and *Lophoziopsis* (*Lophozia*) *polaris*). Some recently described 'Arctic' liverworts were synonymized with earlier known species (e.g. *Leiocolea katenii* was synonymized with *Leiocolea badensis*). Several species referred by Konstantinova (2000) from the Arctic were collected in the alpine belt of the Caucasus in southern Russia (e.g. *Cephaloziella aspericaulis*). Moreover a majority of liverwort species considered previously as Arctic have been collected in the mountains of Siberia and the Russian Far East. These areas are phytogeographical corridors (or 'bridges') between the Arctic and the mountains of South and East Asia.

Nowadays only a few liverworts species can be considered as true Arctic endemics. They were recently described and only known from a single locality (e.g. *Scapania matveyevae*) or several localities (*Gymnocolea fascinifera*, *Schistochilopsis hyperarctica*). It is quite possible that most of such taxa will turn out to be more widespread in the Arctic.

Most of the Arctic, sub-Arctic and alpine species ('meta-Arctic' species) have a circumpolar distribution. Several species are really 'old' endemics, some are evidently neoendemics (Schuster & Konstantinova 1996).

The majority of 'old' isolated species occur in the Beringian sector of the Arctic (e.g. *Pseudolepicolea fryei*, *Radula prolifera*), and such species are absent in W Siberia and E Canada. Thus as for vascular plants Beringia is an important refugium of a presumably relictual tertiary bryophyte flora (see also Schuster & Konstantinova 1996).

### 9.3.7. Trends

We refrain from speculations about changes in bryofloras, due to insufficient knowledge in many Arctic areas. There are no known threatened species.

### 9.3.8. Conclusions and recommendations

The estimated species number of the bryophyte flora of the Arctic is moderate (c. 900) compared with that of lichens (c. 1,750) and vascular plants (c. 2,218). But it is likely that this number will increase significantly in the course of future studies. Arctic endemism is not strongly pronounced, and is displayed mainly on an infra-species level. The Arctic bryoflora is rather uniform. Almost 80% of the species have a broad circumboreal and circumpolar distribution. In rather stable, wet-to-moist sites they strongly contribute to vegetation biomass, and they also contribute to species richness of many vegetation types in other habitats. Their ecosystem function is poorly studied, and overall the bryofloras of most Arctic regions are still incompletely known. Moreover, Arctic material in the majority of taxonomic groups needs revision using modern molecular phylogenetic approaches (cf. Konstantinova & Vilnet 2009, Söderström *et al.* 2010). Records of localities of rare and recently described species need verification. There are no known threatened species. The use of bryophytes by indigenous peoples is very restricted. A circumpolar checklist according to uniform taxonomic concepts and nomenclature is urgently needed and will be highly beneficial for vegetation and ecosystem studies, especially for monitoring and interpretation of change in the face of climate change.

## 9.4. ALGAE

This section surveys both freshwater and marine environments by inventorying the biodiversity of the algal flora at a pan-Arctic scale in terms of species richness and distribution. The current exercise should be taken as a snapshot of the present situation regarding the accumulated knowledge of the biodiversity of these micro- and macroalgal organisms.

Algae are oxygenic autotrophic eukaryotes characterized by chloroplasts containing chlorophyll and other associated pigments, and reproducing by the formation of spores and gametes. They differ from vascular plants in physiological, cellular and morphological aspects. However, the cyanobacteria are addressed here since they were classified as blue-green algae with the Cyanophyceae for many years and are functionally oxygenic autotrophic prokaryotes. All algae contain the photosynthetic chlorophyll *a* pigment. The eukaryotic algae comprise heterogeneous and evolutionarily different groups. The origin and development of the first eukaryotic algae is explained through an endosymbiotic event where a heterotrophic eukaryote acquired or enslaved an ancestral cyanobacterium (cf. Reyes-Prieto *et al.* 2007). After genetic reduction and transformation, this event gave rise to primary plastids (chloroplasts) present in the Glaucophyta, Rhodophyta (red algae) and Chlorophyta (green algae); the three lineages are classified as Plantae with the higher plants (van den Hoek *et al.* 1993, Adl *et al.* 2005, Raven *et al.* 2005, Cocquyt *et al.* 2010). The Chlorophyta are ancestral to the algal Streptophyta and hence to the bryophytes (Bryophyta) and vascular plants (Tracheophyta). All are predominantly green with chlorophyll *b* as a secondary pigment.

Other algae are polyphyletic, lacking an identifiable common ancestor, and for the most part, their chloroplasts originated as a secondary endosymbiotic event where a single-celled pre-rhodophyte alga was acquired or enslaved by another heterotrophic protist (see Lovejoy, Chapter 11). Over time, this ancestral red lineage is thought to have given rise to other major algal phyla (e.g. Friedl *et al.* 2003, Falkowski *et al.* 2004, Reyes-Prieto *et al.* 2007, Armbrust 2009, Cocquyt 2009). Chlorophyll *c* is a secondary pigment common to most of these other algae, and the Chromalveolata is a term used to designate a supergroup of all the chlorophyll *c* containing algae and their non-chloroplastic relatives. These algae include the Dinophyta and the diverse heterokont algae. Two algal phyla, the Cryptophyta and Haptophyta, with chlorophyll *c* are now thought to have arisen through separate endosymbiotic events with different protists (Baurain *et al.* 2010), and since their phylogenetic positions are uncertain, the term Chromalveolata is used descriptively in this text. There are two other algal phyla that arose from endosymbiotic events where single-celled green algae gave rise to chlorophyll *b*-containing chloroplasts in the photosynthetic Euglenophyta and Chlorarachniophyta. Several dinoflagellates from diverse lineages have lost their original secondary, endosymbiotically acquired chloroplast and have acquired new chloroplasts directly from green algae, cryptophytes and even diatoms in what are termed tertiary endosymbiotic events (Keeling 2010).

Algae are ecologically very important, contributing to the biogenic carbon flux throughout aquatic systems, being at the base of marine and freshwater food webs (Forest *et al.* 2011). Algae have a worldwide distribution occurring in nearly all wet or aquatic habitats, on land (terrestrial), in freshwater (limnic) and in seawater (marine). They occur either free in the upper water column (pelagic) and known as phytoplankton which encompass autotrophic, single-celled eukaryotes ranging in size from 0.2 to 200 µm, and further segregated into pico- (< 2 µm), nano- (2-20 µm) and micro-sized (20-200 µm) fractions of the scaling plankton classification (Sieburth *et al.* 1978). In a broader sense, plankton includes microzooplankton, non-autotrophic eukaryotic protists, bacteria, Archaea and viruses (Thomas *et al.* 2008, Poulin *et al.* 2011). Algae are also associated with polar sea ice (sympagic, Różańska *et al.* 2009, Poulin *et al.* 2011), or attached to soft and hard bottom substrates (benthic, Totti *et al.* 2009). Single-celled algae as well as large macroalgae (seaweeds) live in the intertidal zone. Attached, benthic marine macroalgae are the main habitat structuring agents of several major marine ecosystems, such as kelp forests and sub-tidal red algal crusts.

Marine phytoplankton and sympagic algae are at the base of the Arctic marine food web. Marine phytoplankton are responsible for more than 45% of the annual net primary production of the Earth (Falkowski *et al.* 2004, Simon *et al.* 2009). Diatoms alone are responsible for 20% of the Earth's annual net primary production, generating as much carbon as all terrestrial rainforests together (Armbrust 2009). In Arctic seas, sympagic algae contribute 57% of the total primary production in the central Arctic Ocean (Gosselin *et al.* 1997) and up to 25% on Arctic shelves (Legendre *et al.* 1992).

Algae exhibit a tremendous variability in morphology from unicellular solitary and colonial microalgae to multicellular macroalgae (e.g. seaweeds). Their size range varies from 0.2 µm for pico-sized cells to more than 100 m long Phaeophyta in giant kelps (Thomas *et al.* 2008). Algae differ from vascular plants, bryophytes and lichens by their diversified cell wall compounds, which can be taxonomically specific with, for example, the siliceous casing characterizing the Bacillariophyta (diatoms) or the calcium carbonate distinctive of the Haptophyta coccolithophorids. Other algae have cell walls containing cellulose or chitin. In addition to some differences in the main chlorophyll pigments, accessory pigments also differ among algae, with different phyla having specific profiles of xanthophylls (carotenoids with molecules containing oxygen). Cryptophyta and a few dinoflagellates with cryptophyte-origin plastids contain phycobiliproteins that also absorb photons. Storage products also differ with starches, sugars and lipids found among different phyla in various proportions. Life cycles are haplontic, diplohaplontic or diplontic, without embryonic stadia (e.g. van den Hoek *et al.* 1993, Raven *et al.* 2005), and algae do not produce an early sporophytic generation embedded in parental tissue (Friedl *et al.* 2003). The mode of locomotion among algae is highly diverse; only the Rhodophyta and centric diatoms do not usually have a flagellated stage. However, benthic pennate diatoms are well known for their movement on substrates and vertical migration through soft ediments (Round *et al.* 1990). In addition, most algal groups lack functional anatomical and morphological differentiation as shown in vascular plants (e.g. van den Hoek *et al.* 1993, Raven *et al.* 2005).

Cyanobacteria (blue-green algae) in the domain of Bacteria (van den Hoek *et al.* 1993, Raven *et al.* 2005) are fundamentally different from autotrophic eukaryotic algae. Cyanobacteria lack a membrane-bound nucleus and organelles. Most do not have accessory chlorophylls (*b* or *c*). Cyanobacteria exhibit a very diverse morphological range from solitary coccoid cells to colonies with simple thalli of a more restricted size range compared with eukaryotic algae. Their blue-green color is caused by high amounts of the accessory pigments phycocyanin and allophycocyanin (e.g. van den Hoek *et al.* 1993). In marine systems as well as in some deep freshwater environments, the accessory pigment phycoerythrin masks the phycocyanin giving a pink coloration to the cyanobacteria. Cyanobacterial mats exposed to high ultraviolet radiation in polar regions have high concentrations of photoprotective sunscreen and other pigments and can be black or orange (Vincent 2000). They are able to fix atmospheric nitrogen and are thus key players in global nitrogen budgets as well as in carbon flux.

Additionally, both green and blue-green algae can be the photosynthetic partner for fungi to form lichens (see Dahlberg & Bültmann, Chapter 10). They can also live independently of lichens and with bryophytes and lichens they cover bare soil as ‘black crusts’ and improve growth conditions for vascular plants, which is particularly important in the Arctic (Elster *et al.* 2002).

## 9.4.1. Major algal groups

The diversity of marine phytoplankton is impressive. About 25,000 species are known to date (Norton *et al.* 1996, Poulin & Williams 2002, Falkowski *et al.* 2004, Poulin *et al.* 2011). Over the last 15 years with the increasing use of molecular tools there has been some upsurge in taxonomic descriptions, especially among some of the smaller, less speciose groups such as Chlorarachniophyta (Ota *et al.* 2011). The major taxonomic divisions discussed in the following sections are presented in Tab. 9.8, with phylogeny based on a consensus of recent works (Adl *et al.* 2005, Raven *et al.* 2005, Cocquyt 2009, Baurain *et al.* 2010, Cocquyt *et al.* 2010, Keeling 2010, Marin & Melkonian 2010).

Among the Chlorophyta (chlorophytes, green algae *sensu stricto*), the most frequently reported classes in the Arctic are Chlorophyceae, Mamiellophyceae, Pedinophyceae, Prasinophyceae and Ulvophyceae. The Chlorophyceae are often found in snow and ice (Müller *et al.* 1998, Larose *et al.* 2010), whereas the Prasinophyceae are mainly planktonic but also occur frequently in Arctic sea ice (Poulin *et al.* 2011). The Pedinophyceae and Mamiellophyceae are truly planktonic, and all known species are less than 5 µm in size. One phylotype of *Micromonas* in the Mamiellophyceae is likely the most abundant single-celled type in the Arctic Ocean (Lovejoy *et al.* 2007).

The Streptophyta (streptophytes) include all green land plants and Charophyceae as well as the Zygnematales (Leliaert *et al.* 2012). Charophytes (stoneworts) and Zygnematales occur predominantly in freshwater habitats, and they have a worldwide distribution. The Zygnematales are highly diverse and often used as indicator species of water quality; they have been reported from Arctic tundra streams (Sheath *et al.* 1996).

**Table 9.8.** Worldwide recognized and estimated numbers of algal species. Sources: Norton *et al.* (1996) and Poulin & Williams (2002).

| Taxonomic group | Recognized taxa | Estimated taxa |
|---|---|---|
| Prokaryotic algae | | |
| **Cyanophyta** | c. 2,000 | ? |
| Eukaryotic algae | | |
| **Archaeplastida** | | |
| Chlorophyta (1) | | |
| Prasinophyceae incl. Pedinophyceae | 120-140 | 500 |
| Ulvophyceae | 1-1,000 | 3,000 |
| Chlorophyceae | 2,500 -2,600 | 10,000-100,000 |
| Streptophyta (2) | | |
| Charophyceae incl. Zygnematales | 11,000-13,000 | 20,500 |
| Glaucophyta | 13 | 50 |
| Rhodophyta | 4,000-6,000 | 5,500-20,000 |
| **Chromalveolata** | | |
| Cryptophyta | 200 | 1,200 |
| Haptophyta (Prymnesiophyceae) | 300-500 | 2,000 |
| Dinophyta (7) | 2,000-4,000 | 3,500-11,000 |
| Stramenopiles (8) | | |
| Dictyochophyceae incl. Pedinellophyceae | 10 | 15 |
| Eustigmatophyceae | 12 | 1,000-10,000 |
| Pelagophyceae | 7 | 20 |
| Bacillariophyceae | 10,000-12,000 | 100,000-200,000 |
| Phaeophyceae | 900-1,000 | 2,000 |
| Xanthophyceae | 600-700 | 2,000 |
| Chrysophyceae | 1,000-2,000 | 2,400 |
| Rhaphidophyceae | 15-27 | 100 |
| **Excavata** | | |
| Euglenophyta (9) | 900-1,000 | 2,000 |
| **Opisthokonta** | | |
| Choanoflagellidae (10) | 60 | ? |
| **Rhizaria** | | |
| Chlorarachniophyta (11) | <5 | 20 |

The Rhodophyta are also highly diverse, and although many have a tropical distribution, they occur in cold waters and are present in freshwater, including in the Arctic (Sheath *et al.* 1996).

The Chromalveolata constitute the group with the highest diversity of autotrophic eukaryotic algae with chlorophyll *c* pigment, including two major groups: the stramenopiles and the alveolates. The alveolates are defined by their cell wall characteristics, and include ciliates, dinoflagellates and parasitic taxa (see Lovejoy, Chapter 11). The autotrophic alveolates, with a few exceptions, are in the Dinophyta (dinoflagellates). The stramenopiles (heterokonts) have the highest diversity within the Chromalveolata. There are six major groups of algae within the stramenopiles that are frequently reported from the Arctic. The Bacillariophyta (diatoms) are planktonic, sympagic and benthic, occurring in terrestrial, freshwater and marine habitats. The Eustigmatophyceae, Raphidophyceae and Dictyochophyceae are mostly marine planktonic species and have been rarely reported from Arctic seas (Comeau *et al.* 2011, Poulin *et al.* 2011), except perhaps for *Dictyocha speculum*, which occurs regularly all year round in Arctic seas. The Chrysophyceae (golden-brown algae) are mostly limnic and often dominate Arctic and sub-Arctic lakes (Charvet *et al.* 2011) and tundra streams (Sheath *et al.* 1996), occasionally occurring as Arctic marine phytoplankton (Lovejoy *et al.* 2002, 2006, Poulin *et al.* 2011), with *Dinobryon balticum* dominating in late summer – early fall around Svalbard. Most species are single cells but some species are colonial including the spectacular arborescent colonies of *Dinobryon*. The Xanthophyceae (yellow-green algae) are mostly freshwater species. Among the macroalgal stramenopiles are the Phaeophyta (Phaeophyceae, brown algae), widespread along the Arctic coasts.

Also within the Chromalveolata, the Cryptophyta (cryptophytes) and Haptophyta (haptophytes or prymnesiophytes) branch apart from other chlorophyll *c* containing algae and also from each other (Baurain *et al.* 2010). The Cryptophyta are unicellular organisms and can have a variety of colors derived from the phycoerythrin and phycocyanin pigments. The cryptophytes are reported from both cold marine and limnic environments (Lovejoy *et al.* 2002, 2006, Charvet *et al.* 2011, Poulin *et al.* 2011). The Haptophyta are unicellular algae and they are mainly marine and coastal, although the calcium-carbonate-scale-bearing coccolithophorids are scarce in Arctic regions. Small flagellated haptophytes that do not have coccoliths are common in polar marine plankton.

The Euglenophyta (euglenids) belong to the lineage Excavata and are mainly limnic, unicellular flagellates, with some species present in Arctic seas (Poulin *et al.* 2011). The chlorarachniophytes (Chlorarachniophyta) have been reported in the Arctic from molecular biological surveys (see Lovejoy, Chapter 11) and the group belongs to the Rhizaria lineage. The Opisthokonta are represented by small celled, non-autotrophic choanoflagellates considered in the broader sense as belonging to marine phytoplankton. They are characterized by the formation of a siliceous lorica protecting the cell and have been recorded mainly in coastal Arctic seas (Thomsen *et al.* 1997).

### 9.4.2. Arctic algal taxonomic diversity and regionality

The taxonomic diversity of algae on a worldwide scale is estimated to be extremely high (Norton *et al.* 1996, Poulin & Williams 2002). Many phycologists assume that the number of described species, varying between 30,000 and 40,000, is only a small fraction of the total number of undescribed species estimated to vary between 400,000 and more than 10 million (Norton *et al.* 1996), this last figure having to be taken with great caution. More recently, the number of diatom species was estimated around 200,000 by both Poulin & Williams (2002) and Armbrust (2009). Recent environmental surveys using molecular techniques suggest that the diversity at all levels has been underestimated, and much work needs to be done to even make informed estimates of how many species of algae exist on Earth.

The total species number of algae in the Arctic is unknown and assumed to be much lower than in warmer regions of comparable size (e.g. van den Hoek 1984, Lüning 1985, Norton *et al.* 1996, Kerswell 2006), although recently Archambault *et al.* (2010) reported a lower number of marine seaweeds and a higher number of marine phytoplankton in the Canadian Arctic compared with eastern and western Canada. Seaweeds from the Arctic were characterized by Kjellman (1883) as having "monotony and luxuriance." Species diversity of the seaweed Chlorophyta, Phaeophyta and Rhodophyta (Norton *et al.* 1996; Tab. 9.8) showed distinctly lower species numbers for the Arctic regions: 80 and 252 taxa for the Bering Sea and Arctic Ocean, respectively (Kjellman 1883), and 201 and 280 taxa for Arctic Canada and Greenland, Iceland, Svalbard and northern Norway, respectively (South & Tittley 1986). Species numbers of algae from temperate and tropical regions were generally much higher, with up to 1,058 species in the Caribbean and adjacent waters (Wynne 1986) and 1,510 in Japan (Yoshida *et al.* 1990).

The species diversity of microalgae in the Arctic, as elsewhere, is generally poorly known. Okolodkov & Dodge (1996) reported the occurrence of 250 species of planktonic dinoflagellates from various localities in the Arctic Ocean. All species appeared common in Arctic-boreal marine waters, and species diversity was higher in regions influenced by an influx of warmer water from the south. In Arctic regions, marine diatoms are very diverse and abundant in both annually formed sea ice and pelagic waters (von Quillfeldt *et al.* 2003, Różańska *et al.* 2009, Poulin *et al.* 2011).

Recent molecular studies reported a high diversity in the smallest sized-fraction of the phytoplankton in polar regions, frequently contributing to more than 50% of the total phytoplankton biomass and production (Lovejoy *et al.* 2006, Poulin *et al.* 2011). A more recent study using high throughput sequencing technology to better capture rare species indicates that in the Beaufort Sea, western Canadian Arctic, alone there may be on the order of 10,000 single-celled eukaryotic species, at least half of which are likely autotrophic (Comeau *et al.* 2011).

The knowledge of taxonomic biodiversity and geographical variation of marine, freshwater and terrestrial algal floras across the Arctic regions is obviously less than that of the predominantly terrestrial vascular plant and bryophyte floras. The knowledge of terrestrial and freshwater algae, including cyanobacteria, of the comparatively well-explored Svalbard archipelago was considered "still in its infancy" by Skulberg (1996), whereas the bryophyte and vascular plant floras are comparatively well known (Elvebakk & Prestrud 1996). Nevertheless, knowledge of the diversity of marine microalgae distinctly increased in the last decades because of increased and improved sampling techniques and culture protocols, advanced microscopy and molecular biology research methods, electronic archiving databases and gene libraries, and increased international cooperation through climate change and biodiversity research programs (e.g. ArcticNet, Conservation of Arctic Flora and Fauna, Arctic Ocean Diversity-Census of Marine Life).

The main difficulties in assessing biological diversity at the subgeneric levels are the dissimilarities that exist in the taxonomic species concept and classification among the circumpolar countries. Moreover, current species concepts from traditional morphological assessments are challenged by the latest molecular phylogenetic analyses (e.g. Pröschlod & Leliaert 2007), which may or may not support traditional classifications. In particular for microalgae, this dichotomy between fundamental morphological and molecular phylogenetic interpretations makes the assessment of their geographical distribution very hard (cf. Rindi *et al.* 2009). The morphological variation in picophytoplankton (< 2 µm) is poorly addressed with current microscopic investigations, whereas its molecular biodiversity is enormous (Lovejoy *et al.* 2006). A major challenge facing biodiversity assessments will be matching morphology of a single-celled alga to a given gene sequence, which obviously will mean developing better sampling strategies and culture techniques for these small-sized microalgae.

Since the first algal biodiversity census by Norton *et al.* (1996), various floristic or biogeographic reports of local or regional character have been reported (e.g. Lee 1980, Okolodkov & Dodge 1996, von Quillfeldt 1997, Cremer 1998, Okolodkov 1998, Stenina *et al.* 2000, von Quillfeldt *et al.* 2003, Kerswell 2006, Lindstrom 2006, Matuła *et al.* 2007), including more recent pan-Arctic algal biodiversity assessments (e.g. Adey *et al.* 2008, Wulff *et al.* 2009, Bluhm *et al.* 2011, Poulin *et al.* 2011).

The present contribution can be regarded as a snapshot of the algal diversity obtained from a number of regional studies as well as a few more recent pan-Arctic surveys. It is far from an exhaustive account of the algal diversity of terrestrial, freshwater and marine habitats; more inventory work is still needed to get a good picture of the situation across the immense polar region. Here, the Arctic pertains to the Arctic lands (CAVM Team 2003, Walker *et al.* 2005), their bordering seas (Beaufort Sea, Canadian Arctic Archipelago straits and channels, Hudson Bay system, Melville Bay, Baffin Bay, Denmark Strait, Greenland Sea, Barents Sea, Kara Sea, Laptev Sea, East Siberian Sea, northernmost Bering Sea and Chukchi Sea) and the Arctic Ocean (cf. Fig. 6.4 in Christiansen & Reist, Chapter 6).

#### 9.4.2.1. Russia

Okolodkov (1992) studied the sympagic flora of 125 stations in the Laptev, East Siberian and Chukchi Seas. Over 120 algal species were identified, predominantly diatoms, primarily of the genera *Navicula* (24 species) and *Nitzschia* (20). Allochtonous freshwater diatoms and many marine planktonic *Chaetoceros* and *Thalassiosira* species were recorded as well. Okolodkov (1998) also presented a checklist of dinoflagellates recorded since 1878 in the Russian Arctic and the central Arctic Basin. Apart from several *incertae sedis* (organisms of unknown taxonomic placement), 189 species were recognized belonging to 16 families and 34 genera. Peridinales species were most prominent, followed by Gymnodiniales and Gonyaulacales. The genera *Protoperidinium* (c. 50 species), *Peridinium* (20), *Dinophysis* (20) and *Gyrodinium* (18) were well represented. The diversity and distribution of marine benthic diatoms in the Laptev Sea were studied by Cremer (1998), who recorded the occurrence of 345 taxa in 56 genera, including 78 taxa mainly from Arctic and sub-Arctic areas. Species-rich genera included *Navicula* (72 species), *Pinnularia* (27), *Nitzschia* (21), *Cymbella* (20), *Eunotia* (20), *Fragilaria* (20) and *Achnanthes* (16). The taxonomic biodiversity of limnic phytoplankton of the Pechora Delta and adjacent tundras was studied by Stenina *et al.* (2000). They recorded the occurrence of 440 species and 523 subspecific taxa (Tab. 6.2.7. in Stenina *et al.* 2000). Diatoms showed the highest diversity with 360 taxa in 44 genera and 19 families, followed by blue-green algae with 79 taxa in 26 genera and 18 families, and chlorophytes with 72 taxa in 34 genera and 21 families. Xanthophyta, Chrysophyta and Dinophyta were less common. The diatom genera *Navicula*, *Nitzschia*, *Pinnularia*, *Fragilaria*, *Achnanthes* and *Cymbella* appeared very species-rich. A last report by Ratkova & Wassmann (2005) listed the occurrence of 306 algal species in the phytoplankton and sea-ice communities of the White Sea and Russian Barents Sea, with 156 species common to both environments. Most species observed in the sea ice were similar to those recorded in other Arctic regions.

More recently, Poulin *et al.* (2011) listed the most frequently recorded marine phytoplankton diatoms (*Chaetoceros contortus*, *Thalassiosira gravida*, *T. nordenskioeldii*, *Cylindrotheca closterium*, *Thalassionema nitzschioides*) and dinoflagellates (*Protoperidinium brevipes*, *P. pellucidum*) from the Russian Arctic seas, as well as the most commonly recorded sea ice diatoms (*Melosira arctica*, *Cylindrotheca closterium*, *Entomoneis kjellmanii*, *Fragilariopsis cylindrus*, *F. oceanica*, *Navicula directa*, *N. transitans* var. *derasa*, *Nitzschia frigida*, *N. polaris*, *Pseudo-nitzschia delicatissima*). Many of these sea ice diatoms are also well known from, and commonly occurring during, the spring blooms at the ice edge zone.

#### 9.4.2.2. Svalbard

In Svalbard, Hansen & Jenneborg (1996) recorded the occurrence of 163 species of benthic marine algae and cyanobacteria, including 38 chlorophytes, 60 phaeophytes and 59 rhodophytes, whereas some 200 marine microalgae were reported by Hasle & von Quillfeldt (1996) and Okolodkov *et al.* (2000). Diatoms (108 species) and dinoflagellates (60) are the most diverse groups, with *Chaetoceros* (21) and *Thalassiosira* (16) as the most prominent diatom genera, and *Protoperidium* (18) in the dinoflagellates. Werner *et al.* (2007) studied sympagic algae in pack ice during winter and identified 54 taxa. Diatoms appeared prominent with at least 24 species. Conversely, Skulberg (1996) listed a total of 766 species of terrestrial and limnic algae and cyanobacteria, including a number of *incertae sedis*: more than half the species (i.e. 409) are represented by diatoms with the most speciose genera being *Navicula* (97 species), *Pinnularia* (49), *Cymbella* (49) and *Epithemia* (25). Matuła *et al.* (2007) identified 150 algal species from several terrestrial habitats in W Svalbard, including 100 blue-green algae, with 55 species new to Svalbard.

In the European Arctic, macroalgal composition and zonation patterns are most well known from Svalbard, especially the Kongsfjorden area (Wulff *et al.* 2009). A total of 80 seaweed species, mostly brown algae, are known from various Svalbard fjords (Wulff *et al.* 2009). The distribution of these polar seaweeds depends mainly on exposure and depth. Kelp species, *Laminaria digitata* and *Saccharina latissima* (syn. *Laminaria saccharina*), are dominant at depths between 5 and 15 m. A similar macroalgal flora to the Svalbard archipelago extends eastwards along the Russian Arctic coast, but is less speciose than in Svalbard.

#### 9.4.2.3. Greenland

There are a fair number of old and detailed local and regional floristic monographs on algae of Greenland, such as those on marine macroalgae (Rosenvinge 1893, 1898, Lund 1951, 1959a, 1959b, Pedersen 1976), marine phytoplankton (Grøntved & Seidenfaden 1938), and freshwater desmids (Grönblad 1952), diatoms (Foged 1953, 1955, 1973) and algae (Hansen 1967). A rather poor knowledge of freshwater algal species diversity was summarized by Kristiansen (2003). The most speciose estimated algal groups were the diatoms (1,000 taxa), the desmids with the Mesotaeniaceae and Desmidiaceae (400) and the chlorophytes (200), followed by chrysophytes (83), dinoflagellates (21) and cyanobacteria (127), with several confined to hot spring environments. The total number of algal species was estimated at about 1,900. The species diversity of marine phytoplankton, considered to be very fragmentary for Greenland, was reviewed by Burmeister (2003) and Poulin *et al.* (2011). Diatoms are the most speciose group of microalgae in pelagic waters with some 250 species, mainly from the following dominant genera: *Chaetoceros*, *Nitzschia* and *Thalassiosira*, followed by prymnesiophytes (38 species), chrysophytes (15) and cryptophytes (10). An estimated 50 species of Pedinophyceae occur in the coastal waters around Greenland. Benthic macroalgae are far better known in Greenland with a long history of floristic surveys. Eight classes of benthic algae occur along the coasts of Greenland, with a total number of 215 species consisting of 83 brown, 53 green and 52 red algae (Tab. 16 in Pedersen 2003).

Already in old times the zonation of macroalgae and their main players along the Greenland rocky coast were well known by the indigenous peoples, because these informed the kayak hunters about the tidal conditions (see Robbé 1994).

#### 9.4.2.4. Canada

The Canadian Arctic has been surveyed for its freshwater and marine algal flora, but unfortunately without entirely covering this immense polar region. The first significant algal records came when the eastern Canadian Arctic was inventoried by Ross (1947), Seidenfaden (1947) and Whelden (1947). Ross (1947) recorded a total of 245 freshwater diatom taxa, with the Naviculaceae being the most speciose family (170 taxa) mainly represented by the genera *Navicula* (47 taxa) and *Pinnularia* (43), while the genus *Nitzschia* was represented by 16 taxa. Whelden (1947) surveyed 423 algal taxa mainly from freshwater habitats with only a few from the marine shoreline. The main algal groups were the Chlorophyceae (284 taxa), Cyanophyceae (112), Phaeophyceae (12) and Rhodophyceae (8). Among the green algae, the desmids (Desmidiaceae) showed the highest diversity with 220 taxa mainly dominated by the genera *Cosmarium* (90 taxa) and *Staurastrum* (70), while *Lyngbya*, *Gloeocapsa* and *Nostoc* were the dominant genera in the Cyanophyceae with 12, 10 and nine species, respectively. Finally, marine phytoplankton were inventoried by Seidenfaden (1947), who reported a total of 128 taxa, including 84 diatoms, 39 dinoflagellates and five small flagellates. The two most speciose phytoplankton genera were the diatom *Chaetoceros* (23 taxa) and dinoflagellate *Peridinium* (19).

In the 1980s, Sheath & Steinman (1982) listed the freshwater algal flora of 279 bodies of waters from the Northwest Territories, which consisted of 1,577 taxa in 212 genera. The major algal classes included the Bacillariophyceae with 761 taxa, followed by Chlorophyceae (481) and Cyanophyceae (173), which accounted for 90% of the total freshwater flora diversity. The most speciose genera were *Navicula* (119 taxa), *Cymbella* (78), *Pinnularia* (73), *Eunotia* (55), *Nitzschia* (52), *Achnanthes* (45) and *Gomphonema* (44) for the Bacillariophyceae; *Cosmarium* (156 taxa), *Staurastrum* (56) and *Closterium* (35) for the Chlorophyceae (Desmidiaceae); and *Oscillatoria* (18 taxa), *Anabaena* (13), *Chroococcus* (12), *Lyngbya* (12) and *Nostoc* (12) for the Cyanophyceae. In 1980, Lee reported the occurrence of 183 marine seaweed taxa from more than 105 sites scattered throughout the Canadian Arctic, including 37 new records. The most speciose genera were the green alga *Enteromorpha* (8 taxa) and the brown algae *Laminaria* (7) and *Fucus* (5). Later, Haber (1995) reported a total of 171 marine benthic algae across the Canadian Arctic, with *Saccharina latissima* (syn. *Laminaria saccharina*) as the most common species.

Generally speaking, benthic algal diversity increases with decreasing latitude and decreasing longitude from the west to east along Parry Channel, the main marine corridor linking the Beaufort Sea-Arctic Ocean to Baffin Bay-North Atlantic Ocean. Hsiao (1983) recorded a total of 685 marine phytoplankton and sea-ice microalgal taxa across the Canadian Arctic, which mainly consisted of 561 diatom taxa followed by 95 dinoflagellates, 22 chrysophytes, four chlorophytes and three euglenids.

For northern Baffin Bay in the eastern Canadian Arctic, Lovejoy *et al.* (2002) reported a total of 192 marine phytoplankton taxa, mainly represented by 75 diatom taxa, 58 dinoflagellates, 46 flagellates and 13 *incertae sedis*. The most speciose genera were the diatom *Chaetoceros* (17 taxa) and the dinoflagellate *Gymnodinium* (12). In the central Canadian Arctic near Resolute Bay, Riedel *et al.* (2003) recorded 180 marine phytoplankton and sea-ice algal taxa consisting of 99 diatoms, 45 dinoflagellates, 26 flagellates and 10 *incertae sedis*, with the most speciose genera belonging to the diatoms *Navicula* (17 taxa), *Nitzschia* (14) and *Chaetoceros* (8), and the dinoflagellates *Gymnodinium* (8 taxa) and *Gyrodinium* (8). In the northernmost part of the Canadian Arctic Archipelago, Antoniades *et al.* (2008) described and illustrated 362 benthic diatom taxa from various freshwater habitats, primarily consisting of these dominant genera: *Pinnularia* (37 taxa), *Navicula* (29), *Nitzschia* (25), *Eunotia* (15), *Gomphonema* (14), *Neidium* (14), *Caloneis* (12), *Cymbopleura* (12), *Encyonema* (12) and *Stauroneis* (12).

In a recent circumpolar biodiversity assessment of the marine unicellular eukaryotes, Poulin *et al.* (2011) recorded a total of 1,350 phytoplankton and sea-ice algal taxa for the entire Canadian Arctic, including the Hudson Bay system (e.g. Hudson Bay, Hudson Strait, Foxe Basin). They reported the most frequently occurring phytoplankton species, which mainly consisted of the diatoms *Attheya septentrionalis*, *Chaetoceros decipiens*, *C. furcillatus*, *C. wighamii*, *Eucampia groenlandica*, *Thalassiosira gravida*, *T. nordenskioeldii*, *Cylindrotheca closterium*, *Fragilariopsis cylindrus*, *F. oceanica*, *Nitzschia frigida* and *Pseudo-nitzschia seriata*. They also reported the most commonly occurring sea-ice diatom taxa, consisting of *Attheya septentrionalis*, *Melosira arctica*, *Cylindrotheca closterium*, *Entomoneis kjellmanii*, *Fragilariopsis cylindrus*, *Navicula directa*, *N. transitans*, *Nitzschia frigida*, *N. longissima* and *Pauliella taeniata*.

#### 9.4.2.5. Alaska

Historical seaweed collections from Alaska were reviewed by Lindstrom (2006). The total number of recognized seaweed species for Alaska increased from 376 in 1977 to about 550 today. Marine unicellular eukaryotes from the Alaskan Arctic were addressed by Poulin *et al.* (2011) who reported a total of 443 phytoplankton and sea-ice microalgal taxa, mainly represented by diatoms (331 taxa) and dinoflagellates (74). The low number of freshwater and marine algae reported for the Alaskan Arctic can be explained by the low number of investigations conducted in these regions.

### 9.4.3. Pan-Arctic surveys

As a constant feature of the Arctic regions, snow offers a suitable habitat for the development of freshwater microbial communities (e.g. Gradinger & Nürnberg 1996, Müller *et al.* 1998, Takeuchi *et al.* 2001, Vincent *et al.* 2004, Larose *et al.* 2010). Such microbial mats were recorded from ice floes in the Arctic Ocean (Gradinger & Nürnberg 1996), snow fields in Svalbard (Müller *et al.* 1998, Larose *et al.* 2010), Devon and Penny ice cap glaciers in the Canadian Arctic (Takeuchi *et al.* 2001) and on the ice shelf in the Canadian high Arctic (Vincent *et al.* 2004). Algae on snow fields and on the surface of ice floes are mainly represented by the chlorophytes *Chlamydomonas nivalis* (green and red forms) and *Chloromonas nivalis* (Gradinger & Nürnberg 1996, Müller *et al.* 1998), while Larose *et al.* (2010) recorded 19 different bacterial classes from 16S rRNA gene sequencing, mainly dominated by *Betaproteobacteria* and *Sphingobacteria* from snow fields in Svalbard. Exposed microbial mats on Arctic ice shelves were dominated by the chlorophyte genera *Chlorosarcinopsis*, *Pleurastrum*, *Palmellopsis* and *Bracteococcus*, and the cyanobacteria *Nostoc*, *Phormidium*, *Leptolyngbya* and *Gloeocapsa* (Vincent *et al.* 2004). Glaciers farther inland such as the Devon and Penny ice caps on Devon and Baffin Islands, respectively, exhibit a microbial community characterized by seven chlorophyte and cyanophyte taxa (Takeuchi *et al.* 2001).

Biodiversity assessments of algae across the Arctic are extremely scarce with only a handful of reports on marine seaweeds and unicellular eukaryotes (e.g. Kjellman 1883, van den Hoek 1984, Lüning 1985, Wiencke *et al.* 2007, Wulff *et al.* 2009, Poulin *et al.* 2011). This type of information is simply lacking for the freshwater and terrestrial polar environments. Arctic species counts are likely to be underestimated due to few collections, extremely remote areas and sampling logistics.

According to Lüning (1985), there are approximately 150 seaweed species across the Arctic; the most recent estimates total 210-215 (Pedersen 2003, Archambault *et al.* 2010). The Arctic seaweed flora is of Atlantic and by and large Pacific origin (Adey *et al.* 2008), with many species having a circumpolar distribution and a few cosmopolitan or endemic species (Kjellman 1883, Lüning 1985, Wiencke *et al.* 2007, Wulff *et al.* 2009). About a dozen seaweed species are restricted to the Arctic, including the brown algae *Punctaria glacialis* and *Platysiphon verticillatus*, and the red alga *Petrocelis polygyna* (Wiencke *et al.* 2007). Most species have a southern range extension into the temperate region, such as the kelp *Laminaria solidungula* and the red algae *Devaleraea ramentacea*, *Turnerella pennyi*, *Neodilsea integra* (now *Dilsea socialis*)

**Table 9.9.** Survey of total numbers of marine unicellular eukaryote taxa in Arctic regions (Poulin *et al.* 2011).

| Algal group | Alaska | Canada | Scandinavia | Russia | Total |
|---|---|---|---|---|---|
| **Archaeplastida/Plantae** | | | | | |
| Chlorophyta | 12 | 34 | 3 | 17 | 55 |
| Prasinophyta | 1 | 42 | 25 | 18 | 60 |
| **Chromalveolata** | | | | | |
| Centric diatoms | 99 | 199 | 132 | 202 | 297 |
| Pennate diatoms | 232 | 604 | 251 | 563 | 930 |
| Bicosoecida | 0 | 7 | 5 | 1 | 10 |
| Chrysophyceae | 9 | 22 | 18 | 8 | 38 |
| Dictyochophyceae | 3 | 14 | 9 | 9 | 19 |
| Pelagophyceae | 1 | 0 | 0 | 0 | 1 |
| Rhaphidophyceae | 0 | 2 | 1 | 2 | 3 |
| Synurales | 0 | 3 | 3 | 0 | 6 |
| Xanthophyceae | 1 | 3 | 0 | 0 | 3 |
| Cryptophyceae | 0 | 23 | 10 | 9 | 30 |
| Prymnesiophyceae | 2 | 33 | 45 | 10 | 70 |
| Dinoflagellates | 74 | 266 | 183 | 257 | 441 |
| **Excavata** | | | | | |
| Euglenida | 3 | 14 | 4 | 10 | 20 |
| Kinetoplastea | 1 | 8 | 1 | 0 | 9 |
| **Ophistokonta** | | | | | |
| Choanoflagellates | 0 | 30 | 39 | 9 | 46 |
| **Cyanophyta** | 0 | 4 | 0 | 9 | 12 |
| *Incertae sedis* | 5 | 42 | 25 | 4 | 56 |
| Total species number | 443 | 1,350 | 754 | 1,128 | 2,106 |

and *Pantoneura baerii* (Lüning 1985). At a pan-Arctic scale, macroalgal species richness tends to decrease with increasing latitude and from the Atlantic sector to the Pacific sector (Wiencke *et al.* 2007). Arctic seaweeds are almost entirely subtidal with, however, some specialized species exclusively in the supralittoral or spray zone such as the green alga *Prasiola crispa* and the red alga *Bangia atropurpurea* (Wiencke *et al.* 2007).

The pan-Arctic diversity of marine pelagic and sea-ice unicellular eukaryotes was thoroughly reviewed by Poulin *et al.* (2011) based on current inventories and literature. A total of 2,106 marine single-celled eukaryote taxa were reported from the four main Arctic regions, namely Alaska, Canada, Scandinavia and Greenland, and the Russian Federation (Tab. 9.9): 1,027 sympagic taxa associated with sea-ice and 1,874 phytoplankton taxa. More than three-quarters of the total microalgal flora belongs to diatoms (1,227 taxa; 58%) and dinoflagellates (441; 21%), with pennate and centric diatoms accounting for 44% (930 taxa) and 14% (297), respectively.

Landfast and pack ice are predominantly colonized by pennate diatoms. Some colonial diatoms *Entomoneis kjellmannii*, *Fragilariopsis cylindrus*, *F. oceanica*, *Nitzschia frigida*, *Pauliella taeniata*, and solitary pennate diatoms *Cylindrotheca closterium*, *Navicula directa*, together with the colonial centric *Melosira arctica* and solitary, epiphytic *Attheya septentrionalis* are considered highly associated with or strictly confined to the Arctic sea ice, whereas *Navicula frigida* can be regarded as the sentinel endemic species of sympagic communities (Różańska *et al.* 2009, Poulin *et al.* 2011). Some colonial centric diatoms such as *Chaetoceros furcillatus*, *Thalassiosira gravida*, *T. nordenskioeldii* and pennate *Fragilariopsis oceanica* together with the solitary pennate diatom *Cylindrotheca closterium* are marine cold water plankton and widespread across the Arctic seas. The biodiversity of the smaller cell-sized phytoplankton (< 20 µm) is not very well known and is estimated at 20% of the diversity of the known pan-Arctic unicellular marine pelagic and sea-ice eukaryotes (Poulin *et al.* 2011). Nanoalgae mainly consist of cyanobacteria, prasinophytes, dinoflagellates, diatoms and prymnesiophytes (Tab. 6.1 in Thomas *et al.* 2008). In addition to this first biodiversity assessment of the marine unicellular eukaryotes, there are 37 potentially toxic species recorded including 25 dinoflagellates, nine diatoms, two prymnesiophytes and one raphidophyte (Tab. 4 in Poulin *et al.* 2011).

### 9.4.4. Trends

It is extremely hazardous to provide estimates of trends in Arctic phytoplankton, sea ice and benthic seaweed assemblages due to insufficient and fragmented knowledge of this algal biodiversity. However, recent studies have provided further information about the various marine algal groups present across the Arctic (Wiencke *et al.* 2007, Li *et al.* 2009, Różańska *et al.* 2009). For instance, it has been reported from the Arctic Ocean that the size class of marine phytoplanton is changing from large to small cells (Li *et al.* 2009). It has now to be seen if this trend will effectively apply to the entire Arctic region. Therefore, indeed more inventories and monitoring of micro- and macroalgae are needed to better define populations and assess trends across the Arctic.

### 9.4.5. Conclusions and recommendations

The total number of recognized algal species for the Arctic is at present likely around 4,000, which represents 10% of the world's recognized species. There are between 30,000 and 40,000 described species of algae worldwide, which correspond to only a small fraction of the estimated number of about 200,000 species (Poulin & Williams 2002). The total species number of algae and cyanobacteria in the Arctic is still largely unknown, especially in terrestrial and freshwater environments. Regarding their huge ecological importance for all life on Earth, both in the sea and on land, better inventories and monitoring of algae are strongly needed, particularly considering that the Arctic regions are and will be severely impacted by global warming.

> "The urgent need for more studies of all aspects of the biodiversity and ecology of polar algae has never been more apparent than at present" (Wulff *et al.* 2009).

> "Such an initiative will require that the field of taxonomy be better financially supported by the pan-Arctic countries … it would also be imperative to develop some training of the next generation of expert scientists in the field of phytoplankton taxonomy and systematics, which has been entirely neglected at present" (Poulin *et al.* 2011).

A major effort should be undertaken to establish a complete baseline of the biodiversity of marine and freshwater phytoplankton and macroalgae and polar sea ice microalgae, especially since these algae will become part of the CAFF Circumpolar Biodiversity Monitoring Program (CBMP). Reaching that goal requires more taxonomic studies in order to elucidate the species concept and harmonize it across the Arctic. The fields of taxonomy and systematics should be considered more than a descriptive exercise and rather as fundamental tools of discovery, conservation and management. Future efforts should focus particularly on the biodiversity of small-celled (< 20 µm) microalgae. Finally, all this research effort should be undertaken through international networks leveraging the costs associated with such pan-Arctic programs.

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Appendix 9: www.abds.is/aba-2013-appendix-9

The golden colored blackening waxcap *Hygrocybe conica* var. *aurantiolutea* is a colorful member of waxcaps that grows in grasslands in the low and sub-Arctic zones. At appropriate climatic conditions, the cryptically growing long-lived mycelia produce sporocarps in August-September. Waxcaps are sensitive to nitrogen, and their occurrence is strongly reduced in temperate and boreal zones due to anthropogenic deposition of nitrogen and fertilization. Tasiusaq at Qassiarsuk in South Greenland, 1987. Photo: Flemming Rune.

## *Chapter 10*

# Fungi

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## Contents

> » **I want to tell you something I learned about plants from the late Kakkik that I tried myself. My sister's late husband used to know about nirnait, caribou lichen, the plants that caribou eat. They are long and you pull them out. They tend to grow in swampy areas. I boiled them when all the people in our camp were sick. I was the only one up and about when we were living in a fishing camp. My mother had been admitted to the hospital and we were waiting for her return in August. Six of my family members were sick in bed. I boiled some caribou lichen in a pot for a long time, following my brother in-law's advice. He told me to stop boiling them when the water turned black. I waited for them to cool down and I gave each sick person some to drink. The next day, they were all up and about. It looked like the cough syrup in a bottle.**
>
> Aalasi Joamie in Joamie *et al.* 2001.

## SUMMARY

Fungi are one of the most species-rich groups of organisms in the Arctic. While the occurrence, distribution and ecology for lichenized fungi (lichens)[1] are reasonably well known, less is known about non-lichenized fungi (normally just called fungi), including lichenicolous fungi (fungi living on lichens)[2] and in particular, microfungi[3]. The known number of fungal species in the Arctic is presently about 4,350, of which 2,600 are macrofungi[4] and 1,750 are lichens, the rest are microfungi. The fungi have largely a cryptic life form and have therefore not been exhaustively inventoried. Hence, total fungal-species richness in the Arctic may exceed 13,000. Local species richness is typically high and can be very high, e.g. about 50 lichen species on less than 1 $m^2$. Most species appear to be present throughout the Arctic, and they also occur in alpine habitats outside the Arctic, particularly in the northern hemisphere. Few fungi are endemic to the Arctic. Of the lichens, 143 species are listed as Arctic endemics, but it is likely that the major part will prove to be synonyms of other species.

Fungi are pivotal in Arctic terrestrial food-webs. Mycorrhizal, saprotrophic[5] and pathogenic fungi drive nutrient and energy cycling, and lichens are important for primary production. Reindeer lichens *Cladonia* subgenus *Cladina* spp. form dominant vegetation types in many areas and function as keystone species.

As for other inconspicuous organism groups, it is obviously desirable to gain a better knowledge of the identity, occurrence and functions of fungal species, and particularly the large number of unrecorded species (mainly microfungi). An evaluation of the conservation status of Arctic fungi is feasible, and the mapping of rare and endemic species is necessary. Enhanced monitoring and functional research would enable more accurate prediction of how fungal diversity and the ecosystem functions of fungi will develop with climate change.

Effects of climate change on diversity of Arctic fungi are predicted to be gradual but radical over time, due to changes in vascular plant flora and vegetation, especially the expansion of shrubs. Most fungal species associate with living or dead parts of specific vascular plants and will respond directly to changing composition, abundance and location of the vegetation. Similarly, terricolous[6] lichen communities will be affected by increased competition from vascular plants. The changing vegetation will transform the fungal diversity and thereby affect ecosystem services provided by fungi, such as plant's uptake of nutrients, decomposition and long-term carbon sequestration in soil, although unknown how and to what degree. The conservation status of Arctic fungi is predicted to scarcely be affected within the next decades but greatly changed over the long term.

## 10.1. INTRODUCTION

Fungi are an extraordinary group of organisms. They constitute a large portion of Arctic biodiversity and are essential in the functioning of Arctic terrestrial ecosystems. A substantial part of the fungi is lichenized and generally termed lichens. The remaining part of the fungi is in general terms just called fungi and will here be referred to as fungi. Given favorable weather conditions, some may produce short-lived, sometimes prominent, sporocarps (mushrooms), but predominantly, and for many species exclusively, they exist as cryptic and hidden mycelia in e.g. soil and in living or dead insect or plant tissues. The most well-known group of fungi in the Arctic is the lichenized fungi (lichens) because they grow on substrate surfaces and often contribute conspicuously, and colorfully, to Arctic vegetation. This is particularly apparent in the high Arctic and in reindeer lichen[7]-dominated vegetation types in the sub-Arctic.

Here we review the knowledge and status of Arctic macroscopic fungi, i.e. visible sporocarps of fungi, and lichens. Microfungi constitute the most species-rich fungal group in the Arctic, but are only briefly mentioned due to scarcity of knowledge.

## 10.2. STATUS OF KNOWLEDGE

### 10.2.1. Fungal life strategies and ecosystem functions

Fungi are heterotrophic, i.e. they cannot fix carbon but need organic carbon for growth and therefore rely on photosynthetically derived energy from plants, including algae and cyanobacteria. Their strategies to access this energy are to be (1) mutualistic[8] (i.e. to associate

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[1] Lichenized fungi live in symbiosis with photosynthetic green algae or cyanobacteria and form stable structures called lichens.

[2] Lichenicolous fungi live exclusively on lichens, commonly as host-specific parasites, but also as broad-spectrum pathogens, saprotrophs or commensals.

[3] Microfungi are defined as fungi either lacking known reproductive structures, with microscopic reproductive structures or small sporocarps, typically less than 2 mm. They constitute the majority of known species and likely the overwhelming majority of the yet unknown and undescribed fungi.

[4] Macrofungi are defined as fungi with visible, sporocarps, typically larger than 2 mm.

[5] Saprotrophic organisms decompose dead plant, animal or fungal tissues.

[6] Organisms living on or in the soil.

[7] Despite being lichens, reindeer lichens are sometimes called "reindeer or caribou moss".

[8] Mutualism is a relationship between two species of organisms in which both benefit from the association, e.g. fungi and plants in mycorrhizae and fungi and green algae or cyanobacteria in lichens.

with photosynthetic organisms), (2) endophytic[9], (3) saprotrophic (i.e. they decompose dead plant, animal or fungal tissues) or (4) parasitic.

Fungal mutualism may be in the form of lichen or mycorrhiza. Lichens are an intimate, long-lived and stable association between fungi and green algae and/or cyanobacteria. Each lichen species has a unique fungus or mycobiont that determines its appearance and properties as well as its taxonomy, while the photosynthetic symbionts (photobionts) consist of relatively few species (148 according to Voytsekhovich *et al.* 2011), which are globally widespread and sometimes free living (Nash 2008). Lichens are classified and named after their fungal symbionts. The majority of Arctic vascular plants species form different types of mycorrhizae (Gardes & Dahlberg 1996, Newsham *et al.* 2009). The complex mycorrhizal organ, consisting of plant root and fungal hyphae, enlarge the surface area for absorbing water and nutrients from soil, explore for nutrients more extensively than vascular-plant roots, and mobilize organically bound nutrients. The fungal association provides the fungus direct access to the plant's carbohydrates, while the plant gain benefits from improved mineral and water absorption through the fungal mycelium. Ectomycorrhizal fungi are common in the Arctic where they associate with roots of mountain avens *Dryas* spp., willows *Salix* spp., birch *Betula* spp. and alpine bistort *Bistorta* spp. and in the sub-Arctic with additional species of bushes and trees. Ectomycorrhizal fungi belong mostly to genera forming conspicuous sporocarps, e.g. boletes (e.g. *Leccinum* spp.), amanitas *Amanita* spp. and milk-caps *Lactarius* spp. Arbuscular mycorrhizae are widespread in Arctic species of the true grasses Poaceae, the buttercup family Ranunculaceae, the aster family Asteraceae, the saxifrage family Saxifragaceae and the rose family Rosaceae (e.g. Gardes & Dahlberg 1996, Olsson *et al.* 2004, Ormsby *et al.* 2007, Peters *et al.* 2010, Walker *et al.* 2010). Ericoid mycorrhizae are widespread in Arctic species of the heather family Ericaeae, e.g. huckleberry *Vaccinium* spp., bell-heather *Cassiope* spp. and crowberry *Empetrum* spp. (Walker *et al.* 2011). The fungal symbionts in arbuscular and ericoid mycorrhizae are microfungi and typically need microscopic root examination to be seen, or molecular tools to be detected and identified.

The few studies conducted of Arctic fungal endophytes indicate a high species diversity, e.g. in above ground tissues of mountain avens (Higgins *et al.* 2007) and associated with Arctic plant roots, as so called dark septate endophytes (Newsham *et al.* 2009). Recently, fungal endophytes have been found common in lichen thalli (Arnold *et al.* 2009, U'ren *et al.* 2010).

Saprotrophic fungi are characterized by their dependence on dead organic materials as sources of energy and nutrients. They consist predominantly of microfungi, including a large number of anamorphic (asexual) ascomycetes and yeasts but also macrofungi (Ludley & Robinson 2008). Hitherto, the information on microfungi has largely been restricted to culturable mycelia from soil and plants (Ludley & Robinson 2008). Molecular tools are now providing exciting opportunities to resolve the diversity, distribution and function of fungal mycelia in the Arctic. The saprophytic macrofungi producing larger sporocarps include puffballs *Calvatia*, funnels *Clitocybe*, *Galerina* and *Leptoglossum*. Pyrenomycetes is a common group of saprophytic microfungi mostly apparent as black dots on dead plants that are frequent in the Arctic (Lind 1934, Savile 1963).

Fungal parasites are normally specialized microfungi attacking plants, animals, in particular invertebrates, and sometimes also fungi. They may have large effects on the population sizes of their hosts, but have not been extensively studied in the Arctic (but see Savile 1963). Examples of Arctic parasites are rust fungi such as *Melampsora* that commonly cause mortality of willows (Parmelee 1989, Smith *et al.* 2004) and smuts (Ustilaginales), parasitizing plants of Cyperaceae (Scholler *et al.* 2003). Another group of frequent pathogens in the Arctic are the snow molds that attack mosses and vascular plants under snow-cover when plant resistance is lowered (Tojo & Newsham 2012).

Fungi are pivotal for the cycling of carbon and nutrients (including N) in terrestrial ecosystems of the Arctic (Ludley & Robinson 2008, Newsham *et al.* 2009). Until recently, in ecological studies fungi were lumped with other microbes into a 'black box', and both the identity and roles of fungi in Arctic regions were largely unknown (Callaghan *et al.* 2004). The majority of Arctic plants' nutrient uptake is accomplished by mycorrhizal symbioses. Lichens are significant primary producers in the Arctic, and their contribution of biomass ranges from 2% in low Arctic to over 18% in high Arctic tundra and 65% in polar desert habitats (Webber 1974, Longton 1988). The proportion of Arctic vegetation biomass associated with mycorrhizal fungi has been estimated to range from 17% to 100% (Olsson *et al.* 2004). The cyanobacterial photobionts of Arctic lichens contribute significantly to nitrogen fixation (Crittenden & Kershaw 1978). Note that while the fungal part in lichens constitutes the major part of the lichen biomass, the mycorrhizal fungi constitute only a minute part of the plant biomass.

The decomposition of dead organic matter and recycling of nutrients in Arctic terrestrial systems is mainly conducted by saprotrophic fungi, with contributions by mycorrhizal fungi, and to a lesser degree by bacteria (Ludley & Robinson 2008, McMahon *et al.* 2009). Fungi have a major advantage over bacteria in this regard due to their ability to redistribute nutrients and carbohydrates within their extended hyphae and thereby overcome spatial deficiencies.

The presence and diversity of fungal species is largely determined by the distribution, diversity and abundance

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[9] Fungal endophytes are microfungi living inside plants without causing apparent symptoms.

of vascular plants and for lichenicolous fungi[10] of the lichens. Fungi parasitizing insects rely on the occurrence of their host animals. Some fungal species are confined to a single plant species, whereas others may associate with a few or several plant species. The majority of Arctic lichenicolous fungi are confined to one lichen genus (Zhurbenko 2010a). On the other hand, common Arctic lichen species or genera may host many lichenicolous fungi (e.g. about 20 on *Stereocaulon* spp. or *Thamnolia* spp.; Zhurbenko 2010b, 2012). Lichens ecologically resemble bryophytes. Their distribution depends primarily on habitat conditions (e.g. substrate type: rock-soil-bark, pH, microclimate, etc.) and competition by other plant species.

### 10.2.2. Fungal properties and adaptations to Arctic conditions

The short growing season and restricted opportunities for reproduction in the Arctic is thought to have selected for high longevity in individual fungi, slower population growth, and hence lower turnover than in more productive biomes (cf. Gardes & Dahlberg 1996). Local spreading relies primarily on mycelial growth or asexual spores rather than sexual reproduction. Population dynamics of fungi have not been studied in the Arctic, but may be inferred from boreal and temperate biomes (cf. Dahlberg & Mueller 2011). There, soil-inhabiting fungal genotypes may potentially, in stable conditions, exist for years, centuries or even longer as mycelia. Furthermore, patterns of sporocarp fairy rings and molecular studies reveal that genotypes of mycorrhizal and other soil-dwelling macrofungi typically extend from a few to several hundred square meters. In contrast, substrate-bound saprotrophic and pathogenic fungi are restricted in age and space. However, they may also disperse by asexual spores and sometimes as mycelia by insects, enabling genotypes to spread and persist longer than their host substrates.

Many lichen genotypes can most easily disperse by thalli fragmentation, and subsequently be transported by wind, water or animals over considerable distances. Some lichens even have specialized organs for fragmentation composed of fungal hyphae and algal cells, i.e. isidia, small thallus outgrowths that easily break off, or soredia, smaller powdery propagules. Hence, whereas single genotypes are localized in soil-dwelling fungi, they are typically more scattered and dispersed in lichens (e.g. Scheidegger & Werth 2009, Geml *et al.* 2010). Significant genetic differentiation at the landscape level has been shown in two Arctic lichens, a crustose *Porpidia* and a fruticose reindeer lichen, *Cladonia arbuscula* (Werth 2010). Most Arctic rock-dwelling crustose lichens reproduce sexually and are dispersed by spores (Fahselt *et al.* 1989).
Analyzing the increment of thallus radius over time (*Rhizocarpon geographicum* is frequently used in lichenometry), large thalli of rock-dwelling crustose lichens have been estimated to be up to several thousands years old (Matthews & Trenbirth 2011). These estimations are based on circumstantial evidence and linear extrapolation of growth rates derived from data for several decades or a few centuries. It is possible that exceptionally large crustose lichen thalli may be formed by the coalescence of neighbouring thalli rather than by slow radial growth and are not genetic 'individuals', though this is not probable for *R. geographicum* (e.g. Clayden 1997). Similar estimates of potential longevity of reindeer lichen genotypes are not possible, as the older portions at the base of thalli decay after about 30 years (Holt & Bench 2008). The annual growth of Arctic-alpine lichen thalli is seldom expressed as a change in surface area, thickness or biomass. Usually, it is measured and reported as a radial change that ranges from 0-0.5 mm per year in some crustose species (e.g. *R. geographicum*) to about 6 mm per year in reindeer lichens (Pegau 1968, Werner 1990, Armstrong & Bradwell 2010, Matthews & Trenbirth 2011, Bültmann & Daniëls 2012).

Arctic fungi have evolved physiological mechanisms to maintain mycelial activity and growth at low temperatures and low water potential (Robinson 2001). Even when soils are frozen, microbial processes in the Arctic continue. Fungi contribute 10 times more to Arctic soil microbial biomass than cohabiting bacteria. Microbial processes, i.e. predominantly of fungal origin, reach their annual peak under snow (e.g. Schadt *et al.* 2003), take up carbon from the environment and grow in frozen soils at least down to -2 °C (McMahon *et al.* 2009). Arctic lichens may have a positive net primary photosynthesis balance at low temperatures (many studies by K.A. Kershaw and co-workers, e.g. Larson & Kershaw 1975, Kershaw 1985), even under snow and ice, and survive extremely low temperatures and levels of water content (Kappen *et al.* 1996, Sommerkorn 2000).

Arctic and alpine ectomycorrhizal mushrooms species have evolved substantially smaller sporocarps and a reduced number of gills compared with their forest counterparts, probably as a response to restricted assimilate accessibility and the dry, harsh environmental conditions (Knudsen 2006). Similarly, sporocarps of many microfungi (observed in the pyrenomycete group) tend to be smaller in the Arctic (Savile 1963). The short growing season has also pushed parasitic species of Arctic rust and smuts to have simplified lifecycles, e.g. perennial habits which enable growth as soon as the season starts (Lind 1927, Savile 1982). Finally, lichenization is relatively more common in Arctic than in temperate areas. For example, the number of lichens vs. the number of macrofungi is about 1:1 in Greenland and 1:2 in Great Britain (Knudsen 2006), and the percentage of lichenized

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[10] Lichenicolous fungi constitute a functional non-taxonomic group of mainly ascomycetes and rarely basidiomycetes or other groups that forms obligate associations with lichens, as commensals, parasites or rarely saprotrophs. They are typically included in lichen checklists. Infection of lichens is very obvious in some Arctic vegetation types, e.g. snow beds. Thus, lichenicolous fungi could be expected to influence the growth of lichens (see Lawrey & Diederich 2003).

fungi of all known fungi is about 20% at the global level and 35% for the Russian Arctic (Zhurbenko 2010a).

### 10.2.3. Historic and present investigations

The first overviews of Arctic fungi were published for Svalbard by Karsten (1872) and for Greenland by Rostrup (1888) (for an extensive overview, see Elvebakk & Prestrud 1996, Gulden & Torkelsen 1996, Knudsen 2006). A brief history of the early mycology in the Canadian Arctic is presented by Savile (1962). Due to the ephemeral and irregular occurrence of sporocarps combined with the low accessibility for humans to the Arctic, macrofungi are collected with considerably less frequency than lichens, and hence the knowledge of their distribution and ecology is correspondingly lower. Regional species lists are available for Greenland, Iceland, Svalbard and the Russian Arctic, but a combined checklist for Arctic fungi has not yet been compiled (Elvebakk & Prestrud 1996, Karatygin *et al.* 1999, Hallgrímsson & Eyjólfsdóttir 2004, Borgen *et al.* 2006, Hallgrímsson 2010). Unfortunately, regional lists cannot easily be combined because of varying taxonomy. Therefore, knowledge of macrofungal distribution is presented at the level of Arctic Russia, Greenland and Svalbard. Iceland is also considered, although most of that country is classified as sub-Arctic. The Russian Arctic fungal checklist also includes species from the sub-Arctic and reports the recorded species numbers in the Arctic proper to be 20-30% less than when the sub-Arctic is included (Karatygin *et al.* 1999). No comprehensive checklist exists for the main North American Arctic, although the distributions of some Arctic species in Canada are reported by Redhead (1988). Arctic species tend to have wide distributions, more or less throughout the Arctic (experiences by authors and e.g. Lind 1934, Cripps & Horak 2006, 2010, Ronkier & Ronkier 2010).

Information on fungal specimens in Arctic herbaria is increasingly accessible through the global biodiversity information facility, GBIF (2012), but is still very incomplete. To promote the development of Arctic and alpine mycological knowledge, mycologists have cooperated in the International Symposium of Arcto-alpine Mycology network (ISAM) since 1980 and have arranged nine symposia with more than 100 participants in total and almost 100 scientific papers presented (Laursen & Ammirati 1982, Laursen *et al.* 1987, Petrini & Laursen 1993, Mukhin & Knudsen 1998, Boertmann & Knudsen 2006, Høiland & Økland 2008, Cripps & Ammirati 2010).

By necessity, Arctic mycological research has been primarily exploratory, focusing on identification, description and recording of fungal taxa. Few analyses of patterns and dynamics of macrofungal communities and of Arctic fungal ecology have been made (e.g. Lange 1957, Petersen 1977). Recent advancements in molecular approaches enable the detection, genetic characterization and quantification of fungi in environmental samples, e.g. soil and plant tissues. These data will significantly help to increase knowledge of Arctic mycology by complementing studies based on sporocarps or mycelial isolations (Fujimura *et al.* 2008, Bjorbækmo *et al.* 2010, Fujiyoshi *et al.* 2011, Walker *et al.* 2011, Geml *et al.* 2012, Timling *et al.* 2012).

The history of lichenological exploration of the Arctic is long. Lichens are easy to collect and preserve, and samples were brought home even by early Arctic expeditions. Therefore, the distribution of lichens is reasonably well known, though crustose microlichens are underrepresented. The distribution of their associated lichenicolous fungi is much less known (Zhurbenko 2009a). The first major work was a lichen flora of Arctic Europe and Greenland (Fries 1860). Details of lichen exploration are reported in several checklists and floras (e.g. Lynge 1947, Krog 1968, Thomson 1979, 1984, 1990, 1997 for North America, Elvebakk & Hertel 1996 for Svalbard, Printzen 2008 for a summary). Greenland is represented by many floristic studies (e.g. Alstrup 1982, 2005, Alstrup *et al.* 2000, numerous papers by E.S. Hansen, as Hansen 2008, Hansen *et al.* 1987). Recently, a Panarctic Lichen Checklist including their associate lichenicolous fungi was compiled by Kristinsson *et al.* (2006, 2010). The exploration of Arctic lichenicolous fungi is reviewed by Zhurbenko (2010a). The diversity of lichenicolous fungi is relatively well known for Greenland, Svalbard and Russia (Alstrup & Hawksworth 1990, Alstrup & Elvebakk 1996, Zhurbenko & Santesson 1996, Lawrey & Diederich 2003, Alstrup 2005, Zhurbenko 2007, 2009a, 2009b, 2010a).

General characteristics of Arctic macrolichen[11] communities have been summarized for lichen-rich vegetation in general (Ahti & Oksanen 1990), in Alaska (Holt *et al.* 2007), on rock in Greenland (Daniëls 1975) and for Arctic terricolous lichen communities (e.g. Nimis 1981, 1985, Daniëls 1982, Bültmann 2005, Bültmann & Daniëls 2009).

Lichens are established bioindicators for air purity (e.g. Nimis *et al.* 2002), but effects of air quality on species composition of Arctic lichen have not been reported. Lichens have been used as accumulation indicators for contaminants such as heavy metal cations, radionuclides, nitrogen, sulphur and organic compounds in the Arctic (e.g. Nash & Gries 1995, Walker *et al.* 2003).

Monitoring of fungi has not taken place in the Arctic. Two local monitoring studies in Greenland that include lichens show no trends for any aspect of lichen diversity as yet (Elberling *et al.* 2008 for 1997-2007 at Zackenberg, Daniëls *et al.* 2011 from 1968 to 2007 in Ammassalik). The site at Zackenberg is continuously monitored (Hansen 2006, Elberling *et al.* 2008), and monitoring

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[11] Macrolichen are defined as foliose (including squamulose) and fruticose lichens, which can mostly be identified macroscopically, while microlichens are crustose lichens, mostly visible to the naked eye, but require microscopical means to be identified.

## Box 10.1. Lichens and reindeer

Reindeer or caribou depend on lichens as winter food (e.g. Llano 1956, Inga 2007). Reindeer dig through the snow to feed on soil lichens. Most important are the reindeer lichens i.e. species of *Cladonia*, subgenus *Cladina*, and *Stereocaulon* spp. (see Box 10.1 Fig. 1). In boreal areas, reindeer also feed on lichens on tree trunks and twigs. Only older forests have enough epiphytic lichen biomass for food. Long-term studies showed a significant decrease of reindeer food lichens in Alaska (Joly *et al.* 2009). Higher winter temperatures caused by climate change will cause an increase in ice on top layers of snow by refreezing or rain making it more difficult for reindeer to dig out the lichens (e.g. Putkonen & Roe 2003 and Large Herbivore Network 2012). The ability of lichens, as of other fungi, to accumulate cations of heavy metals including radioactive elements is also problematic. Thus reindeer kept for human consumption should not graze in areas subjected to pollution with heavy metals. Especially in the sub-Arctic, the availability of and access to lichens for the reindeer of the indigenous peoples in the north of Eurasia is a complex and sometimes politically difficult topic. Some state-imposed reindeer management systems, such as the *Paliskunta*-system in Finland, have disrupted the traditional knowledgeable management of pastures, which has led to severe depletion of lichen in some areas (Mustonen *et al.* 2011).

**Box 10.1 Figure 1.** Terricolous lichen vegetation is suitable for reindeer with reindeer lichens (here *Cladonia mitis* & *C. rangiferina*), *Stereocaulon* spp. and *Flavocetraria cucullata*. Photo: Helga Bültmann, Narsarsuaq, S Greenland.

results are published regularly in annual reports (e.g. Hansen 2006).

Wild mushrooms have rarely been used by indigenous Arctic peoples in the past (e.g. as hallucinogen: an *Amanita* species by Chukchi shamans (M.P. Zhurbenko unpubl.), *Amanita muscaria* and the shelf fungus *Polyporus sulphureus* in Yakutia (Jakutija 2007) and species of puffball for the treatment of wounds and cuts (Joamie *et al.* 2001, Cuerrier & the Elders of Kangiqsujuaq 2011). Only during the last decades have interest and use developed for edible mushrooms, for example in Chukotka due to Russian immigration (Yamin-Pasternak 2007).

In contrast, lichens have historically been used frequently as mild antibiotics (e.g. *Cetraria islandica* and the reindeer lichens) in medicine and food preserving, as food when half-digested in the stomachs of ruminants and, occasionally undigested, but mostly as famine food (e.g. 'rock tripes' *Umbilicaria* spp.), as dyes and as fuel or tinder or even soap (Llano 1956, Oswalt 1957, Richardson 1974, Søchting 1990, Joamie *et al.* 2001, Cuerrier & the Elders of Kangiqsujuaq 2011). A concise summary and bibliography of lichen use is compiled by Sharnoff (2012). Terricolous macrolichens are the main sources of food for reindeer and caribou with *Rangifer tarandus* (Box 10.1) constituting 70-75% of their annual diet, and periodically also used by other species including muskoxen *Ovibos moschatus*, lemmings (subfamily Arvicolinae) and hares *Lepus* spp. (Llano 1956). Even mushrooms such as bolete species of *Leccinum* contribute to the summer diet of reindeer (Knudsen 2001).

## 10.3. THE FUNGI OF THE ARCTIC

### 10.3.1. Species richness

The total number of known fungal species in the Arctic is > 4,350 (Tab. 10.1). Of these, 1,750 are lichens and about 2,600 are fungi[12]. Lichens consist almost exclusively of ascomycetes, while in fungi most are ascomycetes and 837 are basidiomycetes. About 2,030 of the fungal ascomycetes and basidiomycetes are macrofungi (non-systematic group), while the rest are microfungi consisting mainly of ascomycetes but also some Chytridiomycota, Zygomycota and Glomeromycota plus rusts and smuts (Tab. 10.2). 373 of the fungi have a lichenicolous life form.

These figures correspond to 4% of the globally known total number of fungi (> 99,000), but as much as 10% of the globally known lichens and > 20% of the globally known lichenicolous fungi (Tab. 10.1; Hawksworth 2001, Lawrey & Diederich 2003, Feuerer & Hawksworth 2007, Blackwell 2011). However, it has been estimated that more than 90% of the global fungal species remain to be discovered and described, and the current working estimate suggests that their number on the Earth is at least 700,000 and likely 1.5 million (Hawksworth 2001, Schmit & Mueller 2007). These authors suggest a general relation between numbers of species of fungi to vascular plants to be 5-8:1. The status of lichens is rather well known in contrast to that for fungi. Microfungi are particularly poorly investigated. In the Arctic, 2,218 vascular plant species have been recorded, which is roughly half as many species as for fungi (cf. Daniëls *et al*, Chapter 9). With a proportion of 6:1 of fungi:plants, the number of fungi would amount to ca. 13,000 fungal species in the Arctic.

**Table 10.1.** Known and estimated total species richness of Arctic fungi.

| Fungal group | Taxonomic and functional group | Known total number of species | Estimated total number of species |
|---|---|---|---|
| Lichens | | 1,750[1] | ~1,750[2] |
| Fungi[3] | | >2,600[4] | 11,000[5] |
| | Chytridiomycota | 83 | |
| | Zygomycota | 45 | |
| | Glomeromycota | 11 | |
| | Ascomycota | 1,245 | |
| | Basidiomycota | 837 | |
| | Lichenicolous fungi | 373[6] | >440[7] |
| | Non-lichenized macrofungi | 2,030[8] | |
| Total number of Arctic fungi | | >4,350 | >13,000 |

1) The mycobionts of lichens predominantly consist of ascomycetes, but here they are treated as a functional group and not included in the taxonomic groups (Appendix 10.1).

2) Svalbard and W Greenland are the two best know areas where macrolichens are considered to be completely sampled, constituting 31% and 37%, respectively, of the known number of lichen species, mean 34%. Macrolichens also constitute 34% of the known number of Arctic lichens, and thus we expect the total number of lichens in the Arctic not to be much higher than the known number.

3) Fungi refer to non-lichenised fungi.

4) Calculated from the highest number of known species for each fungal group in Greenland, Iceland, Svalbard or Arctic Russia.

5) Estimated from the suggested relationship between vascular plant and fungi 1:5(-1:7) (Hawksworth 2001, Schmit & Mueller 2007.

6) Lichenicolous fungi are predominantly ascomycetes, but are here treated as a functional group and not included in the taxonomic groups (Appendix 10.1).

7) Estimated from a relationship of 4:1 between lichens and lichenicolous fungi (after Zhurbenko 2007 and Diederich *et al.* 2011).

8) Sum based on the species richness of macrofungi of Ascomycota (e.g. not anamorphic taxa) and Basidiomycota (cf. Tab. 10.2) and lichenicolous fungi.

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[12] We conservatively estimate the number of (non-lichenized) fungal species in the Arctic to be the highest species number recorded for each of the major taxonomic groups in the existing regional checklists.

**Table 10.2.** Compilation of reported number of fungi (non-lichenized fungi) species from different Arctic regions. No compilation exists for the main North America.

| **Fungal group** | **Iceland**[1] | **Greenland**[2] | **Svalbard**[3] | **Arctic Russia**[4] | **Highest number used to infer known number of Arctic species** |
|---|---|---|---|---|---|
| Chytridiomycota | 83 | 3 | 3 | | 83 |
| Zygomycota | 45 | 15 | 27 | | 45 |
| Glomeromycota | 11 | | | | 11 |
| Ascomycota | 620 | 680 | 226 | 800 | |
| Pyrenomycetes | | (180) | | (470) | 470 |
| Leotiales | | (200) | | (100) | 200 |
| Pezizales | | (150) | | (50) | 150 |
| Anamorphic | 425 | 200 | 103 | 300 | 425 |
| Basidiomycota | 716 | 837 | 201 | 650 | 837 |
| Lichenicolous fungi[5] | 14 | 231 | 75 | 140[6] | 373[7] |
| Total number of known non-lichenized fungi | 1,903 | 1,947 | 635 | 1,890 | 2,594 |
| Known number of macrofungi | 1,350 | 1,579 | 502 | 1,410 | 2,030 |

1) Hallgrímsson & Eyjólfsdóttir 2004, Hallgrímsson 2010. Lichenicolous fungi refers to low Arctic in Iceland, other fungal groups refer to all of Iceland (low and sub-Arctic).

2) Borgen *et al.* 2006, Knudsen 2006.

3) Elvebakk & Prestrud 1996.

4) Karatygin *et al.* 1999.

5) Consists mainly of ascomycetes, but includes also basidiomycetes (Appendix 10.1).

6) Zhurbenko 2010a reports 250 species for the Russian Arctic, however including areas not corresponding with the Arctic as defined here (e.g. with Kola Peninsula).

7) Known Arctic species richness (Appendix 10.1).

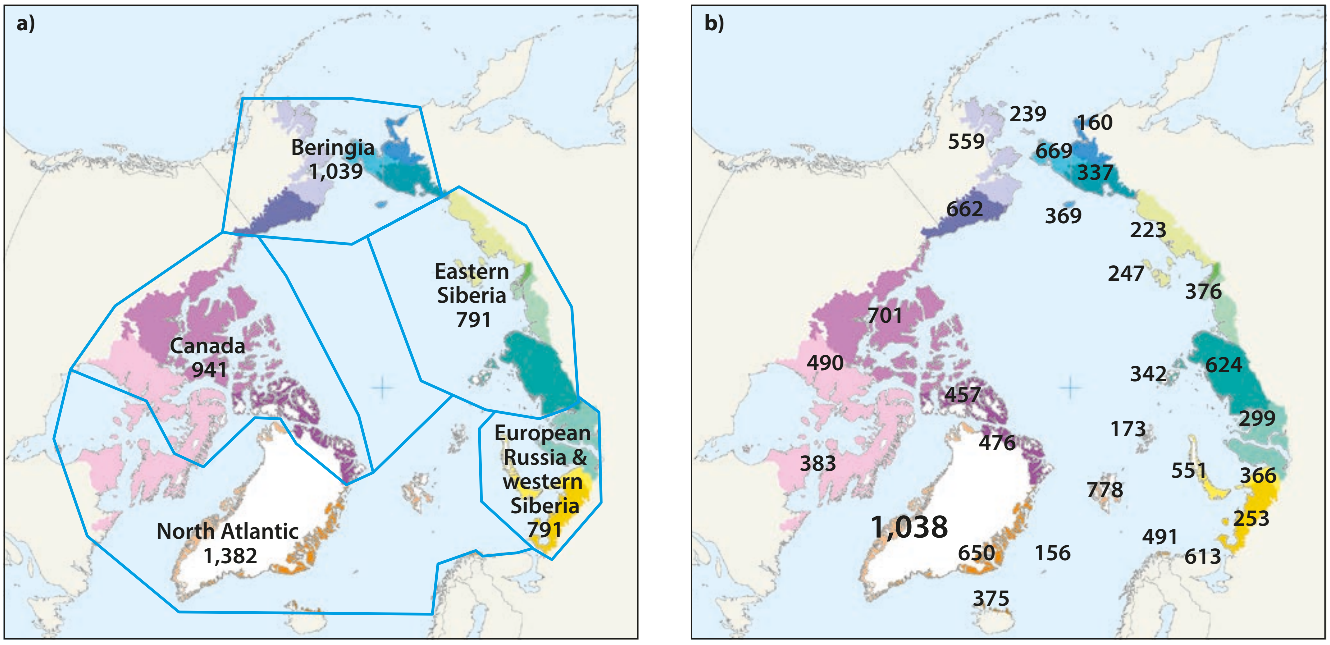

**Figure 10.1.** Species richness of lichens in Arctic (a) sectors and (b) floristic provinces. Provinces are shown with different colors (n = 1,750). Continental species richness: North America 1,026, Greenland 1,136, Europe 1,075 and Asia 1,178.

## 10.3.2. Species richness in different geographical regions

The distributions of Arctic lichens and lichenicolous fungi are known in greater detail than those of other fungi (Fig. 10.1 and 10.2). The two best investigated areas concerning fungal diversity are Greenland and Svalbard with high documented species richness for fungi, lichens and their associated lichenicolous fungi (Tab. 10.2, Fig. 10.1 and 10.2). W Greenland is accessible from the coast and has been intensively studied historically and in recent years. It includes a small area with sub-Arctic birch forests in the very south, but only about 30 lichen species and 200 fungi are exclusively found in this sub-Arctic enclave (Jensen 2003). Svalbard is rather small and consists exclusively of high Arctic habitats. It has attracted many lichenological and mycological studies (e.g. Øvstedal *et al.* 2009, Bjorbækmo *et al.* 2010, Geml *et al.* 2012). No compilation of fungi is available from the main American Arctic, but a molecular study of ectomycorrhizal roots from 326 plants of Arctic willow *Salix arctica* and mountain avens *Dryas octopetala* collected along a gradient from the low to the high Arctic in north America identified 242 different ectomycorrhizal fungal species and no decline in species richness (Timling *et al.* 2012).

The difference in the number of recorded species among regions is due to several factors, including area size, the diversity and number of different habitats, and relative survey effort. The relatively lower species richness in many of the vast Arctic areas in North America and Russia, for example, is probably caused by fewer surveys having been conducted there.

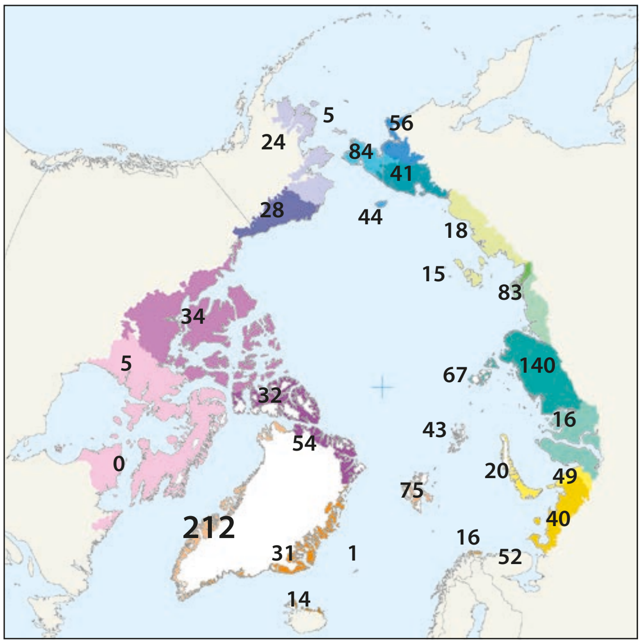

**Figure 10.2.** Species richness of lichenicolous fungi in Arctic floristic provinces. Species richness in Arctic sectors: Beringia 157, Canada 89, North Atlantic 256, European Russia & western Siberia 90 and eastern Siberia 176 (see Fig. 10.1 for delimitation). Continental species richness: North America 80, Greenland 231, Europe 111 and Asia 243.

**Table 10.3.** Species richness of lichens in sub-, low and high Arctic Greenland on different substrates (n = 1,694 species, distribution unknown for 56 species).

| | All substrates | Bark | Wood | Soil | Rock |
|---|---|---|---|---|---|
| High Arctic | 1,230 | 101 | 33 | 358 | 738 |
| Low Arctic | 1,450 | 215 | 53 | 413 | 769 |
| Sub-Arctic Greenland | 671 | 88 | 25 | 211 | 347 |

Exclusively sub-Arctic Greenland: 32 species, low Arctic: 432 species; high Arctic: 204, in low & high Arctic: 1,018 species, sub- & high Arctic: 8 species.

## 10.3.3. Distribution of species within different Arctic zones

Knowledge of the distribution of fungal species in the low and the high Arctic, respectively, is fragmentary and has not yet been compiled and analyzed. However, these species are largely dependent on the occurrence and abundance of plants, and hence their distribution may be inferred from the distribution of plants. Plant species richness and abundance decline from the low to the high Arctic, which support 2,183 and 111 species of vascular plants, respectively (Daniëls *et al.*, Chapter 9). The occurrence of specific plant species determines which species may be present, and different plant species are associated with different numbers of fungi. High Arctic root-associated fungal communities are reported to be quite distinct for six plant species (Fujimura & Egger 2012). In contrast, the two principal ectomycorrhizal Arctic plants, mountain avens and arctic willow, form ectomycorrhizae with more than 250 fungal species that they largely share (Bjorbækmo *et al.* 2010, Timling *et al.* 2012).

The distribution of Arctic lichens is better known than that of fungal species. Almost 60% of the lichen species occur in both the low and the high Arctic (Tab. 10.3). On average, lichen species richness declines by 15% from low to high Arctic in contrast to species richness in vascular plants, which declines by 95% (Tab. 10.3; Daniëls *et al.*, Chapter 9). Most of the decline in lichens is among species growing on bark and wood and there is some decline among species growing on soil and rocks. In some high Arctic areas, e.g. in Canada and Svalbard, lichen species richness can be higher than in the low Arctic (Appendix 10.2).

Arctic fungal diversity hotspots on a landscape scale are not known, but compared with the low plant diversity in Arctic communities, the species richness and heterogeneity of lichen communities is high (e.g. Lünterbusch & Daniëls 2004, Bültmann 2005, Bjorbækmo *et al.* 2010, Geml *et al.* 2012, Timling *et al.* 2012), as high as in species-rich communities outside the Arctic such as calcareous grasslands (Bültmann 2011).

**Table 10.4.** Examples of Arctic studies documenting high small-scale species richness of lichens in relation to vascular plants and bryophytes within study plots of different size in homogeneous vegetation (Greenland: all low Arctic, Canada: high Arctic).

| Country | Total species richness within plot | Number of species thereof | | | Reference |
|---|---|---|---|---|---|
| | | Lichens | Vascular plants | Bryophytes | |
| Greenland | 70/0.16 m$^2$ | 38 | 11 | 21 | Lünterbusch & Daniëls 2004 |
| Greenland | 71/0.25 m$^2$ | 47 | 9 | 15 | Bültmann 2005 |
| Greenland | 83/4 m$^2$ | 48 | 11 | 24 | Lünterbusch & Daniëls 2004 |
| Greenland | 90/9 m$^2$ | 56 | 18 | 16 | Sieg *et al.* 2009 |
| Canada | 95/25 m$^2$ | 40 | 17 | 38 | Vonlanthen *et al.* 2008 |

Species richness of 700 lichens and of 100 lichenicolous fungi is documented for hotspots in mountain areas in the boreal zone, adjacent to Arctic areas (Elvebakk & Bjerke 2006: 709 lichens, 94 lichenicolous fungi in N Norway, and Spribille *et al.* 2010: 668 lichens, 98 lichenicolous fungi in Alaska). Species richness in potential Arctic hotspots could be expected to be slightly lower because of the decline in the number of epiphytic lichens. However small-scale diversity in vegetation study plots in the Arctic has been shown to be very high, in most cases due to a large number of lichens; up to 50 species on less than 1 m$^2$ (Tab. 10.4). For soil fungi, a molecular study detected 332 fungal taxa in 600 soil cores in Svalbard (Geml *et al.* 2012).

## 10.3.4. Distribution of different life forms and at different substrates

The most well-known fungal life form in the Arctic is lichens, comprising 40% of the known species, while ectomycorrhizal fungi constitute at least 6% and lichenicolous fungi about 9% of known species. The remaining known species are predominantly saprotrophic, the majority litter- and soil-dwelling with a few wood-inhabiting species, and only a few are parasitic species (e.g. rust and smuts). Most Arctic lichen species are rock dwellers (56%), followed by lichens on soil (26%), bark (14%) and wood (4%; Appendix 10.2. The proportions of lichen species growing on these substrates are similar in boreal and temperate biomes, except for the proportion of 'bark' species which is higher there, about 30% (Bültmann 2010). In the Arctic, as in the other biomes, a larger portion of lichen species grows on acidic substrates rather than on calcareous substrates (Appendix 10.2; see also Bültmann 2010). Most species of lichenicolous fungi are found on lichens with soil or plant debris as substrate (for the Russian Arctic: 63%; Zhurbenko 2010a). Fewer are associated with rock-dweller (33%) and bark/wood-dweller species (4%). Most Arctic lichens (66%) are crustose, i.e. microlichens, while 34% are macrolichens (7% of squamulose, 13% of leaf-like (foliose) and 14% of small-shrubby (fruticose); Appendix 10.2).

## 10.3.5. Specificity to the Arctic and rarity

Few species if any, of fungi are exclusively confined to the Arctic. The potential degree of endemism is probably less than 2% in fungi (H. Knudsen pers. com.). Some genera and several species are predominately Arctic-alpine circumpolar in their distribution, while the remaining species also may occur in boreal and temperate habitats (Gulden & Torkelsen 1996, Knudsen 2006). The distribution of 422 circumpolar Arctic microfungi was reported and discussed by Lind (1927). More recently, circumpolar distribution has been examined and reported for a few species of Arctic macrofungi (Knudsen & Mukhin 1998, Cripps & Horak 2006, Cripps *et al.* 2010, Ronkier & Ronkier 2010, E. Larsson pers. com.). DNA sequence analyses of the identity of Arctic ectomycorrhizal fungi in mycorrhizal host roots imply that many may be distributed globally and are found also in boreal, temperate and Mediterranean biomes (Geml *et al.* 2012, Timling *et al.* 2012).

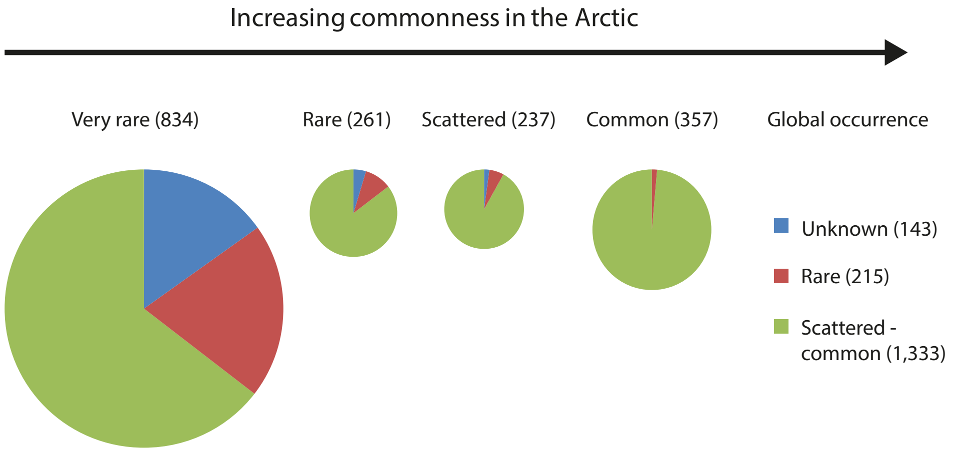

**Figure 10.3.** The commonness of lichen species in the Arctic in four categories: very rare, rare, scattered and common. The sizes of the pie charts correspond to the species number. The estimated global occurrences of these species within each category are shown within each pie chart (see Appendix 10.1; n = 1,691, insufficient data for 59 of the 1,750 known species in the Arctic).

**Table 10.5.** Numbers of potentially endemic lichens in the Arctic together with lichen species that are rare outside the Arctic, distributed by low and high Arctic, province or sector and their life form. Only species with known distribution are included (n = 358; endemic: 143, rare: 215). For explanation of province and sector, see Fig. 10.1.

| | Low | High | Only low | Only high | Only in 1 sector | Only in 1 province | Microlichens | Macrolichens |
|---|---|---|---|---|---|---|---|---|
| **Endemic** | 83 | 103 | 36 | 56 | 84 | 72 | 125 | 18 |
| **Rare** | 152 | 138 | 41 | 48 | 98 | 80 | 174 | 41 |

Microlichens: crustose, Macrolichens: squamulose, foliose and fruticose

The majority of Arctic lichen species have more limited distributions. About 25% are known from the entire Arctic, a further 25% from three or four sectors (delimitations of sectors see Fig. 10.1), while 49% are known from only one or two sectors. This is a wider distribution than reported for vascular plants, for which about 70% of the taxa are found in one or two sectors and 10% in all five (Elven 2007 onwards). The lichen species known only from one geographic region are mostly very rare in the Arctic. Overall, 48% of the Arctic lichens are classified as very rare in the Arctic (Appendix 10.2). The majority of those (64%) are common or scattered outside the Arctic (Fig. 10.3).

At the moment, 143 lichen species are listed as Arctic endemics (Appendix 10.1). Five of these are widely distributed within the Arctic while the majority is classified as very rare (Appendix 10.1 and 10.2). These Arctic endemics are mainly rock-dwelling microlichens occurring in the high Arctic (Tab. 10.5). However, a taxonomic revision is needed for many of these lichens in order to settle their taxonomic status (Kristinsson *et al.* 2010). A recent critical reexamination of 52 rare lichen taxa reported in Norway concluded that only 30% of them were appropriately identified to the species level and that the remaining were probably synonyms to more common species (Jørgensen & Nordin 2009).

Most lichens with scattered or common distribution in the Arctic are also scattered or common outside the Arctic (Fig. 10.3). The 215 Arctic lichen species that are rare outside the Arctic are predominantly rock-dwelling crustose microlichens (Tab. 10.5).

## 10.4. TRENDS, CAUSES AND PROSPECTS

Arctic climate and vegetation, including fungal communities, have undergone major changes during past glacial and interglacial periods (Lydolph *et al.* 2005, de Vernal & Hillaire-Marcel 2008). Fungal species have repeatedly disappeared and re-colonized the present Arctic, the fungi following their associated plants, and the lichens responding to availability of suitable habitats. There is growing evidence that the advance of flowering plant vegetation is speeding up as is the 'greening' of Arctic tundra, similar to related changes occurring in mid-latitude alpine regions (Wookey *et al.* 2009; see also Ims & Ehrich, Chapter 12). Altered vegetation drives fungal communities to change. Increasing productivity and increasing biomass in the low and the high Arctic – including increasing shrub cover in the low Arctic – will result in increased fungal activity and biomass, alter composition of fungal communities and may subsequently affect fungal ecosystem processes (e.g. Wallenstein *et al.* 2007, Deslippe *et al.* 2011). These changes will mainly be a response to altered composition of plants and increased photosynthesis levels, but other biotic and abiotic factors may also play roles.

It is obvious that the occurrence and abundance of fungi will track those of their associated plants, but so far the fungal consequences of climatically induced vegetation changes have only been studied to a limited extent (Pickles *et al.* 2012, Timling & Tayler 2012). One of the few studies of vegetational changes and fungal diversity reports large effects on the composition and functions of ectomycorrhizal fungi in an 18-year long-term experimental greenhouse warming of dwarf birch *Betula nana* (Deslippe *et al.* 2011). This experiment resulted in higher mycelia biomass in ectomycorrhizal fungi characterized by mycelia of long distance exploration types and capacity to mobilize organic nitrogen (e.g. in webcaps *Cortinarius* spp.). At the same time, there was a reduction of fungi with mycelia of the contact exploration type, like brittle gills *Russula* spp.; these have an affinity to labile inorganic nitrogen. The authors infer that warming may profoundly enhance decomposition of soil organic matter and increase the connectivity of dwarf birch through mycorrhizal networks of larger size. These changes may further facilitate shrub expansion by enhancing nitrogen acquisition and nutrient redistribution to dwarf birch. The reports of earlier spring and later autumn fruiting behavior of macrofungi in Europe due to current climatic warming (Kauserud *et al.* 2008, 2010, 2012) reflect increased fungal activities below ground; such changes are also likely to take place in the Arctic.

The predicted profound influence of increased average air temperature and annual average precipitation in the Arctic will have effects on ecosystem functions that are difficult to predict (ACIA 2005). The effects on global carbon cycling and atmospheric $CO_2$ levels will significantly depend on how the diversity and functions of fungal communities are affected due to their key roles in terrestrial carbon cycling (e.g. Ludley & Robinson 2008, Pickles *et al.* 2012). The uncertainty of how the large Arctic soil pool of carbon will change with changing vegetation, soil temperature and permafrost will also depend on (1) how vegetation patterns will change and feed back to climate, (2) how diversity of fungal and bacterial communities will change in relation to vegetation change, and (3) how the subsequent fungal and bacterial carbon-cycling processes will be affected. It has recently been reported that a major portion of stored carbon in boreal forests derives from roots and root-associated microorganisms, probably with ectomycorrhizal fungi as key-players (Clemmensen *et al.* 2013). As fungi similarly may be important for the carbon flux in Arctic soils, changing vegetation and fungal communities may affect the amount of stored carbon. Yet, the abundance, diversity, functions and potential reactions to climate change of fungi in the Arctic are not well understood.

Lichens are autotrophic and less dependent on vascular plants, though some may compete with plants and some grow on bark. The majority of lichen species, including most endemic and rare species, grows on rock surfaces and do not compete with vascular plants. Nevertheless, changes in temperature and moisture regime will gradually cause changes in the species composition of lichen communities. The Arctic epiphytic lichens may be favored by the spreading of shrubs and trees to the north, while terricolous lichens can be expected to face increasing competition from vascular plants.

The recently established local long-term monitoring of lichen communities at Greenland has not detected any effects of climate change. In the Netherlands, long-term monitoring of lichen communities has revealed changes that are suggested to be partly due to warming since 1990 with a rather rapid increase in some and a decrease in other species (van Herk *et al.* 2002, Aptroot 2009). However, these findings are only partly applicable to the Arctic. In the Netherlands, the increase in (sub-) tropical species concerns mainly species recovering from the losses by former $SO_2$-pollution, and the decrease in boreo-montane/Arctic-alpine species concerns mainly terricolous species suffering from changes in land management of semi-natural grassland and heath-land and is fuelled by anthropogenic emissions of nitrogen compounds (primarily $NO_3$ and $NH_3$; e.g. Hauck 2009).

Increasing nitrogen input to ecosystems has large direct and indirect effects on species diversity of both ectomycorrhizal fungi (e.g. Lilleskov *et al.* 2002) and lichens. Atmospheric nitrogen deposition in the Arctic is expected to increase in the future (Callaghan 2005). Such input of nitrogen will increase vascular plant growth and competition with a negative effect for the Arctic terricolous lichen, including the lichens essential as reindeer food. Field experiments document that increased vascular plant vegetation results in a decline in soil-inhabitating macrolichen abundance in the sub- and low Arctic, including reindeer food lichens (Joly *et al.* 2009), but this is not yet apparent in the high Arctic (Cornelissen *et al.* 2001).

It is possible to infer potential future distribution of fungi by combining predicted changes in habitat types or vegetation cover in the Arctic with their ecology. Hence, it would be feasible to initiate monitoring programs for any of these fungal groups. Lichens would best be monitored through visual surveys (e.g. Elberling *et al.* 2008) and fungi through a combination of sporocarp observations and molecular analyses of environmental samples. Recent advances in molecular methods, e.g. pyrosequencing, efficient bioinformatics and increasing sizes of databases of fungal reference sequences are promising in this regard (e.g. Buee 2009, Geml *et al.* 2012, Timling *et al.* 2012). Soil animals are increasingly being monitored using such methods (Heger *et al.* 2012).

The conservation status of macrofungi and lichens has not been evaluated for any fungal group at the circumpolar level, for Arctic-alpine environments or at the global level (IUCN 2012). None of the three globally ad hoc red-listed fungal species (two lichens and one fungal species) occurs in the Arctic (IUCN 2012). Given the relatively large distributional and ecological knowledge of Arctic lichens (Kristinsson *et al.* 2010), a red-list evaluation and the conservation status of Arctic lichens could be established. It is a challenge that many rare lichens are known only from ancient collections. The evaluation of conservation status should include detailed information about the distribution of rare and endemic Arctic lichens to avoid unintentional destruction of rare lichens by e.g. construction works, such as reported by Thomson (1997) as a possibility for a type locality in Alaska. Similarly, the conservation status of Arctic macrofungi, although based on substantially less knowledge, may for a large share of the species be evaluated based on published and anecdotal knowledge in combination with data on habitat trends (Dahlberg & Mueller 2011).

Field surveys, monitoring programs and research are needed to maintain and develop knowledge of Arctic fungi. However, today's knowledge of Arctic fungi relies on a very small number of experienced and skilled people. There is a general concern that universities and government agencies rarely hire field-experienced scientists with a broad taxonomic knowledge. This is particularly true for Arctic fungal specialists. Without opportunities for such positions, Arctic fungal biodiversity will attract little attention and loss of fungal diversity may go unnoticed and undocumented resulting in causes for changing fungal-dependent ecosystem processes be less understood.

## 10.5. CONCLUSIONS AND RECOMMENDATIONS

Fungi is a key group of organisms with high species richness and large significance for ecosystem processes in the

Arctic. Except for macrolichens, however, their presence and significance has often been overlooked and poorly appreciated in the Arctic, despite being species rich, abundant and pivotal in carbon and nutrient cycling. Distributional and ecological knowledge is reasonably good for macrolichens but sparser for fungi and microlichens.

Even with these caveats, present knowledge largely enables us to predict the future of Arctic fungi. The unavoidable greening of the Arctic will steadily and significantly affect the distribution and abundance of fungi, as habitat conditions gradually transform the distribution and abundance of plants. This change is in progress already, but studies of Arctic soil fungal communities imply that the response as yet is relatively slow (Timling & Taylor 2012). Therefore, we judge that these changes will only rarely affect their conservation status in the immediate future. However, over time the effects of climate change and subsequently transformed vegetation will have profound effects on the distribution and composition of fungi and consequently also their ecosystem functions. Most of the species are circumpolar and also distributed outside the Arctic. However, a large proportion of them are confined to Arctic-alpine habitats of which the greater part is located within the Arctic and few are true Arctic endemics.

The following actions would enable a more thorough analysis of the status and trends of Arctic fungi.

- Long-term funding is necessary to maintain and train Arctic specialists in mycology and lichenology and to ensure research and monitoring to take place.
- The identity and taxonomy of species with unclear status (e.g. poorly known fungi and potentially endemic lichens) should be critically examined. The large potential of fungal analysis of deep sequenced environmental samples will largely benefit by clarified fungal taxonomy.
- A check-list for Arctic fungi should be compiled.
- The knowledge of distribution and ecology for all fungi, but in particular for non-lichenized fungi, should be improved.
- Conservation status should be assessed for Arctic lichens and fungi, preferentially at both the Arctic and global scales.
- Long-term monitoring within representative Arctic habitats would enable us to document and follow fungal species shifts over time.
- Analyses of how vegetation changes may, based on knowledge of fungal ecology, predict potential habitats for fungi in space and time.
- Efforts to analyze the effects of slowly shifting fungal communities on ecosystem processes such as nutrient cycling and carbon fluxes are needed.
- Analyses of how the supply of reindeer food lichen communities will alter due to vegetation change should be conducted in order to better predict future conditions for populations of reindeer/caribou.

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Appendix 10: www.abds.is/aba-2013-appendix-10

Microorganisms are numerous almost everywhere. Here is an epi-fluorescene micrograph from a northern Baffin Bay water sample. The sample was treated with a fluorescent probe which stains the DNA inside of the cells. Bacteria and the nucleus of single celled eukaryotic plankton appear in blue. The smaller points are bacteria and the larger are Eukarya. Photo: Connie Lovejoy.

## *Chapter 11*

# Microorganisms

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## Contents

## SUMMARY

Microbes, defined here as Bacteria, Archaea and single-celled Eukaryota (protists) are ubiquitous and diverse members of all biological communities. In marine and many freshwater systems, photosynthetic microbes form the base of the food chain supporting higher trophic levels. Among the photosynthetic species are biologically diverse small flagellates that also graze on bacteria and other protists and hence are functional heterotrophs at times. Strictly phagotrophic protists are also diverse and contribute to the complexity of microbial food webs, with a multitude of trophic interactions. The fate of Arctic primary production emerges from the assembly of the entire microbial community. Heterotrophic bacteria break down fixed organic carbon and recycle nutrients, while other bacteria and Archaea with diverse metabolic capacities are active in the remineralization of carbon, nitrogen and other elements. There is a lack of long-term comprehensive baseline data on microbial biodiversity in terrestrial, freshwater and marine systems that largely impedes understanding ecosystem structure and resilience over both local and regional scales.

Because of their small size and often large populations, microbes in principle may have global distributions as they are transported by moving masses of air and water. Microbial communities are strongly selected for by their immediate environment, and successful global transport will be influenced by the ability of organisms to remain viable during transport between favorable environments. Species are more likely to have geographically restricted distributions if they lack a dormant stage or are specialists, and if their preferred environments are rare and distant from each other. Local communities may also resist invasions in the absence of physical or ecological perturbations that would give invading species or ecotypes an advantage. In the absence of ice cover, increased light availability and increased water column stratification can influence microbial community structure, affecting both phototrophic and heterotrophic species. Both the duration of the productive season and the species composition of protists have implications for higher food webs, thus ecosystem services by microbes are of direct relevance to wildlife and fisheries biologists as well as local communities. In addition, microbial community interactions largely determine the efficacy of the biological carbon pump.

The diversity of heterotrophic protists and other microbes is largely unknown, since for the most part they cannot be identified morphologically. Hence, sound historical records are lacking. New tools are being used to identify these heterotrophs from their DNA and RNA collected from the environment. Even among larger species of phytoplankton, cryptic species have been identified from DNA sequences. The small sub-unit ribosomal RNA (SS rRNA) gene is the most common target for gene surveys and enables the identification of microbes at the level of genus and even species and ecotype for some groups. In addition, genomic and transcriptomic signatures of microbes from the Arctic will provide valuable insight into the resilience and capacity of Arctic ecosystems. The recent rapid advances in sequencing technology will enable the expansion of microbial surveys, facilitating the integration of microbial biodiversity data into coupled biogeochemical climate models. Further, monitoring could provide the means to test whether there are linkages between climate change, environmental perturbation and the emergence of southerly species, enabling robust projections about dynamic shifts in ecosystem structure over time. For these reasons there is an urgent need to increase knowledge of microbial communities at the finest taxonomic and functional levels.

## 11.1. INTRODUCTION

Microbes represent the majority of biodiversity on Earth and are integral components of all ecosystems. In terms of numbers, microbes also dominate with c. one million cells per milliliter (ml) of seawater and most freshwaters. Marine sediments host an even more impressive number of bacterial cells per ml (in the order of 1 billion). Sea ice also harbors distinct microbial communities that live within brine channels and at high local concentrations (Deming 2002). Distinct communities can be found attached to the bottom of first year ice and occurring in surface melt ponds (Mundy *et al.* 2011). Concentrations of bacteria in Arctic soils are less than in temperate soils, but can still reach substantial numbers in key microhabitats (Yergeau *et al.* 2010, Wilhelm *et al.* 2011). Although heterotrophic protists and other microbes are the primary drivers of marine food webs and play key roles in freshwaters and soils, they are rarely included in general assessments of biodiversity (Archambault *et al.* 2010).

As reported in other chapters, climate and environmental change is rapidly reshaping northern ecosystems. These perturbations include the loss of summer ice, changes in the annual production cycle and changes in the depth of the most biologically active layers in both pelagic water columns and soils. Such environmental changes will have a direct effect on visible animals and plants (Falk-Petersen *et al.* 2009) and also have direct impact on the microbial food webs that support higher trophic levels.

In addition, as mentioned in other chapters, terrestrial and aquatic habitats merge over much of the sub-Arctic and Arctic. Distinct ponds and lakes are formed in polygons and runnels surrounding polygons within the permafrost, and in the high Arctic water increasingly remain as ice over the year. Deeper lakes are also scattered throughout the Arctic, and the microbial community structure of ponds and lakes is influenced by their depth, catchment area, orientation and underlying basin geology. Freshwater microbes are poorly studied with only sporadic reports of species. Most surveys of soil microbes have focused on disturbed sites with few reports on the microbes from pristine regions (Steven *et al.*

2008a, Martineau *et al.* 2010, Niederberger *et al.* 2010, Wilhelm *et al.* 2011). In this chapter, I provide a brief summary of existing knowledge, identify key gaps and suggest strategies for monitoring microbial biodiversity.

## 11.2. STATUS AND KNOWLEDGE

### 11.2.1. Bacteria

Prior to the application of molecular techniques, all that was known about the identity of bacteria in the Arctic was from culture studies of isolates. This approach continues to be valuable and provides unique insights into the metabolic capacity of microorganisms, especially those from extreme environments (Steven *et al.* 2008b, Niederberger *et al.* 2009a, 2009b). Sea ice bacteria are also represented in culture collections (Junge *et al.* 2002, 2003), but few unequivocally planktonic polar bacteria have ever been cultured. An alternative approach to culture studies are gene surveys, where the taxonomically informative gene coding for 16S ribosomal RNA (rRNA) is amplified by polymerase chain reaction (PCR), cloned and sequenced (Crump *et al.* 2003, 2009, Hollibaugh *et al.* 2007, Kellogg & Deming 2009, Jungblut *et al.* 2010, Harding *et al.* 2011, Lovejoy *et al.* 2011). The combination of culture studies and environmental gene surveys can reveal greater diversity than either alone (Wilhelm *et al.* 2011). Recently, high throughput sequencing technologies have been used to tag samples and enable massive parallel sequencing without cloning. This technique was first applied to marine Arctic water samples as part of the International Census of Marine Microbes (ICOMM; Galand *et al.* 2010, Kirchman *et al.* 2010). Those results indicate, as with most open ocean systems, that bacterial diversity has been underestimated by earlier approaches and showed that biogeography, history and water mass distribution were important determinants in the makeup of pelagic microbial communities. Similar studies of soil systems and freshwater have also indicated that bacterial diversity is much greater than previously thought (Yergeau *et al.* 2010, Wilhelm *et al.* 2011, Comeau *et al.* 2012a).

Salinity and oxygen are primary environmental drivers that select for microorganisms at the level of phyla. Freshwaters are dominated by *Betaproteobacteria* and freshwater clades of *Bacteroidetes*. *Bacteroidetes* are also commonly found in sea ice and marine Arctic surface waters along with *Gammaproteobacteria*. Sea ice communities vary within ice core horizons, and multiyear ice may be distinct from more biologically active first year ice (Staley & Gosink 1999, Bowman *et al.* 2012, Comeau *et al.* 2012b). *Alphaproteobacteria* are more frequent dominants in marine pelagic waters (Galand *et al.* 2008, 2010). *Gammaproteobacteria*, *Deltaproteobacteria*, *Actinobacteria* and *Alphaproteobacteria* are the most common classes in Arctic marine sediments (Ravenschlag *et al.* 1999, Li *et al.* 2009, Teske *et al.* 2011, Bienhold *et al.* 2012). *Acidobacter* and *Actinobacteria* have been reported from sub-Arctic and Arctic freshwaters and may be selected for by particular environmental characteristics (Liebner *et al.* 2008). *Actinobacteria*, *Alphaproteobacteria* and *Bacteroidetes* tend be most abundant in the high Arctic, however as in other soil environments bacteria are very patchy both in terms of abundance, species composition and species turnover (Pellerin *et al.* 2009, Wagner *et al.* 2009). Seasonal changes in bacterial communities have also been reported with one sulphur-oxidizing species in the genus *Thiomicrospira* forming macroscopic streamers during winter and disappearing during the Arctic summer (Niederberger *et al.* 2009a). Similar species and associated communities are also reported from Svalbard thermal springs (Reigstad *et al.* 2011) indicating the importance of specialized micro-environments harboring microbial biodiversity. Recent metagenome analyses revealed that during transition from a frozen to a thawed state there are rapid shifts in many microbial, phylogenetic and functional gene abundances and pathways (Mackelprang *et al.* 2011).

Polar seas are well oxygenated, and bacterial chemosynthetic primary production has not been widely studied, although methane production is reported from ice covered waters (Damm *et al.* 2010) suggesting microbial activity apart from heterotrophy. Energy availability in the form of phytodetritus was suggested to be a main driver of diversity and activity for benthic bacterial communities at the Laptev Sea continental slope, which implies that changes in primary production and subsequent flux to the benthos will likely influence bacterial community structure and activity, with subsequent impacts on ecosystem functioning, such as C-cycling (Bienhold *et al.* 2012).

Ponds formed by permafrost thaw and polygon collapse may be major contributors to greenhouse gases via respiration of ancient carbon: both $CO_2$ and methane can be released from these systems (Rivkina *et al.* 1998, Wagner *et al.* 2009). Methane production may also be balanced by methane oxidation, where methanotrophs use methane as a source of carbon and energy (Liebner *et al.* 2009, 2011). Gene sequences of 16S rRNA associated with these methanotrophs, though rare, have also been recovered from polar seas (Galand *et al.* 2010, Kirchman *et al.* 2010). Overall, the dynamics and community composition in these systems is poorly understood. The suite of rare and occasional abundant taxa found in water columns, marine benthos and soil are likely involved in other diagenetic processes and require further study.

### 11.2.2. Archaea

Archaea are a separate domain of life apart from Bacteria and Eukarya. When they were first discovered, Archaea were thought to be uniquely extremophiles, inhabiting hot springs, supersaturated saline waters and highly acidic environments. They are now recognized as being ubiquitous in all marine waters and frequent members of freshwater microbiota (Galand *et al.* 2006, Pouliot *et al.* 2009). In terms of numbers, Archaea may be more important in polar seas compared with other systems and are especially abundant in winter (Alonso-Saez *et al.* 2008). The two most abundant archaeal phyla in the ocean belong to the Euryarchaeota (Marine Groups: MGII, MGIII and MGIV) and Thaumarchaeota, also referred to as Marine Group I (MGI) and originally classified with Crenarchaeota (Spang *et al.* 2010). The only free living cultivated representative of MGI, *Nitrosopumilus maritimus*, is able to oxidize ammonia and fix inorganic carbon (Konneke *et al.* 2005, Walker *et al.* 2010), and the majority of Thaumarchaeota in the oceans appear to have the ammonia monooxygenase gene (*amoA*) involved in ammonium oxidation and nitrification (Francis *et al.* 2007). Thaumarchaeota and the Archaeal *amoA* gene have been widely reported from soils generally (Leininger *et al.* 2006) and specifically from Arctic soils (Wilhelm *et al.* 2011) as well as Arctic freshwaters (Pouliot *et al.* 2009). Thaumarchaeota and the *amoA* gene are found throughout the marine Arctic (Hollibaugh *et al.* 2007).

Marine Group II Euryarchaeota are widespread and reported from throughout the world oceans, but they have remained uncultivated. Although some are reported to take up amino acids (Ouverney & Fuhrman 2000), and a recent study using enviromental gene assembly found evidence of a heterotrophic capacity (Iverson *et al.* 2012), some groups are likely chemolithotrophic[1] as well (Martin-Cuadrado *et al.* 2008). Even less is known about Marine Group III Euryarchaeota, which are rare in the global oceans, but appear to be common in the mesopelagic zone of the Arctic (Galand *et al.* 2009a). As with MGII, there is no clear understanding of the functional role of these microorganisms in the sea, but if they are chemolithotrophic, their sheer numbers suggest they could contribute to oceanic inorganic carbon fixation.

### 11.2.3. Heterotrophic and mixotrophic protists (Eukarya)

Protists are morphologically more diverse than Bacteria and Archaea. They are also phylogenetically and functionally diverse; the term protist is for convenience, not a valid taxonomic classification (Adl *et al.* 2005, 2007), and evolutionary relationships at the highest taxonomic ranks remain controversial. While larger protists such as ciliates, testate amoeba and dinoflagellates have a well-defined taxonomy based on morphology, the diversity of smaller flagellates is underestimated, and the lack of qualified taxonomists working on specific groups is problematic. As with Bacteria and Archaea, investigations using high throughput sequencing technology will facilitate comparisons among sites and seasons (Comeau *et al.* 2011). The need for taxonomic verification of samples to match historical records to their genetic signature remains a major challenge.

Photosynthetic microalgal groups are reported in the chapter on plants (Daniëls *et al.*, Chapter 9). However, it is important to reiterate that these are not plants; many of these algae are also mixotrophic, supplementing their energy and nutrient requirements via phagotrophy[2] and sometimes osmotrophy[3]. Mixotrophic Chrysophyceae are particularly common in Arctic freshwaters (Kristiansen 2008, Charvet *et al.* 2012) and are also reported from sea ice and Arctic marine waters (Lovejoy *et al.* 2002, Rozanska *et al.* 2008) and include everything from small free living flagellates to large tree shaped colonies of *Dinobryon balticum* and other colonial species. In addition to Chrysophyceae, other mixotrophs among the stramenopiles[4] (Heterokonta) include members of the Dictyophyceae, Pelagophyceae, Raphidophyceae (Scott & Marchant 2005, Poulin *et al.* 2011) and Bolidophyceae, which are all frequently recovered in marine Arctic 18S rRNA gene surveys (Lovejoy *et al.* 2006, 2011).

Recent work suggests that the Parmales, which have siliceous walls and have been reported from electron microscopy studies of polar waters (Kosman *et al.* 1993), are closely related to or within the flagellated bolidophytes (Ichinomiya *et al.* 2011). In Antarctic sediment cores, Parmales have been considered paleoenvironmental indicators of cold water (Franklin & Marchant 1995), but to my knowledge have not been reported as such in the Arctic. Other major phyla level groups, which are mixotrophic, are also commonly reported from Arctic seas, sea ice and freshwaters, including Euglenozoa, Cryptophyceae, Haptophyceae and many small dinoflagellates (Lovejoy *et al.* 2002, 2006, Poulin *et al.* 2011, Charvet *et al.* 2012). Chloroarchniophytes, which are Cercozoa with chlorophyll *b* (derived from a green algal secondary endosymbiosis), have been recovered from most surface marine 18S rRNA gene surveys (Lovejoy *et al.* 2006, 2011, Lovejoy & Potvin 2011).

There have been fewer studies on primarily heterotrophic protists that depend on bacteria and other protists for energy (nutrition). Key non-marine, larger heterotrophic protists from Arctic freshwater habitats were treated in the chapter on terrestrial invertebrates, where it was noted that ciliates and testate amoebae are common (Hodkinson, Chapter 7). Smaller heterotrophic protists can be assumed to be common in sub-Arctic to high Arctic ponds and lakes, but very few reports are available. One recent 18SrRNA gene survey found that ponds and lakes have typical freshwater phylotypes of non photosynthetic heterokonts, as well as choanoflagellates, Cercozoa and bodinids (Charvet *et al.* 2012). Extensive surveys of smaller protists in Arctic soils using molecular techniques are planned but have not been undertaken (S. Adl pers. com.)

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[1] Organisms that obtain energy from the oxidation of inorganic compounds.

[2] Particles such as bacteria that are engulfed by a cell; protists are often phagotrophic feeders.

[3] The uptake of dissolved organic material by an organism, where the solute permeates the membrane. Fungi and bacteria commonly use osmotrophy to obtain energy.

[4] The collection of organisms that either currently or ancestrally had two different types of flagella, specifically a flimmer flagella and a smooth flagella; these include the diatoms, brown algae, chrysophytes and related phyla.

Compared with freshwaters, marine waters have been better investigated both by way of microscopy (Appendix 11; Vørs 1993, Ikävalko & Gradinger 1997, Lovejoy *et al.* 2002) and more recently using molecular 18S rRNA gene surveys. Such surveys have highlighted the diversity and distribution of small heterotrophic protists (Lovejoy & Potvin 2011, Terrado *et al.* 2011), many of which have never been brought into culture (Appendix 11). Among the small marine flagellates are choanoflagellates, Katablepharidia, *Telonemia*, cerozoans, diplomonads[5] and diverse marine stramenopiles (MASTS; Massana *et al.* 2006). MASTS are only known from their 18S rRNA gene sequences, but most are thought to be phagotrophic (Massana *et al.* 2004). One group, MAST 3, is reported to be related to an epibiont[6] of marine algae (Gomez *et al.* 2011). Also among heterotrophic flagellates are uncultured flagellates that were designated picobiliphytes or biliphytes (Not *et al.* 2007). These cells are phylogenetically distant from other protist groups, and recent genome sequencing of an enviromental cell population indicates that they are probably heterotrophic (Yoon *et al.* 2011). The biliphytes are nearly always recovered in Arctic clone libraries (Lovejoy *et al.* 2011) and appear to be most common in winter (E. Medrinal and C. Lovejoy unpubl.).

In marine waters, classic Rhizaria (Polycystinea, Acantharia) are also frequently recovered from 18S rRNA gene libraries from the Arctic; often the sequences are most similar to sequences from the deep ocean (Lovejoy & Potvin 2011). These fragile cells are not well preserved from net or bottle samples, but their frequency in environmental gene surveys suggest they may be important phytoplankton predators in polar waters. As in other oceanic regions, alveolates, which include dinoflagellates, ciliates and uncultivated groups, are common and very diverse. Dinoflagellates and ciliates have long been noted in microscopic surveys (Okolodkov & Dodge 1996, Okolodkov 1999, Lovejoy *et al.* 2002) and are also frequently recovered in 18S rRNA gene surveys. While about half of known dinoflagellates are photosynthetic, it is likely that all prey on phytoplankton and other protists (Taylor *et al.* 2008). Ciliates also graze on phytoplankton, other protists and each other (Montagnes *et al.* 2010).

Gene surveys have also revealed uncultivated alveolates mostly falling into two major clades (Group I and Group II Alveolates; Lopez-Garcia *et al.* 2001). These two groups are found in nearly all marine samples including the Arctic (Lovejoy *et al.* 2006). These uncultivated alveolates are within or related to the parasitic Syndiniales (Skovgaard *et al.* 2005, Guillou *et al.* 2008). The most commonly recovered clade in the Arctic belongs to Syndiniales Group II, which contains the dinoflagellate parasitoid, *Amoebophyra*. Others are related to fish parasites (Skovgaard *et al.* 2009). All known representatives of the Syndiniales have complex life stages and are either parasitoids, parasitic or commensally dependent on a host.

## 11.3. STATUS AND TRENDS

### 11.3.1. Endemic species, population sizes and genetic diversity

While there are phylum-level similarities among communities from the different habitats, at the genus and species levels there is strong environmental selection with freshwater, brackish, sympagic and marine species very distinct from one another. Despite this, it has been strongly debated whether or not microbes have a biogeography or if endemic microbes even exist (Finlay & Fenchel 2004, O'Malley 2007). The debate centers on major differences between single-celled, mostly asexual-reproducing organisms and multicellular, mostly sexual species (Medlin 2007, Yang *et al.* 2010). The frequency of genetic exchange is the major difference; in addition microbes can attain very high populations via clonal division, which in combination with their small size could lead to global transport by winds and water given sufficient time. The original proposition that, for microbes, everything is everywhere came with an important proviso; the environment selects (de Wit & Bouvier 2006 citing Beijerinck 1913). In addition, as with plants and animals, some groups of microbes are better able to disperse between favorable environments and maintain viability over long periods.

The bipolar distribution of several sea ice bacteria (Staley & Gosink 1999) and protist taxa has been used to argue for lack of endemism among microbes; e.g. the cyst-forming dinoflagellate *Polarella glacialis* is found associated with ice in both the Arctic and Antarctic (Montresor *et al.* 2003). Until recently, this debate was largely semantic based on expert opinion on the definition of species, as most microbes are not in cultivation and type specimens do not exist. As more sequences from widely dispersed regions become available, biogeographic studies are becoming more common, and a level of similarity among taxa from different regions can by defined at levels from genera to strain, depending on the resolution of the marker (Koester *et al.* 2010). Cloning and sequencing studies of the 18S rRNA gene suggest a certain level of, if not endemic, then certainly restricted distribution of several marine Arctic protists (Lovejoy & Potvin 2011). A recent survey of over 2,500 sequences of small potential mixotrophs originating from Arctic 18S rRNA gene clone libraries indentified 14 potential Arctic taxa. Since most are not cultivated these were refered to by their designated type clone names (in parenthensis). Specifically these were: one Prasinophyceae (NPK2_194), two Haptophyceae (NOR50.28 and CFL133DA03), one Cryptophyceae (MD65.37), one Dictyochophyceae (05M80r.07), three Pelagophyceae (NW614.28,

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[5] Organisms that belong to the Diplomonadida, which are mostly parasites and include Giardia and other vertebrate parasites.

[6] An organism that grows on the surface of other organisms.

05M80r.43, and CB1901L07) two Chrysophyceaceae (ES069_E8 and AN0678L07) and finally three distinct taxa withing the bolido-parmales (CB1901S35, NW617.26 and NW614.34). All of these sequences were retrived from at least two independent studies and are therefore probably common and widespread in the Arctic Ocean (Terrado *et al.* 2012). Among other protists with possible restricted distributions are several ciliates, dinoflagellates and Acantharia (Lovejoy & Potvin 2011). Bacterial and Eukaryote SS rRNA gene sequences with best matches to sequences previously reported from freshwater and marine Arctic sites have been recovered from Arctic snow and air suggesting the importance of local transport reinforcing species distribution patterns (Harding *et al.* 2011). It is also important to emphasize that DNA based analysis can only record the historic input of microbes into a system. For example, Hubert *et al.* (2009) report on the occurrence of thermophilic bacteria in Arctic sediments, showing the importance of cold, deep sediments as archives of bacterial diversity.

Environmental gene surveys can be carried out on archived samples where DNA has been preserved, and on new samples collected specifically for monitoring. The application of high throughput sequencing will enable much more extensive comparisons of different regions and habitats (Comeau *et al.* 2011). Since species-specific identification is only as reliable as the reference data base, the need for ongoing studies using culturing and cloning and sequencing the entire SS rRNA gene and other taxonomically useful markers will remain. Global comparisons of the bacterial and archaeal sequences from many different sites are also underway by a group of polar ICOMM researchers. A recent bipolar comparison of marine surface and deep sea bacteria from this data revealed that the communities from the Arctic and Antarctic, while more similar to each other than to communities from the temperate oceans, grouped apart, suggesting isolation at time scales relevant to bacterial evolution (Ghiglione *et al.* 2012).

Knowledge of transcriptomes[7] of isolated species and metatranscriptome[8] data can be used to identify key genes in the environment. At the functional level of the gene, bipolar distributions seem clear at least among Archaea. For example, ammonia monooxygenase gene sequences, which are > 99% similar, occur in both Polar regions (Kalanetra *et al.* 2009). However, whether this reflects species and implied genetic exchange or the conserved nature of the genes being investigated will require single cell sequencing and further cultivation of isolates from both poles. Finally, there is some disagreement on the nature and definition of microbial species. Comparative studies at fine taxonomic levels will require agreement on the definition of a species or ecotype and well-thought-out global surveys. Even putatively closely related species may have vastly different capabilities and be much less similar at the whole genome level compared with higher animals and plants (Bapteste *et al.* 2009, Worden *et al.* 2009). This implies that Arctic ecotypes may be a unique genetic resource regardless of taxonomic assignment, and loss of genetic diversity will be a consequence of habitat loss. In particular, specific adaptations to subzero temperatures at the enzymatic level could be of interest for biotechnology applications (Deming 2002, Varin *et al.* 2012). Bioprospecting for both genes and the bacteria that harbor them is already occurring in the Arctic and is an issue that needs to be considered (UNU-IAS web).

## 11.3.2. Trends

Microbial communities are expected to be influenced by environmental changes that are now underway. General projections of the effect of global environmental changes on microbes in Arctic ecosystems are generally based on the predicted increase in temperature and potential changes in primary production (Kirchman *et al.* 2009, Vincent *et al.* 2009, 2010, Kritzberg *et al.* 2010). According to a study based on data from the western Canadian oceanographic region, recent changes in ice cover have influenced microbial community structure (Comeau *et al*. 2011), likely caused by increased light availability and increased water column stratification (Michel, Chapter 14). Both phototrophic and heterotrophic species are vulnerable to change, as the seasonal open water increases over time and space. There is accumulating evidence that species assemblages among Bacteria, Archaea and Eukarya co-occur, and distinct communities re-appear annually in the same region (Beman *et al.* 2011, Steele *et al*. 2011). There is a need to identify existing patterns in the Arctic to facilitate efforts to predict ecosystem changes and microbial community structure following anthropogenic and climatic forcing (Lovejoy 2011). The timing and extent of the spring surface bloom will change, along with the timing and geographical extent of ice edge blooms with consequences for zooplankton and higher food webs (Soreide *et al*. 2010). Changes in primary productivity and subsequent export to the benthos (Michel, Chapter 14) will also likely have an impact on benthic bacterial community structure and activity (Boetius & Damm 1998, Bienhold *et al.* 2012, see also Josefson & Mokievsky, Chapter 8). Day length can influence food quality as well as species composition (Leu *et al*. 2010). Ongoing loss of ice and earlier blooms could result in a rearrangement of food webs in the Arctic, since annual light availability at high latitudes remains fixed and there is an increased probability of decoupling production patterns from annual animal cycles resulting in major ecosystem shifts (Grebmeier *et al.* 2006).

In addition, microbial community interactions and dominant species largely determine the efficacy of the biological carbon pump where $CO_2$ is drawn down from the atmosphere and sequestered in the deep ocean. This

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[7] The sum of mRNA transcripts found in an organism. Transcripts of genes are used as evidence that a functional gene is being expressed.

[8] The sum of transcripts from a community of organisms, for example all of the microbes in a soil or water sample.

absorption of $CO_2$ by the global ocean is now affecting the pH of oceanic waters and the biological availability of carbonate and aragonite minerals. There are already signs of such changes in the Arctic Ocean (Carmack & McLaughlin 2011), and these pH effects will add to the selection pressures on microbial community structure including effects on organisms with calcium and aragonite scales and structures (see also Josefson & Mokievsky, Chapter 8, and Michel, Chapter 14). Although the main marine microalgae with carbonate scales, coccolithophores, are rare in the Arctic, other calcifying species including some cyst-forming dinoflagellates could well be affected. The influence of pH on the metabolism of microbes in the ocean has been little explored, but a recent study suggests that ocean acidification could have an effect on microbial ammonia oxidizing communities (Kitidis *et al.* 2011). Such communities are key players in the Arctic nitrogen cycle, which is strongly linked to circulation patterns in the Arctic Ocean (Galand *et al.* 2009b), which in turn will be affected by climate change. There is an urgent need to acquire sufficient understanding of community assemblages and functions to predict how these factors will interact.

In sum, there will always be microbial communities, but there will be taxonomic adjustments to new circumstances. Such ecosystem changes may have unforeseen consequences on global biogeochemical cycling and higher trophic levels in the Arctic.

## 11.4. CONCLUSIONS AND RECOMMENDATIONS

### 11.4.1. Sensitive areas and hotspots

In the terrestrial and freshwater habitats, areas identified either as sensitive or as hotspots for animals and plants should also be considered as microbiologically significant regions. In addition, unique or rare habitats such as saline springs should be protected to preserve unique biomes and specialized microbiota. In coastal and oceanic regions, areas where mammals and birds congregate should also be monitored. For example, marine productivity is related not only to the quantity of photosynthetic biomass produced but also the quality. In oceanic regions, the diversity and stability of microbial food webs dictates lipid concentrations in the zooplankton that support higher trophic levels. As longer ice free periods become the norm, microbial food chains are predicted to lengthen, and less energy will be available to the highest trophic levels in the oceans (Lovejoy 2011). Such changes will also have major impacts on benthic communities and on the carbon and nutrient cycling that occurs in the benthos (see also Josefson & Mokievsky, Chapter 8). The potential loss of multiyear ice as a habitat and changes in the duration and type of sea ice with different communities (Comeau *et al.* 2012b) will have consequences for biodiversity and carbon cycling. More research is needed to better estimate which communities may be lost as a result of the loss of summer sea ice. These changes are likely to have significant effects on the diversity and functioning of Arctic ecosystems. In terrestrial based systems, increased liquid water, higher temperatures and longer growing seasons will affect all biological activity, and northward expansion of species can be expected. Although at present much of the Arctic appears poor in life, microbial communities are active and complex, and 'non-hotspot' regions need to be monitored as well as highly productive regions in order to anticipate new distributions and community associations. Microbes will respond to ecosystem changes much sooner than higher plants and invertebrates and are thus sensitive indicators of directional changes.

### 11.4.2. Key knowledge gaps and recommendations

Ecosystem assessments and the role of complex interacting factors, which may influence ecological patterns, can only be explored through long time series of biological collections and surveys at local to regional scales. The only open-ocean long-term observatory in the Arctic is HAUSGARTEN, coordinated by the Alfred Wegener Institute for Polar and Marine Research (Soltwedel *et al.* 2005; see also Josefson & Mokievsky, Chapter 8). The Arctic is vastly under-sampled and heterotrophic protists, Bacteria and Archaea play a critical role in ecosystem support. Currently, there are only a small handful of researchers interested in microbial biodiversity and how it directly relates to ocean ecosystem function. There is a need to foster greater interest in microbial ecology among Arctic researchers. Microbial communities must be included in any Arctic monitoring effort aimed at understanding biodiversity and ecosystem function.

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Wild and semi-domestic herds of *Rangifer* (caribou or reindeer) are almost omnipresent in Arctic tundra. Rangifer management is an important issue, as the herds exert a number of important controls on the Arctic terrestrial ecosystem through their effects on vegetation and carnivore populations, as well as providing essential ecosystem goods to indigenous people. Photo: Susan Morse.

*Chapter 12*

# Terrestrial Ecosystems

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## Contents

> **» It has progressively become warmer. I recall that only in our traditional area did the trees occur, but when I returned there via plane last year, a lot more of the tundra was inundated with trees, small mind you, but they have moved north and east. The area we used to inhabit has been overgrown with vegetation, mainly shrubs and small trees. It has become almost like a mini-forest where we used to have our main camp. We visited the site in 2000 and it was almost unrecognizable due to all of the growth that occurred during our absence. I think this is due to a shorter spring, a longer summer and longer frost free falls.**
>
> Utok; Elders Conference on Climate Change 2001.

## SUMMARY

The Arctic tundra biome is geographically restricted to a strip around the margins of the Arctic Ocean. A key force determining the tundra biome's zonal structure is the bottom-up effect of decreased vegetation productivity and complexity with increasing latitude. Accordingly, there are trends of decreasing diversity within and among trophic guilds of consumers with increasing latitudes. Low food web complexity in the northern parts of the biome is also due to island biogeographic features, as large parts of the high Arctic are located on islands. Similarly, a substantial proportion of the high biodiversity of low Arctic zones stems from 'spillover effects' from sub-Arctic ecosystems. Historic processes have also contributed to shaping the current large-scale regional provinces in terms of Arctic species communities. At sub-regional scales the terrestrial Arctic harbors diverse mosaics of communities that are structured by gradients and disturbances in climate, substrate, hydrology and cryosphere that form unique patterns of within – and among – community diversity. Hot spots of high regional diversity are currently found in some old, topographically and geologically complex regions.

The architecture of tundra food webs is modulated by inter-specific interactions within and between trophic levels. Herbivores can regionally exert strong top-down controls on tundra vegetation, whereas predators often control small mammal herbivores and the reproductive success of ground nesting birds. Multi-annual, cascading bottom-up and top-down interaction cycles mediated by lemming populations are crucial for the maintenance of terrestrial Arctic biodiversity in many tundra ecosystems. Functional traits of plants in interactions with below-ground microbial communities and herbivores maintain essential roles in the regulation of the global climate system through controls on fluxes of greenhouse gasses (GHG) and heat fluxes between the earth surface and the atmosphere. Changes to the composition of terrestrial biodiversity may determine whether the Arctic will become a source or a sink for GHGs in a warming climate.

Climate is historically and currently the most important driver of change of Arctic terrestrial ecosystems, through alteration of coastal sea ice, glaciers, snow and permafrost, changed seasonality and extreme events. At present, a second emerging driver is an increased footprint of human presence within the Arctic. Currently, the most profound ecosystem impacts include (1) increased plant biomass due to growth of tall woody plants that cause lower albedo and possibly enhance GHG emissions and thereby accentuating the Arctic amplification of climate change, (2) collapsed cycles of lemmings and emergent outbreaks of insect herbivores and plant pathogens with cascading impacts on food webs and ecosystem functioning, and (3) increasing abundance of boreal and human commensal species impacting Arctic endemics as predators or competitors.

Recommended actions to conserve Arctic terrestrial ecosystems under the impacts of climatic change and other anthropogenic stressors include conservation of topographically diverse areas with landscape-scale 'buffer-capacity' to maintain cold refuges in a warmer climate and of remote high Arctic islands that are the most physically protected from species invasions from the south and human presence. Prudent management of Arctic herbivores such as reindeer *Rangifer tarandus*, using their capacity for shaping vegetation on landscape scales, may be considered for counteracting encroachment of tall woody vegetation that otherwise will eliminate tundra habitats, while avoiding the negative impacts of herbivore overabundance that have been documented in some regions.

A key message from the present assessment is that essential attributes of terrestrial Arctic biodiversity, some of which have global repercussions, are ultimately dependent on how interactions within ecological communities and trophic webs are impacted by rapidly changing external drivers. Consequently, research, monitoring and management ought to be properly ecosystem-based. Because ecosystems are structurally and functionally heterogeneous across the tundra biome and may also be subjected to external drivers of different strengths, new ecosystem-based observatories that include state-of-the art research, often combined with adaptive management, should be widely distributed across the circumpolar Arctic. Model-based predictions about how Arctic species and ecosystems will respond to the substantial climate change currently projected for the Arctic have limited powers to accommodate surprises in terms of novel climates and ecosystems that may rapidly emerge. New efforts urgently need to be deployed to enable well-designed real-time observations as a basis for empirically based documentation and understanding of cause-effect relationships of future ecosystem changes in the terrestrial Arctic.

## 12.1. INTRODUCTION

The Arctic tundra biome is characterized by low-growing vegetation composed of low shrubs, sedges, grasses, forbs, lichens and mosses (bryophytes) that grow beyond the northern climatic limit of trees (see Section 2 in Meltofte *et al.*, Introduction for this assessment's definition of the Arctic). A polar view of the biome from space reveals that the continental portion of the Arctic tundra occupies a thin strip of land between the Arctic Ocean and the boreal forest (Fig. 12.1). Eighty percent of the lowland portion of the Arctic lies within 100 km of seasonally ice-covered seas. The biome essentially owes its existence to cold sea breezes that keep the temperatures during the growing season below that required for tree growth. One fifth of the total coastline of the world, or about 177,000 km, occurs in the Arctic, a biome that comprises only about 5% of the Earth's terrestrial surface. Three main aspects of the extensive Arctic coastlines make the tundra biome extremely vulnerable to climate warming: (1) the strong climatic influence of the nearby sea ice, (2) narrow bioclimate zonation associated with these coastlines, and (3) extensive lowland plains near most of the Arctic coast (CAVM Team 2003).

In terms of climate, the Arctic tundra can be viewed as a strongly oceanic-influenced biome, but one that varies considerably in the degree of maritime expressions of cloudiness, fog, humidity and equitable temperatures, because the Arctic Ocean is covered by ice to a varying extent during the winter and summer. The longevity of the ice near the coast in summer strongly affects summer land temperatures and local continentality of the climate as well as the diversity of organisms and total productivity of the land (Bhatt *et al.* 2010). Steep temperature gradients occur inland from these coastlines resulting in extraordinarily long and narrow ecological transition zones with several bioclimate subzones compressed near the coast. Permafrost strongly affects the ecosystems of most of the biome, but is not a condition that defines the biome, as permafrost also extends far into the boreal forest in continental areas of Siberia and North America. On the other hand, there are portions of coastal tundra with no or only discontinuous permafrost (Callaghan *et al.* 2004a, AMAP 2011).

The integrity of terrestrial Arctic ecosystems, as shaped by biotic and abiotic processes, is ultimately conditional on low primary productivity resulting from short and cool summers that restrict plant growth and metabolic activity of other poikilothermic[1] organisms, such as bacteria, fungi and invertebrates. The low productivity at the base of trophic chains restricts secondary productivity and the complexity of food webs and decomposer webs. Tundra food webs are usually composed of only three major trophic levels: plants, herbivores and predators (Krebs *et al.* 2003, Ims & Fuglei 2005). The structure of decomposer webs, in which cryptic microbial communities and soil faunas play a central role, is considerably less known (Callaghan *et al.* 2004b), but may be more complex than the more conspicuous food webs composed of green plants and macroscopic animals (see Hodkinson, Chapter 7). Terrestrial food webs also include fewer trophic levels than, for instance, aquatic ecosystems in the Arctic (Wrona & Reist, Chapter 13, Michel, Chapter 14), although high Arctic limnic systems may be as simple as their terrestrial counterparts (van der Wal & Hessen 2009, Wrona & Reist, Chapter 13).

Although Arctic tundra ecosystems have a simple trophic structure, often with relatively low species richness within each trophic level, other structural features of biodiversity can be remarkably complex. Spatial variability in temperature, winds, precipitation, hydrology, cryosphere and soil chemistry creates gradients and complex mosaics of abiotic conditions that shape the composition of species assemblages (i.e. ecological communities) at multiple spatial scales. For this reason, a spatially hierarchical approach to characterize biodiversity patterns in terms of differences in species assemblages as functions of abiotic controlling factors from local to circumpolar scales appears to be particularly applicable to Arctic tundra. In terms of ecosystem functions, and the biotic and abiotic processes that shape these functions, tundra ecosystems are no less diverse than other ecosystems. Some of the ecosystem functions are crucial for the livelihood of local people, such as locally produced food, while others have essential roles in the global climate system, such as controls of exchange of heat and GHG.

In this chapter we start with a review of present knowledge of how natural abiotic and biotic factors shape biodiversity in terms of ecosystem structure, processes and functions within the tundra biome (Section 12.2). This provides the background for assessing past and present trends in terrestrial Arctic biodiversity, and the drivers of such trends (Section 12.3). Towards the end of the chapter we provide a synthesis of the assessment's key findings (Section 12.4) before we conclude with a set of recommendations on how policy makers, managers and ecosystem scientists could act on these findings (Section 12.5).

## 12.2. ECOSYSTEM STRUCTURE, PROCESSES AND FUNCTIONS

*Ecosystem structure* (Section 12.2.1) concerns the contemporary distributions (i.e. spatial pattern) of biodiversity at various levels of biological organization as they are shaped by abiotic factors at a range of spatial scales. *Ecosystem processes and functions* (Section 12.2.2) concerns the biotic processes that shape biodiversity in conjunction with abiotic conditions. Our aim is to present the key patterns, processes and their determinants that are necessary to appreciate the present status and ongoing trends of terrestrial Arctic biodiversity (Section 12.3). Our account is biased towards the most studied parts of the ecosystem for which trend information is available; notably the vegetation and vertebrate animals that form the most conspicuous components of the ecological communities and food webs. As pointed out elsewhere in this volume (Hodkinson, Chapter 7, Dahlberg & Bültmann, Chapter 10, Lovejoy, Chapter 11) there is a strong need for long-term research to document status and trends in biodiversity of other compartments of the tundra ecosystem, notably microbial and invertebrate communities and decomposer webs.

### 12.2.1. Ecosystem structure

Vegetation is the main structuring element of terrestrial ecosystems. Plant community types (e.g. plant associations) constitute the basis of classification of terrestrial biota at the scales of communities, ecosystems and biomes. Indeed, mapping of plant community types and investigations made to understand the environmental factors shaping their composition and spatial distribution have a long scientific tradition (Daniëls *et al.*, Chapter 9). Moreover, a comprehensive hierarchic approach has been

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[1] An organism whose internal temperature varies considerably.

**Figure 12.1.** Circumpolar Arctic Vegetation Map (Walker *et al.* 2005).

developed to describe, explain and map the structure of Arctic vegetation at macro- (global), meso- (regional) and micro- (local) scales by analyzing the variation of plant communities with respect to climate, biogeographic history, topography and parent material (Cantlon 1961, Walker & Walker 1991, Walker 2000). This is the organizing principle behind the Circumpolar Arctic Vegetation Map (Fig. 12.1; CAVM Team 2003, Walker *et al.* 2005).

Here we expand on the CAVM scheme to describe ecosystem structure more comprehensively. We do this by incorporating animal communities and the perspective of food webs. The latter perspective has provided an important theoretical framework to tundra ecosystem science in terms of describing and predicting ecosystem properties (Oksanen *et al.* 1981, Ims & Fuglei 2005, Legagneux *et al.* 2012) as well as for documenting recent trends (Post *et al.* 2009). The structure of food webs depends to a large extent on the vegetation, due to bottom-up trophic processes. Moreover, higher trophic levels are subject to many of the same multi-scale abiotic controls as plants. However, there are also some obstacles to directly linking the CAVM scheme to communities of other taxa. First, while there is a widely used methodological approach for classification of vegetation (the Braun-Blanquet approach; Westhoff & van der Maarel 1978), equivalent approaches are largely missing for other taxa (e.g. animal and microbial communities). Furthermore, while Arctic plant communities are relatively well described (Daniëls *et al.*, Chapter 9), there are still large differences between animal taxa in the degree to which taxonomy is known and species distributions and assemblages (communities or guilds) are described (Reid *et al.*, Chapter 3, Ganter & Gaston, Chapter 4, Hodkinson, Chapter 7). Microorganisms are very poorly known compared with all other Arctic species (Lovejoy, Chapter 11), although they are critically important for ecosystem function (Section 12.2.2.2). A recent global synthesis indicates that soil microbial biomass dramatically exceeds total faunal biomass at the ecosystem scale (Fierer *et al.* 2009). Finally, owing to different types of controls and the spatial and temporal scaling of processes that affect different taxa and trophic levels, the hierarchical scheme for describing vegetation structure (i.e. the CAVM) may not always fit with the spatial structure and temporal dynamics of other ecosystem compartments (e.g. taxa or trophic levels). Descriptions of animal and microbial communities are also often missing at some of the spatial scales that vegetation ecologists examine due to methodological and logistical reasons. Thus our description of vegetation structure with respect to certain spatial scales and/or to some abiotic controls cannot always be accompanied by equivalent accounts on other ecosystem compartments.

Following the spatially hierarchical framework of CAVM we start with a description of how circumpolar-scale bioclimatic factors determine the latitudinal zonation of tundra ecosystems and how other large-scale climate gradients as well as historical contingencies create cross-zonal, longitudinal patterns of biodiversity. Next we proceed to regional- and landscape-level structures and explain how they are influenced at several scales by factors such as topography and substrate chemistry. Finally, we identify locations that stand out as 'hot spots' of diversity at various spatial scales (Daniëls *et al.*, Chapter 9) where certain combinations of present-day and historical factors coincide to create conditions that favor exceptionally high biodiversity.

#### 12.2.1.1. Circumpolar-scale variation

**Latitudinal zonation of vegetation structure, species composition and richness**

At the circumpolar scale, summer temperature is the overriding environmental factor controlling the structure and productivity of *zonal* Arctic vegetation, which is the natural vegetation that develops under the prevailing Arctic climate on moderately drained fine-grained soils with moderate exposure to wind and snow (Vysotsky 1909, Alexandrova 1971, Elvebakk 1999, Razzhivin 1999, CAVM Team 2003). The changes in species diversity, plant productivity and structure of the vegetation along the Arctic climate gradient form the basis of all zonal approaches to subdivide the Arctic (Young 1971, Yurtsev *et al.* 1978, Alexandrova 1980, Edlund 1990, Bazilevich *et al.* 1997, Chernov & Matveyeva 1997, Matveyeva 1998, Elvebakk 1999, Walker *et al.* 2005). A remote-sensing approach that uses land-surface temperatures derived from satellite data provides a detailed picture of the distribution of summer temperatures and the amount of warmth available for plant growth that reflects the bioclimate zones of the CAVM (Box 12.1; Raynolds & Walker 2009).

The 10 °C difference in positive mean July air temperatures along the Arctic climate gradient (from 0-3 °C to 10-12 °C) corresponds to important differences in the total amount of summer warmth available for plant growth and results in major structural differences in plant canopies that are the basis for the delineation of the five latitudinal bioclimate subzones (A-E) of the CAVM (Tab. 12.1 and Fig. 9.1 in Daniëls *et al.*, Chapter 9), where A-C corresponds to the high Arctic and D and E to the low Arctic in North America (Bliss 1997). The corresponding changes in the vertical structure of zonal vegetation range from very small plants < 2 cm tall in a single discontinuous moss layer in subzone A to complex canopies with 2-3 layers that include shrubs exceeding 80 cm tall in subzone E. Likewise, the horizontal structure changes from < 5% cover of vascular plants in subzone A to 80-100% cover in subzone E (Chernov & Matveyeva 1997). The plant growth forms that compose the zonal plant cover also change. Subzone A is dominated by mosses, lichens, liverworts, algae, bacteria and a few small cushion forbs, rushes and grasses; whereas subzone E has complex plant canopies composed of a mixture of dwarf and low deciduous and evergreen shrubs, sedges, grasses, forbs, mosses and lichens. There is also a general trend of increasing shrub abundance and height along the north to south temperature gradient (Tab. 12.1).

Subzone A lacks all woody plants (see Daniëls *et al.*, Chapter 9). Subzones B and C are dominated by creeping prostrate dwarf shrubs (e.g. mountain avens *Dryas* spp., prostrate willows *Salix* spp.) and in parts of subzone C the hemi-prostrate shrub Arctic white heather *Cassiope tetragona* is abundant. In subzone D, dwarf erect shrubs less than 40 cm tall are common (e.g. many species of willow *Salix* spp., dwarf birch *Betula nana/exilis*, crowberry *Empetrum nigrum* and bilberry *Vaccinium uliginosum*). Finally, in subzone E, low shrubs over 40 cm tall are common on most zonal sites, whereas drainages with warm soils and abundant water and nutrients can have tall shrubs over 2 m tall. In most flat regions, the transition from tundra to forest is not a sharp line but a gradual transition along a forest-tundra ecotone with open tundra landscapes over broad areas, often with widely spaced trees or patches of fragmented forest, particularly along streams, grading to continuous forest (Scheffer *et al.* 2012). Trees (e.g. balsam poplar *Populus balsamifera* in Alaska and chosenia *Chosenia arbutifolia* in Chukotka) occur even north of the tundra boundary in small protected enclaves on south facing slopes or near perennial springs (Murray 1980, Bockheim *et al.* 2003, Breen 2010).

The reduced height and number of layers of the vegetation canopy in northern subzones has a critical effect on many species of animals. For example, all the birds and insects directly associated with shrubs disappear from zonal sites at the transition between subzones E and D. Farther north they are present only in warm extra-zonal and intra-zonal habitats, mainly shrubby areas along streams and south facing slopes (Chernov 1995). Clear latitudinal zonation is most evident along the continental portions of Arctic Eurasia and North America. The very large Canadian Arctic Archipelago and more mountainous terrain in Alaska, Greenland and Svalbard makes the zonation more complex in these areas (Bliss 1997), but nonetheless the bioclimate subzone approach developed in Eurasia can be applied to both continents as well as Arctic islands (e.g. Edlund 1983, Edlund & Alt 1989, Elvebakk 1999, Walker *et al.* 2008) and in Arctic mountains (Sieg & Daniëls 2005, Sieg *et al.* 2006).

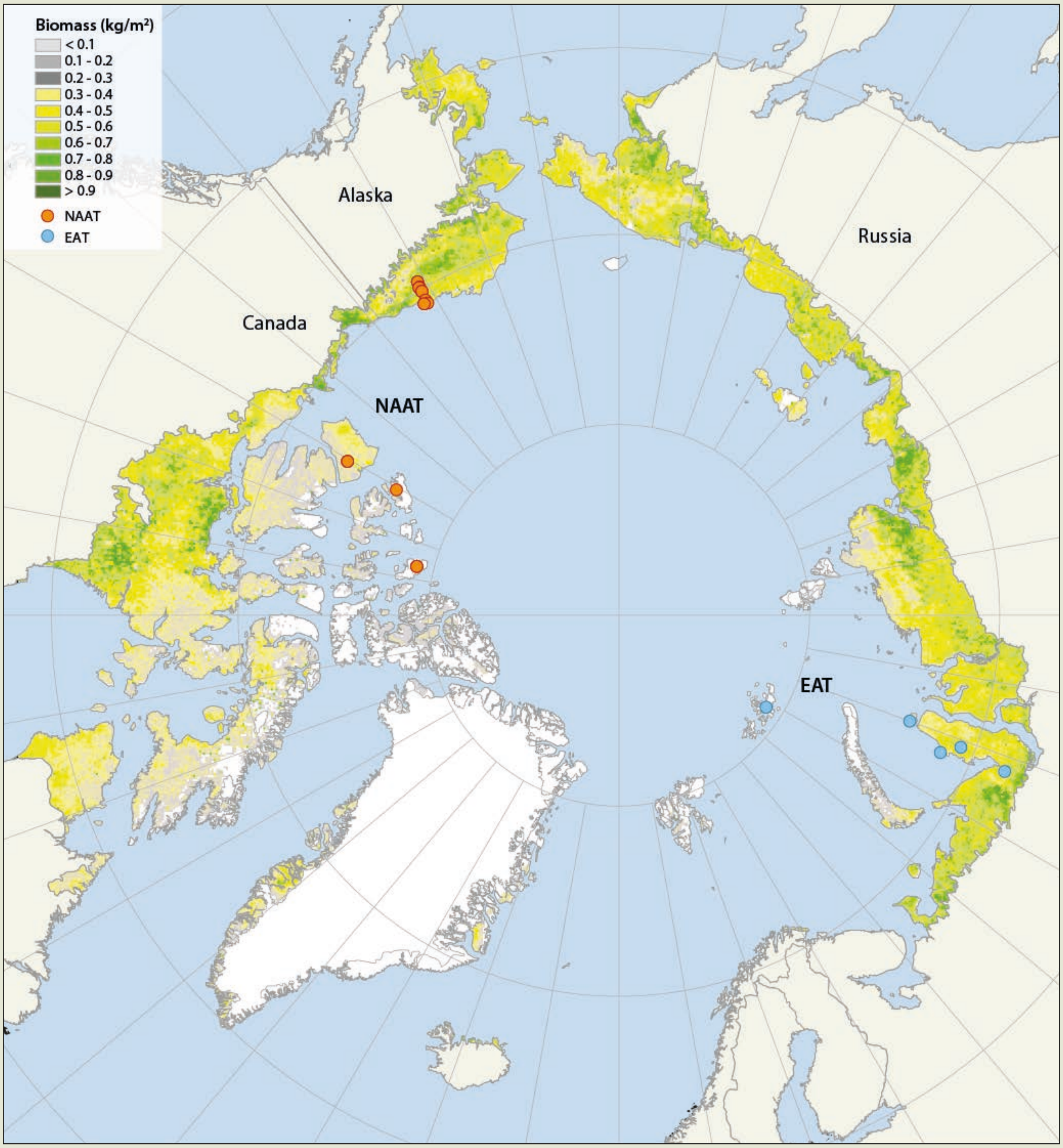
A north to south gradient of increasing plant diversity with temperature has been documented in several Arctic studies (Young 1971, Rannie 1986, Chernov 1989, Daniëls *et al.*, Chapter 9). Similar patterns are observed for animal diversity. Species diversity decreases with decreasing temperature and increasing latitude in most groups, including birds, ground beetles and butterflies (Ganter & Gaston, Chapter 4, Hodkinson, Chapter 7). Latitudinal patterns of diversity differ strongly between groups of animals, however. In general, the decline in diversity is more pronounced in animals than in plants, but in some specialized groups, such as shorebirds and sawflies on willows, there are opposite local

## Box 12.1. Use of remote sensing to map circumpolar patterns of sea ice, land temperatures and aboveground plant biomass

Sensors aboard Earth-orbiting satellites gather data that are used for mapping changing patterns of sea-ice distribution, land-surface temperatures and productivity of vegetation (Bhatt *et al.* 2010). Circumpolar maps of sea ice concentration use Special Sensor Microwave Imager (SSM/I) data (Comiso & Nishio 2008) and Advanced Very High Resolution Radiometer (AVHRR) radiometric surface temperature data.

Maps of the summer land-surface temperature also use the AVHRR surface temperature data with enhanced cloud masking and calibration with in situ ground temperatures (Comiso 2003). The summer warmth index (SWI) is the sum of average May-September monthly surface temperatures above freezing within each pixel, and can be closely related to the bioclimate subzones portrayed in Fig. 9.1 in Daniëls *et al.*, Chapter 9.

The Normalized Difference Vegetation Index (NDVI) is the most common satellite-derived index used to monitor global-scale vegetation productivity. The index is derived from the difference in reflectivity of the land surface in the near-infrared (NIR) band where vegetation reflects strongly, and the red (R) band where vegetation absorbs strongly for photosynthesis. The difference is divided by the sum of reflectances in the same two bands to normalize for differing illumination conditions (NDVI = (NIR-R)/(NIR+R)). The NDVI is interpreted as the photosynthetic capacity of the vegetation (Tucker & Sellers 1986) or its 'greenness' and has been shown to be correlated with ground measurements of biomass, leaf-area index (LAI), intercepted photosynthetically active radiation (IPAR), carbon dioxide flux and other measures of tundra photosynthetic activity (Stow *et al.* 1993). The Global Inventory Modeling and Mapping Studies (GIMMS) data set (now updated to the GIMMS3g), is the most widely used global NDVI data set. The GIMMS3g NDVI is derived from imagery obtained from the AVHRR onboard the NOAA satellite series 7, 9, 11, 14, 16, 17 and 18. This NDVI data set has been corrected for sensor and orbital calibration, view geometry, volcanic aerosols and other artifacts in the data. The data are temporal composites of the maximum NDVI value for two halves of each month, which minimizes the effects of cloud cover. The data set has been used for monitoring trends in vegetation change and biophysical properties of the vegetation in many biomes (Tucker & Sellers 1986, Paruelo *et al.* 1997, Li *et al.* 2002, Fensholt *et al.* 2009) including the tundra biome (Jia *et al.* 2003, Goetz *et al.* 2005, Verbyla 2008, Bhatt *et al.* 2010, Macias-Fauria *et al.* 2012, Xu *et al.* 2013). A circumpolar map of aboveground phytomass has been prepared using the correlation between zonal aboveground biomass and NDVI along two transects in North America and Eurasia (Box 12.1 Fig. 1; Raynolds *et al.* 2012).



**Box 12.1 Figure 1.** Aboveground phytomass in the Arctic in 2010, mapped using the relationship between phytomass and NDVI developed through field sampling of zonal sites along the North America and Eurasia Arctic Transects (NAAT, red dots, and EAT, blue dots). From Raynolds *et al.* (2012).

**Table 12.1.** Vegetation properties in each bioclimate subzone. Adapted from CAVM Team (2003). Vertical and horizontal vegetation structure based on Chernov & Matveyeva (1997).

| Sub-zone | Mean July temp. (°C)[1] | Summer warmth index (thawing °C mo)[2] | Vertical structure of plant cover[3] | Horizontal structure of plant cover[4] | Major plant functional types[5] | Total above-ground zonal phytomass ($g/m^2$)[6] | Number of vascular plant species in local floras[7] |
|---|---|---|---|---|---|---|---|
| **A** | 0-3 | < 6 | Often barren or with biological soil crusts. In favorable microsites, 1 lichen or moss layer < 2 cm tall, very scattered vascular plants hardly exceeding the moss layer | < 5% cover of vascular plants, up to 40% cover by mosses and lichens | b, g, r, cf, of, ol, c | 66-154 | < 50 |
| **B** | 3-5 | 6-9 | 2 layers, moss layer 1-3 cm thick and herbaceous layer, 5-10 cm tall, prostrate dwarf shrubs 5 cm tall | 5-25% cover of vascular plants, up to 60% cover of cryptogams | npds, dpds, b, ns, cf, of, ol | 145-388 | 50-100 |
| **C** | 5-7 | 9-12 | 2 layers, moss layer 3-5 cm thick and herbaceous layer 5-10 cm tall, prostrate and hemi-prostrate dwarf shrubs < 15 cm tall | 5-50% cover of vascular plants, open patchy vegetation | npds, dpds, b, ns, cf, of, ol, ehds*<br>(*in acidic areas) | 297-508 | 75-150 |
| **D** | 7-9 | 12-20 | 2 layers, moss layer 5-10 cm thick and herbaceous and dwarf- shrub layer 10-40 cm tall | 50-80% cover of vascular plants, interrupted closed vegetation | ns, nb, npds, dpds, deds, neds, cf, of, ol, b | 313-563 | 125-250 |
| **E** | 9-12 | 20-35 | 2-3 layers, moss layer 5-10 m thick, herbaceous/dwarf-shrub layer 20-50 cm tall, sometimes with low-shrub layer to 80 cm | 80-100% cover of vascular plants, closed canopy | dls, ts*, ns, deds, neds, sb, nb, rl, ol<br>(*in Beringia) | 740-749 | 200-500 |

1) Based on Edlund (1996) and Matveyeva (1998).

2) Sum of mean monthly temperatures greater than 0°; modified from Young (1971).

3) Based on Chernov & Matveyeva (1997).

4) Based on Chernov & Matveyeva (1997).

5) Codes for plant functional types: b = barren; c = cryptogam; cf = cushion of rosette forb; deds = deciduous erect dwarf shrub; dls = deciduous low shrub; dpds = deciduous prostrate dwarf shrub; g = grass; ehds = evergreen hemiprostrate dwarf shrub; nb = nonsphagnoid bryophyte; neds = nondeciduous erect dwarf shrub; npds = nondeciduous prostrate dwarf shrub; ns = nontussock sedge; of = other forb; ol = other lichen; r = rush; rl = reindeer lichen; sb = sphagnoid bryophyte; ts = tussock sedge. Underlined plant functional types are dominant.

6) Based on Appendix S3 in Walker *et al.* (2012). Range of values for zonal sites along the North America Arctic Transect (NAAT) and Eurasia Arctic Transect (EAT). The values represent landscape-level biomass associated with mapped 100 $m^2$ areas along the NAAT and 2,500 $m^2$ areas along the EAT. Numbers are extrapolated from clip-harvest samples of vegetation types within each mapped area. The values are the mean total standing crop of dead and live plant material within and above the top layer of live green moss.

7) Based mainly on Young (1971).

trends related to habitat and food resource availability (Callaghan *et al.* 2004b). For soil micro-organisms there are no consistent trends in community composition with latitude or altitude (Neufeld & Mohn 2005, Fierer & Jackson 2006, Bjorbaekmo *et al.* 2010, Fierer *et al.* 2011, but see Geml *et al.* 2009 and Timling *et al.* 2012).

Specialization for specific microhabitats decreases also at higher latitudes. In the southern tundra subzones, many more species occur in intra-zonal habitats (habitats where conditions differ from what is typical for the zonal sites, due to, for instance, topography or microclimate), occupying relatively small and isolated sites, than in zonal habitats. The latter contain only a small proportion of the regional flora and fauna. An important consequence of the decrease in number of species with latitude is an increase in dominance. At high latitudes, ecologically plastic species may become 'super-dominant': they occupy a wide range of habitats and have in general a large effect on ecosystem processes (Callaghan *et al.* 2013).

Plant aboveground biomass on zonal sites increases from about 50-150 g per $m^2$ in subzone A to about 750 g per $m^2$ in subzone E (Tab. 12.1). Similarly, annual production increases from about 1 g C per $m^2$ per year in polar desert environments of subzone A to about 90-135 g C per $m^2$ in low Arctic tussock tundra and low-shrub tundra of subzone E (Oechel & Billings 1992, Bazilevich *et al.* 1997). There is, however, considerable regional variation. A recent study measured aboveground biomass of zonal vegetation in all five bioclimate subzones along two transects in Russia and North America, respectively (Walker 2010, Walker *et al.* 2011a, Walker *et al.* 2012). Differences were observed in the growth-form composition of the biomass along the two transects (Fig. 12.2). For example, the North America transect had greater amounts of lichens and evergreen shrubs, and greater total biomass in subzones D and E. Also the North America transect had lower biomass in subzone C compared with that in Russia, and Russia had much lower biomass in subzones A and E. The differences were attributed to variations in precipitation (a drier climate at the Banks Island subzone C location of North America, a much colder and snowier climate at the Franz Josef Land subzone A location in Russia), and to different disturbance regimes, particularly greater amounts of reindeer *Rangifer tarandus* grazing along most of the Eurasia transect (Walker 2010).

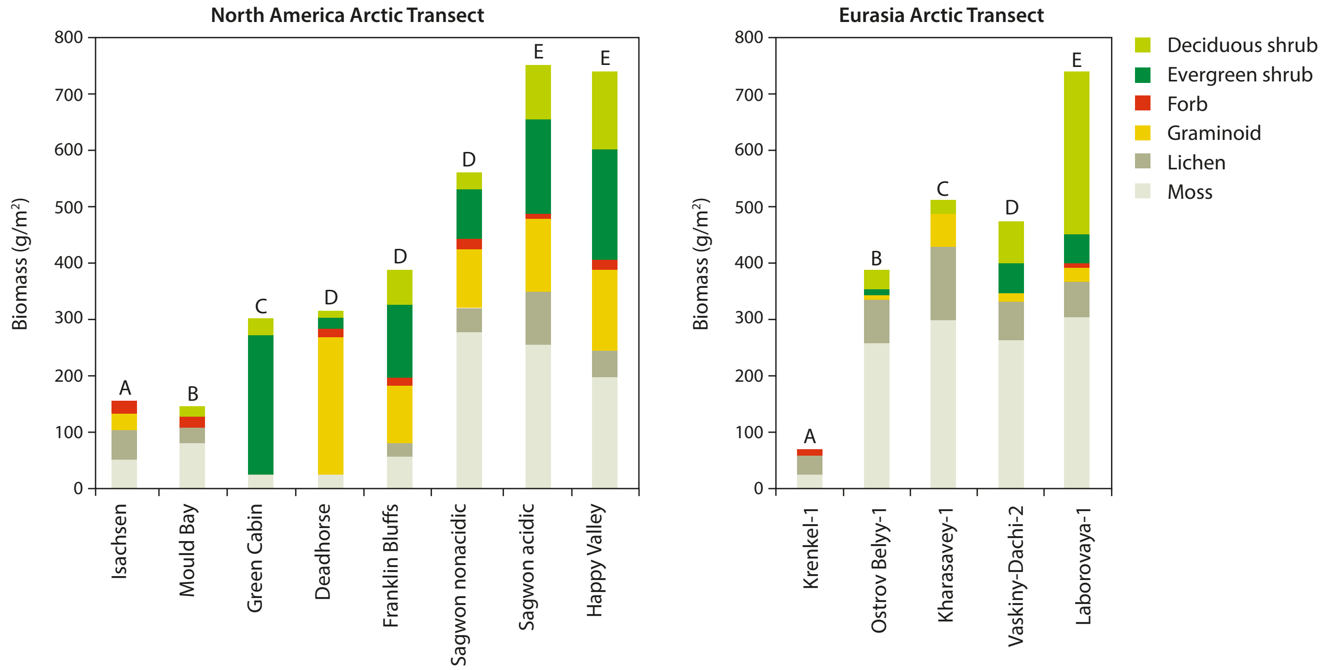


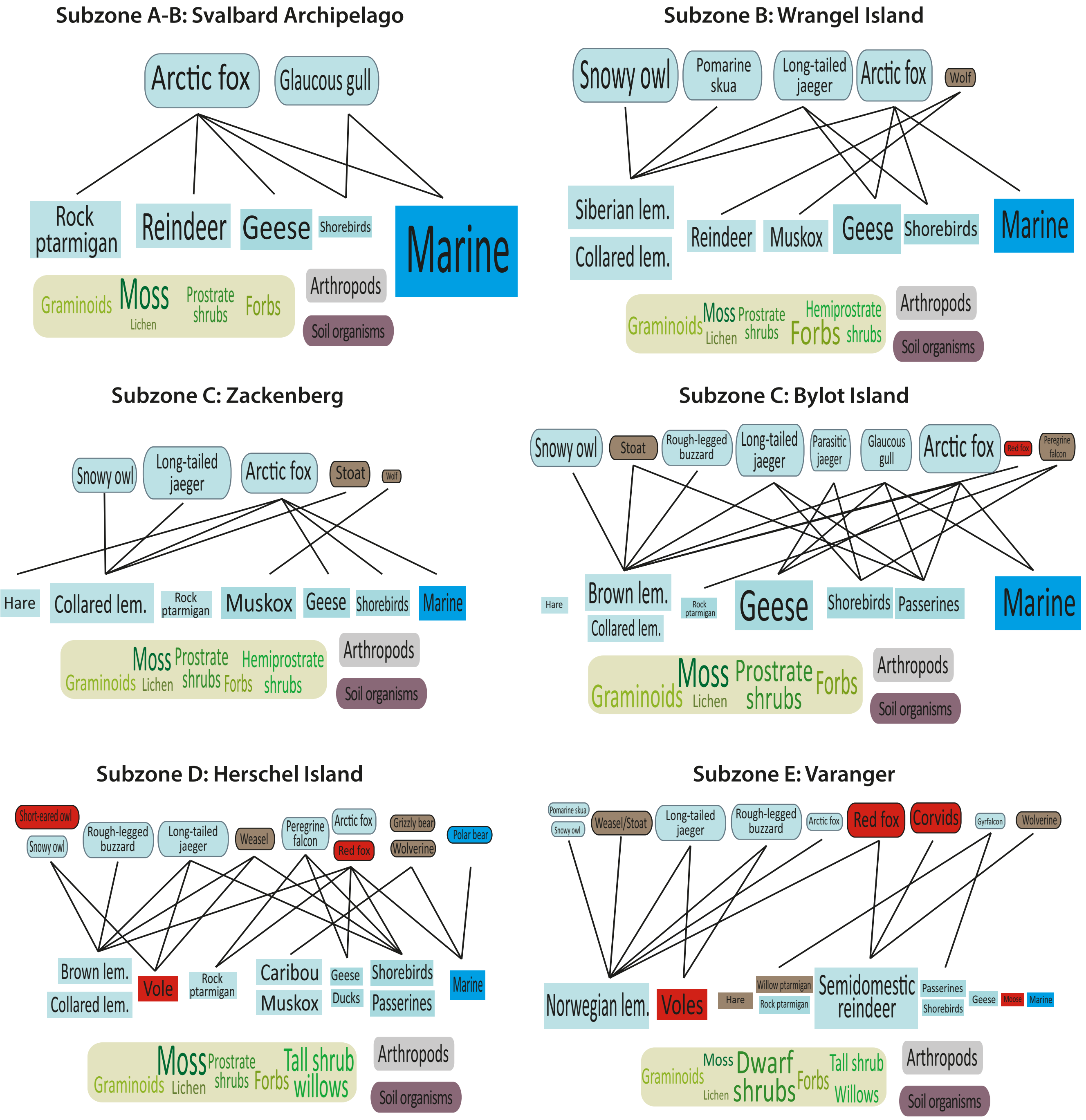
**Figure 12.2.** Total aboveground biomass of zonal vegetation for representative sites along the North America Arctic Transect and Eurasia Arctic Transect, respectively. Values exclude biomass of dead moss, dead lichen, detached dead and biological soil crusts. Bioclimate subzones (A-E) are shown above each bar, and the study sites are marked on Box 12.1 Fig. 1 (from Walker *et al.* 2012).

One of the clearest conclusions from latitudinal studies in Russia and North America is the special nature of both margins of the tundra zone. In the north, subzone A covers a very small area (2% of the Arctic), and mean July temperatures hovering near freezing are likely to make it extraordinarily sensitive to climate change (Walker *et al.* 2008). It truly exists at the margin where even a small summer warming will cause a shift toward vegetation with structure and function characteristic of more southerly subzones. Furthermore, subzone A is situated where some of the largest temperature changes can be expected because it only exists in regions where the summer-long presence of sea ice keeps air temperatures near freezing. At the extraordinarily long forest tundra boundary along the southern extreme of the tundra zone, changes in temperature, primarily summer temperatures, will probably also cause major transitions in ecosystem structure and function. These transitions are likely to be slower in some areas because of natural buffering in tundra soil temperature caused by deep peat, and faster in others because of disturbances caused by thawing permafrost, but everywhere occurring over immense areas associated with the tundra-forest boundary transitions in both North America and Eurasia.

In addition to latitudinal zonation, the Pan-Arctic Flora (Elven *et al.* 2011) divides the Arctic into 21 floristic regions circumscribed by common features independent of the general thermic south-north gradient (Daniëls *et al.*, Chapter 9). These features reflect a combination of glacial history, continental vs. oceanic climate and other historical biogeographic influences. The effect of glacial history and landscape age can be seen using vegetation mapping and remote sensing studies. At a circumpolar scale, Arctic areas show distinctive increases in biomass during the first several thousand years following deglaciation (Raynolds & Walker 2009). Landscape age accounts for 34% of the circumpolar variation in productivity as indicated by the Normalized Difference Vegetation Index (NDVI) (Raynolds & Walker 2009) – landscapes older than 20,000 years in subzones B to E have higher NDVI values (Box 12.1) and greater vegetation cover.

### Latitudinal zonation of food webs

The best studied terrestrial trophic systems in the Arctic are the plant-based food webs where vertebrates usually dominate the higher trophic levels both in terms of biomass and consumption (Batzli *et al.* 1980, Krebs *et al.* 2003, Callaghan *et al.* 2004b). These vertebrates can be classified into *guilds* of species with similar trophic positions. For instance, a particularly important guild of herbivores is formed by small rodents that are associated with a specialized guild of rodent predators (Batzli *et al.* 1980, Ims & Fuglei 2005). As a result of the general trend of decreasing diversity of Arctic organisms with increasing latitude, guilds lose species and become fewer and the food webs get simpler farther north (Callaghan *et al.* 2004b). Whereas in bioclimate subzone E most guilds are typically composed of several species often with fairly even abundances, single super-dominant species that are truly 'Arctic' are features of more northerly subzones. Examples of such super-dominant species are lemmings among the vertebrates (*Lemmus* or *Dicrostonyx* spp.) or springtails among invertebrates (e.g. *Folsomia* spp.). In bioclimate subzones A and B entire guilds are missing in certain areas, resulting in greatly simplified food webs (Fig. 12.3). Note that this may also be due to dispersal barriers as these high Arctic food webs are often located and studied on islands.



Subzone A-B: Svalbard Archipelago

Subzone B: Wrangel Island

Subzone C: Zackenberg

Subzone C: Bylot Island

Subzone D: Herschel Island

Subzone E: Varanger

**Figure 12.3.** Conceptual models for the plant based vertebrate food webs typical for the five Arctic bioclimate subzones represented at six research sites. The graphs illustrate main hypotheses about relative importance of components and trophic links in the food webs taking into account current knowledge about the ecosystem at the respective sites. For vertebrates, mainly boreal species are shown in red, wide-spread boreal and Arctic species in brown and typically Arctic species in pale blue. Only major trophic relationships are represented by lines (based on Chernov & Matveyeva 1997, Matveyeva 1998, Krebs *et al.* 2003, ACIA 2005, Gauthier & Berteaux 2011 and Ims *et al.* 2013).

The following overview of the structural characteristics of the consumer guilds of tundra food webs according to the CAVM scheme for vegetation subzones will primarily be based on information provided by previous large-scale syntheses such as those provided by the IBP (Chernov & Matveyeva 1997, Matveyeva 1998), ACIA (2005) and the IPY-project Arctic WOLVES (Gauthier & Berteaux 2011). Moreover, we will draw on information from research stations and programs spread over most Arctic subzones.

The most complex and species-rich food webs are found in the low Arctic. Ecosystems of subzone E are characterized by a relatively high abundance of boreal species at all trophic levels. The small rodent guild is composed of several species of voles, in addition to the typical Arctic lemmings (Fig. 12.3). Medium-sized herbivores include ptarmigan *Lagopus* spp., hare *Lepus* spp., Arctic ground squirrel *Spermophilus parryii* and geese, whose numbers vary considerably between different geographic regions. The main large herbivore is the caribou/reindeer, although Eurasian elk/moose *Alces alces/americanus* regularly enters the low Arctic in summer, where tall shrubs are abundant. Indeed, the presence of tall shrubs as food or structural habitat is a key factor behind the relatively high species diversity and food web complexity in subzone E. Endemic Arctic predators such as the Arctic fox *Vulpes lagopus* or the long-tailed jaeger *Stercorarius longicaudus* are common, as well as the small rodent specialists weasel *Mustela nivalis* and stoat *M. erminea*, but the most specialized lemming predators such as the snowy owl *Bubo scandiaca* or pomarine jaeger *Stercorarius pomarinus* are mostly lacking. At the same time, widespread predators with strongholds in southerly biomes such as the red fox *Vulpes vulpes*, eagles and corvids may also be common (Killengreen *et al.* 2012). Large predators such as the wolf *Canis lupus*, wolverine *Gulo gulo* and brown bear *Ursus arctos* are less numerous in the tundra than in the boreal forest, and in regions with domestic reindeer their numbers are often under strict anthropogenic control (Reid *et al.*, Chapter 3). In subzone D, Arctic species become more dominant than boreal ones. Thus lemmings dominate the small rodent guild, although voles are present, and typical Arctic predators such as snowy owls can breed there in years with high lemming peaks.

The high Arctic is characterized by endemic tundra food webs in the sense that they are dominated by species whose distribution ranges are restricted to the Arctic tundra biome. Small rodents are represented by one or two species of lemmings, which are distributed as far north as vascular plants are present (Reid *et al.*, Chapter 3). Several species of medium-sized herbivores occur, but are fewer and less abundant than in the low Arctic. Geese, however, can form large colonies, such as the lesser snow goose *Chen c. caerulescens* on Bylot Island (Gauthier *et al.* 2011). Reindeer/caribou are widespread although often at low densities, and muskox *Ovibos moschatus* are present locally. The predator guild is dominated by Arctic species such as Arctic fox, snowy owl and jaegers. Some widespread species, however, still occur. The stoat is an important lemming predator in high Arctic Greenland as far north as Nearctic collared lemmings *Dicrostonyx groenlandicus* are present (Born & Böcher 2001). Large predators such as wolves are rare or absent. Most areas in subzone A and B are located on islands, where fewer vertebrate species are present (presumably due partly to dispersal barriers), and the tundra food web is simplified compared with mainland sites at the same latitude (e.g. on Taimyr Peninsula; Ebbinge & Mazurov 2007). Thus, ptarmigans, hares and small mustelids are absent from Wrangel Island in subzone B (Menyushina *et al.* 2012). In the high Arctic archipelago of Svalbard, which is mostly situated in subzone A, resident terrestrial herbivores are represented only by reindeer and rock ptarmigan *Lagopus muta*. Geese are important in summer. Predators are few, as there is no subsistence for the predator guild that is dependent on lemmings. The main terrestrial predator is the Arctic fox for which marine subsidies constitute important resources (Eide *et al.* 2012).

#### 12.2.1.2. Regional- to local-scale variation

Factors that affect vegetation patterns at regional scales include major substrate differences such as major glaciations, large sand sheets, marine incursions and major topographic variations related to mountains (Cantlon 1961, Walker 2000). At the landscape scale, variations related to smaller hillslope gradients, snow gradients and variations within smaller watersheds become apparent. At local scales, variation in plant communities is caused by such factors as different bedrock types, local drainage conditions, periglacial landforms and small-scale disturbance.

**Altitudinal zonation and hill-slope toposequences**

Topography affects diversity at several scales. Mountain ranges have elevation belts that correspond somewhat to the latitudinal bioclimate subzones. Theoretically, elevation belts are thermally equivalent to the latitudinal zonation and can be determined by the adiabatic lapse rate of -6 °C per 1,000 m elevation with about 333 m steps between the belts (CAVM Team 2003). Studies of alpine vegetation in the Arctic are not numerous (e.g. Jedrzejek *et al.* 2013), but the launch of the Global Observation Research Initiative in Alpine Environments (GLORIA) protocols for analyzing changes in species distribution on high mountain peaks (Pauli *et al.* 2004, Grabherr *et al.* 2010) represents significant progress. GLORIA is organized around the principle that the alpine zonation of many mountain ranges will change because of elevated temperatures. Active GLORIA monitoring sites are located near the Arctic research stations at Toolik Lake, low Arctic Alaska, and Zackenberg, high Arctic NE Greenland.

On a smaller scale, predictable changes in vegetation and soils that occur along hill slopes provide a convenient conceptual means to describe variation in most landscapes (Milne 1935, Billings 1973, de Molenaar 1987, Birkeland 1999). A conceptual framework consisting of five hill-slope positions typically found in hilly Arctic terrain is shown in the upper section of Fig. 12.4 (CAVM Team 2003). The approach provides a way to visualize the common variation in vegetation structure and composition that is attributable mainly to variations in water moving down slope over long periods of time. The changes in plant-community structure along typical toposequences in each Arctic bioclimate subzone are described by Elvebakk (1999; see lower section of Fig. 12.4).

A unique aspect of Arctic and alpine toposequences is the role of snow, which has complex consequences for vegetation patterns and ecosystem processes (Gjærevoll 1956, Billings & Bliss 1959, de Molenaar 1987, Walker *et al.* 1993, Walker *et al.* 2001a). The accumulation of snow can decouple the surface almost completely from air temperatures, resulting in much milder winters beneath the snowpack but correspondingly shorter growing seasons (Scott *et al.* 1993, Zhang 2005). Late snow beds (Bjork & Molau 2007) also influence soil moisture as well as the supply and seasonal availability of nutrients (Fahnestock *et al.* 2000).

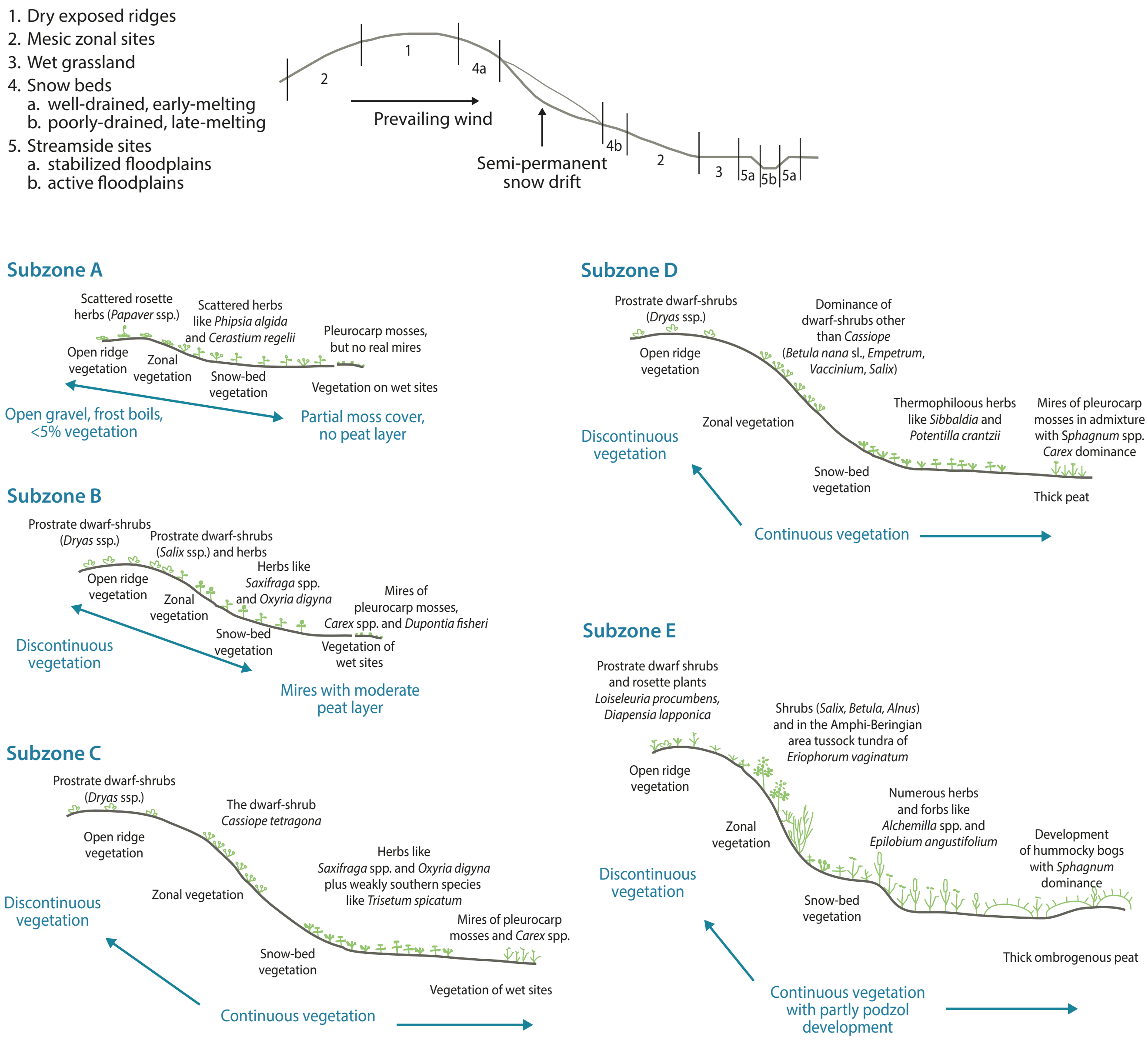


**Figure 12.4.**
Upper section: Conceptual toposequence used for the Circumpolar Arctic Vegetation Map (Walker *et al.* 2005).
Below: Generalized toposequences for vegetation in the five Arctic bioclimate subzones (adapted from Elvebakk 1999).

Snow beds are a key habitat for important tundra herbivores. Lemmings spend the winter under the insulating snow layer, which provides relatively mild and stable conditions necessary for winter breeding (Reid *et al.* 2012). The availability of stable snow cover seems to be a prerequisite for the characteristic lemming outbreaks (Ims *et al.* 2011) – a key biotic process in shaping tundra food webs and maintaining Arctic biodiversity (Section 12.2.2.1).

### Soil pH

Local pH boundaries and gradients are associated with different bedrock types, loess, riparian systems, toposequences along slopes, cryoturbated soils and glaciated landscapes of different age. Soil pH boundaries are particularly noticeable in Arctic and alpine systems because of contrasting near-surface bedrock, extensive loess and coastal marine deposits, and have large consequences for plant community structure and diversity (Edlund 1983, Walker *et al.* 1994). A complex set of soil and ecosystem properties are affected by soil pH, including calcium and phosphorus availability, soil temperature, active layer thickness, photosynthesis, respiration, decomposition rates and fluxes of trace gases together with energy and water (Sjörs 1959, Walker 1985, Bockheim *et al.* 1998, Walker *et al.* 1998).

Soil types and climate are intimately linked. Acidic soils are more common in the southern bioclimate subzones, particularly subzone E, because of accumulations of organic matter in warmer climates, whereas near-surface mineral soils with higher soil pH are more common in the colder regions. However, this is not universally true because sandy soils or acidic bedrock areas in the far North can have acidic soil. Likewise, areas in subzone E with calcareous bedrock, recent glacial till, loess, river alluvium or recent disturbances will often have nonacidic soils. In general, the nonacidic zonal soils have higher species diversity, greater heat flux, warmer and drier soils, deeper active layers, are less of a carbon (C) sink, and are a smaller source of methane ($CH_4$) to the atmosphere (Walker *et al.* 1998). This has implications both for biodiversity but also for phytomass and functional composition (Epstein *et al.* 2008). Also, soil bacterial community composition and diversity in the Arctic is structured according to local variation in soil pH (Chu *et al.* 2010). Many of the physico-chemical factors structuring communities and ecosystems in the Arctic are, however, strongly related, so assigning direct causality is frequently hampered by confounding co-varying factors.

### Glacial history

The effects of past glaciation are clearly expressed in terms of regional plant community diversity (i.e. beta-diversity), which tends to decrease with increasing landscape age. The differences in plant beta-diversity seen on glacial surfaces of contrasting age are also strongly linked to differences in soil pH and soil moisture. These differences often decline over long periods of time as landscapes become paludified[2], and soils become leached and wetter due to the presence of near-surface permafrost.

For example, at Toolik Lake, low Arctic Alaska, distinctly different vegetation types and biomass are found on glacial surfaces differing by more than 100,000 years in age. The oldest surfaces (Sagavanirktok-age, more than 125,000 years since deglaciation) have a dominance of acidic tussock tundra. In contrast, the much younger Itkillik II surfaces (about 11,500 years since deglaciation) have more irregular terrain and more diverse landscapes and vegetation with more lakes, drier vegetation, a dominance of nonacidic tundra and higher percentages of snow-bed vegetation. The diversity of plant communities tends to decrease as time, erosion and vegetation succession proceed (Walker 1995). Many features such as small ponds and diverse glacial landforms become rounded or are eliminated; and large areas become covered by the dominant zonal vegetation (Walker *et al.* 1994). Similar patterns have been shown with vegetation of glacial sequences covering shorter time periods (Zollitsch 1969, Reiners *et al.* 1971, Matthews 1992).

The older landscapes near Toolik Lake and throughout northern Alaska also have higher NDVI and greater amounts of standing biomass (Munger *et al.* 2008, Walker & Maier 2008) and higher production of $CH_4$ (Shippert *et al.* 1995). This is due in part to the relative proportions of dry, moist and wet vegetation types on different-age surfaces. Generally, drier vegetation with lower NDVI is dominant on younger surfaces. The biomass of the *Sphagno-Eriophoretum vaginati* (bog moss-tussock cotton grass association), which grows on the older surfaces, is about 25% greater than its counterpart in younger areas, the *Dryado integrifoliae-Caricetum bigelowii* (entire leaf mountain aven-Bigelow's sedge association). These types also have contrasting key ecosystem properties with respect to differences in soil pH. *Dryado integrifoliae-Caricetum bigelowii*, the zonal vegetation type for subzone D, occurs on moist nonacidic calcareous soils (mean soil pH 6.3) and has the highest species richness of any association sampled near Toolik Lake – 56 species (26 vascular-plant species, 16 bryophytes and 14 lichens) per 20 $m^2$ plot. Several of these species have Beringian or western North American distributions. This is substantially higher than the diversity of the corresponding plant association that occurs on moist acidic soils in the same region (*Sphagno-Eriophoretum vaginati*; mean soil pH 4.6) and has an average of 39 species (15 vascular plants, 14 bryophytes and 10 lichens; Walker *et al.* 1994). The younger Itkillik surfaces also had a stronger NDVI increase during the period of the Landsat satellite record, perhaps due to the somewhat warmer soils, more abundant disturbances caused by non-sorted circles and other periglacial processes, and more gaps in the vegetation canopy (Raynolds *et al.* 2013).

### Disturbance

Natural ecosystem disturbances occur in a hierarchy of spatial and temporal scales from daily needle-ice formation in soils at sub-meter scales to the major glaciations that cover much of whole continents (Walker 1996). Many natural disturbances in Arctic regions are related to the presence of permafrost including the growth and erosion of ice-wedges, thermokarst (e.g. Jorgenson *et al.* 2006), thaw lake drainage, differential frost heave, and mass movements due to thawing permafrost (e.g. Kokelj *et al.* 2009). Many natural disturbances are good analogs of disturbances caused by humans (anthropogenic disturbances are dealt with in Section 12.3.2). The successional processes following disturbances are strong modifiers of diversity, structure and phytomass (Bliss 1997, Callaghan *et al.* 2004a, 2004b). Walker *et al.* (2009) observed that many of the greenest landscapes on the Yamal Peninsula, Russia, are associated with landslides and drainage networks resulting from ongoing rapid permafrost degradation (Fig. 12.5). On older, stabilized slopes there are successional shifts in community composition, for example from pioneer vegetation through grass and forb-dominated communities to willow shrubs. Other disturbances are related to erosion caused by wind, snow or flooding water. The role of wildfires in low Arctic shrub tundra is also increasingly being recognized (Racine *et al.* 2004, Higuera *et al.* 2008). Tundra wildfires have recently scorched thousands of square kilometers in particularly warm and dry summers. Such fires initiate a cascade of processes including release of C to the atmosphere, changed vegetation successional path-ways, thawing permafrost and thermokarst (Mack *et al.* 2011, Rocha & Shaver 2011a, 2011b).

Extreme herbivore abundance owing to erratic or cyclic population outbreaks are also 'pulse events' that may cause considerable physical disturbance to the substrate and the vegetation. Examples are cyclic rodent peak

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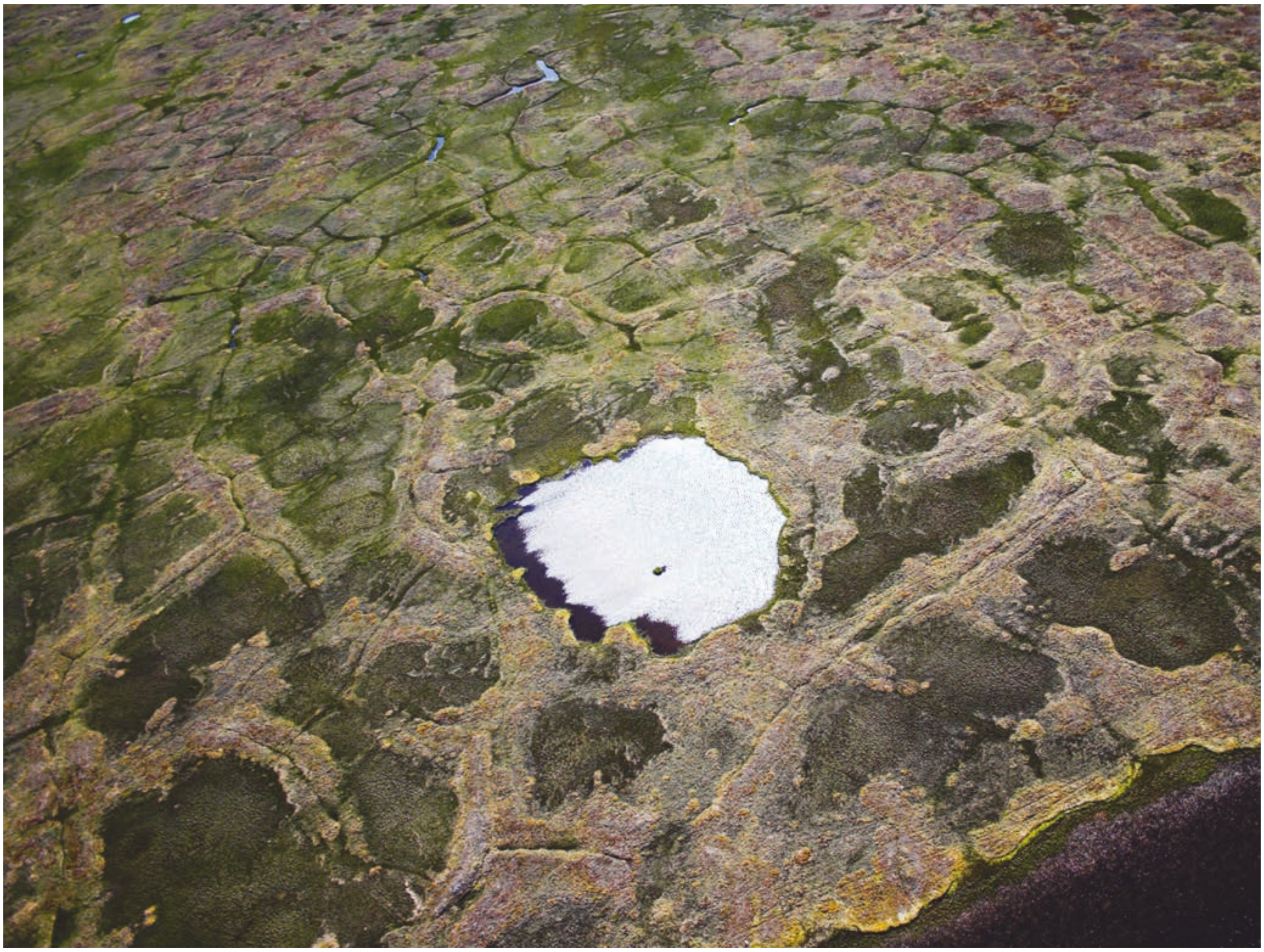
[2] Paludification is a common process by which peatlands in the boreal and Arctic zone are formed.

**Figure 12.5.** Exposed ground-ice thawing along the Se-yakha River within the low Arctic Bovanenkovo gas field in Yamal, Russia. A great deal of terrain within the tundra zone in W Siberia supporting oil and gas infrastructure is underlain by ice-rich permafrost. This surface of marine clay was exposed in the late 1980s and a graminoid cover has regenerated naturally in the intervening decades, but subsidence was still occurring in 2005. See Kumpula *et al.* (2011, 2012) for details. Photo: B.C. Forbes.

**Figure 12.6.** Patterned-ground area in the high Arctic coastal tundra at Barrow, Alaska. These low center polygons (one with standing water) are about 10-30 m across and delineated by ice wedges that are formed by thermal contraction of the ground surface. Photo: George Burba/shutterstock.com



years (Batzli *et al.* 1980) or insect pest outbreaks at the southern margin of the tundra (Jepsen *et al.* 2013, Karlsen *et al.* 2013). Besides the effect of grazing (dealt with in Section 12.2.2), the disturbance effect of such herbivores includes digging of burrows by rodents, grubbing for plant rhizomes and roots by geese, trampling by herds of large ungulates and release of nutrients.

Disturbance and succession are intertwined concepts; the study of one must inevitably consider the other. Disturbance initiates succession, influences its subsequent trajectory and can determine its rate, endpoint and duration through subsequent intervention (Walker 1999). The spatial extent and the frequency of disturbances can be expected to increase in the near future with increased human presence and exploitation, combined with thawing permafrost in a warming climate.

*Patterned ground* features, which are typical for Arctic landscapes that are underlain by permafrost, represent natural disturbances at small scales (Fig. 12.6). Most often these features are caused by a combination of seasonal frost cracking (whereby the ground contracts during winter and cracks into polygons of varying dimensions) and differential frost heave (whereby ice forms in soils and causes it to heave more in some areas than in others). Small, medium and large non-sorted polygons, non-sorted circles (frost boils) and earth hummocks are typical forms (Washburn 1980). These patterns have intrigued geomorphologists and permafrost scientists for decades and have recently been studied by biologists because of their importance notably to local biodiversity and net fluxes of GHG (Kade *et al.* 2005, Ping 2008, Vonlanthen *et al.* 2008).

#### 12.2.1.3. Hot spots of diversity

In addition to the diversity gradients and patterns described above, sites with locally high biodiversity are observed. Such diversity 'hot spots' are often literally hotter, but topography, continentality and historical factors affect the occurrence of extra-zonal Arctic hot spots (Daniëls *et al.*, Chapter 9). Thermal hot spots are often characterized by the presence of anomalously tall shrubs or trees. Alders *Alnus* spp. and tall willows are present in the warmer parts of the low Arctic, occurring mainly on sites where soil conditions permit more luxuriant growth, such as on warm south-facing slopes or along streams and drainages. The tall shrub thickets they form represent hot spots of productivity and diversity, and are important structural elements in the tundra landscape. They provide shelter and food for many animal species such as willow ptarmigan *Lagopus lagopus*, many passerine birds, insects and hares (den Herder *et al.* 2004, Henden *et al.* 2011a, Ehrich *et al.* 2012, Ims & Henden 2012). The presence of balsam poplar, a species with higher thermal requirements than the tall shrubs, is a strong indicator of floristic hot spots because this species often forms small boreal enclaves that occur near springs in limestone bedrock areas or on thermally warm valleys and slopes in the low Arctic (Bockheim *et al.* 2003, Breen 2010). The presence of trees and tall shrubs does not, however, necessarily indicate an area of high plant species diversity. Yet, for some animal taxa like passerine birds, they certainly do (Henden *et al.* 2013), although the high diversity is mostly attributed to the presence of species with their strongholds in the boreal forest (Sokolov *et al.* 2012).

For the diversity of Asiatic and steppe-tundra plant endemics, continentality is more important than temperature. Many of these species evolved in Beringia, where extensive glacier-free areas isolated from oceanic influences during the Pleistocene permitted the evolution of a rich cryo-xerophytic (steppe tundra) flora (Hultén 1937, Hopkins *et al.* 1982, Yurtsev 1982). They were adapted to warm summers, very cold winters, dry year-round climate, warm (in summer) well-drained mineral-rich soils, high disturbance regimes related to the abundant animals, and continual deposition of loess from the floodplains of rivers that were carrying high silt loads from the glacial meltwaters (Guthrie 1982, Yurtsev 1982). At present, these steppe-tundra plants are mostly found in sites that are at a considerable distance from marine influences and also have warm extra-zonal climates, where they form distinct assemblages of xerophytic species.

Locations that have a mix of warm summer soils due to extra-zonal conditions and azonal site factors, such as the occurrence of warm springs, or favorable geology, such as calcareous bedrock, are likely to enhance the probability of high regional species diversity (gamma diversity). Such areas are more common within regions of high habitat diversity (beta diversity), such as mountainous areas with a variety of bedrock types or different-age glacial surfaces, different slope exposures and snow regimes, and large river floodplains with different-age terraces, sand dunes and abandoned channels and meanders. Gamma diversity is furthermore enhanced if the location is in a biogeographic region with high species diversity, such as Beringia. Areas with high plant diversity are also likely to have high diversity of other taxa. For example, pingos (ice-cored mounds up to 50 m high) in northern Alaska are often hot spots of floristic and faunal diversity within 'seas' of wet tundra because of the large variety of microhabitats concentrated within a small area (Walker 1990).

### 12.2.2. Ecosystem processes and functions

The abiotic factors reviewed in Section 12.2.1 set broad constraints on species distribution ranges and thus site-specific community composition and species diversity. Such abiotic factors also constrain functional attributes of the biota such as plant growth forms, their phytomass and primary productivity, as well as the multitude of interactions among ecosystem components (producers, consumers, decomposers and pathogens). In this section we first review current knowledge about how interactions between species within food webs, in conjunction with abiotic factors, contribute to shaping biodiversity patterns in time and space in tundra ecosystems (Section 12.2.2.1), and second, how functional ecosystem properties mainly at the level of broader compartments of terrestrial Arctic biodiversity feed back to the abiotic environment through physico-chemical processes (Section 12.2.2.2). Although obviously linked, the two issues belong largely to separate sub-disciplines within ecosystem science. Food web ecology deals mostly with trophic linkages between macroscopic producer (plants) and consumer (herbivore and predators) species and typically above-ground processes, while functional ecosystem scientists typically deal with linkages between above-ground and below-ground processes, between macro-organism and microbial communities and processes within the decomposer web. However, as separation of the two sub-disciplines is unhelpful for understanding how tundra ecosystems respond to specific drivers of change, we also discuss how trophic interactions are linked to ecosystem functions in terms of physico-chemical processes (Section 12.2.2.3).

Much of the current research on tundra ecosystems is aimed at understanding the impacts of climate change. Research approaches include modeling, field experiments, comparisons across spatial climatic gradients, and time-series analyses. In the present section we review research that provides an understanding of how tundra ecosystems are shaped by climate and are expected to respond to climate change (e.g. by means of modeling, experiments, comparative studies), while research that demonstrates historical, recent and current trends (e.g. by means of time-series analysis) is reviewed in Section 12.3.

### 12.2.2.1. Food web interactions

#### Theoretical framework

There has been a vigorous debate about the relative roles of producers and consumers in controlling the structure and functioning of food webs in different climate settings (Turkington 2009). A prominent theoretical framework, specifically addressing tundra ecosystems, is provided by the Exploitation Ecosystem Hypothesis (EEH; Oksanen *et al.* 1981, Oksanen & Oksanen 2000). EEH focuses on the high energetic costs of maintenance of endothermic animals, and this sets a 'bottom-up' constraint on the number of trophic levels (plants → herbivores → carnivores) that can be maintained along climatic gradients of decreasing primary productivity. Low Arctic climatic zones are predicted to be productive enough to hold all three trophic levels, where predators in turn can provide a 'top-down' control on the abundance of herbivores to the extent that plant communities are little affected by herbivores. In low productivity (or 'harsh') high Arctic environments it is predicted that tri-trophic dynamics are reduced to simple two-level systems (plants → herbivores). In such a situation heavy winter grazing pressure will restrict the above-ground accumulation of biomass and effectively exclude erect woody plants (Oksanen & Oksanen 2000). When released from predator control, herbivores are also predicted to be able to homogenize plant biomass across environmental gradients at the landscape scale, and moreover to be able to bring about gross transitions between alternative tundra vegetation states (Fig. 12.7). Finally, models of both two-trophic and three-trophic level systems show that they are liable to strong multi-annual cyclic fluctuations in interaction strength and biomass (Turchin *et al.* 2000, Ims & Fuglei 2005). One major limitation of the EEH, however, is that it does not include the typical spatial subsidies that tundra ecosystems are often subject to. Below, we review empirical studies of plant-herbivore and predator-prey interaction in light of the predictions from the EEH.

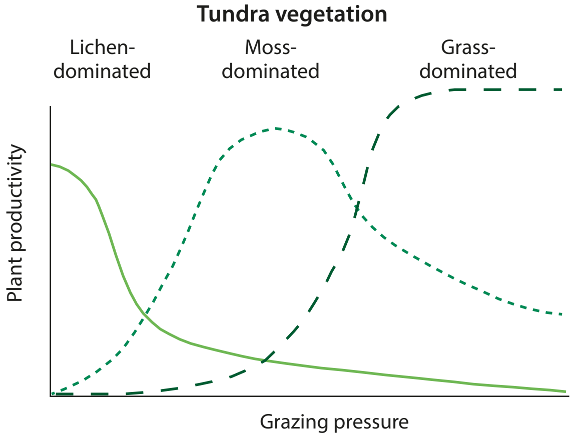


**Figure 12.7.** Predicted transitions between tundra vegetation states with increased grazing impact (from van der Wal 2006).

#### Plant-herbivore interactions

Reindeer/caribou, geese and small rodents are three guilds of herbivores in tundra ecosystems (cf. Fig. 12.3) that are particularly important both in terms of their broad geographic distribution (across bioclimatic subzones and longitudinal eco-regions) and strong impact on vegetation. These keystone herbivores are, however, also fundamentally different in their modes of herbivory (food preferences, grazing/browsing/grubbing behavior), mobility (migratory or resident) and population dynamics (including sensitivity to predation and climatic variability), so there is justification for considering their impacts on the vegetation separately.

Herbivore exclusion experiments in northern Fennoscandia have identified the partial effects of reindeer and small rodents (voles and lemmings) on functionally important shrubs. In this region, reindeer are semi-domestic and have an abnormally high abundance (partly owing to strong anthropogenic control of large predators), whereas the small rodents exhibit distinct 4-5 year population cycles. In low Arctic riparian grasslands, reindeer and small rodents had strong complementary effects on the growth of tall willow recruits, indicating that herbivore community structure matters for the dynamics of tall willow thickets (Ravolainen *et al.* 2011). While the reindeer impose a more constant pressure ('press effect') on the vegetation (Kitti *et al.* 2009), the impact of small rodents is a typical 'pulse effect' associated with cyclic peak abun-

**Figure 12.8.** Thick layer of litter on snow in late June, composed mainly of clipped vegetation mixed with soil and lemming feces, resulting from intense activity of Norwegian lemming *Lemmus lemmus* during a peak-density winter on Varanger Peninsula. This litter, which some Arctic indigenous people term 'lemming hay' (Chernov & Matveyeva 1997), is often flushed by melt water in spring and may appear on the top of remaining snow patches. Photo: R.A. Ims.

dances (Fig. 12.8). Indeed, the pulsed effects of lemming population cycles on dwarf-shrub biomass were strong enough to be picked up as a signal in NDVI (Olofsson *et al.* 2012). Because experimental studies were undertaken during an 'exceptionally warm' decade, it was also possible to identify an interaction between climatic and herbivore effects: while the shrub biomass within herbivore exclosures accumulated strongly in the heath habitat over the > 10 year period in which the experiments were conducted, this was not the case for the open control plots (Olofsson *et al.* 2009). This indicates that there is a significant potential for ungulates and rodents to control biomass of shrubs even in a warming Arctic (see also Post & Pedersen 2008, Post *et al.* 2009, Wookey *et al.* 2009). Aside from direct effects on biomass, ungulate herbivores may also promote diversity within the plant community and prevent reduction of this diversity by warming-induced increases in the dominance of dwarf shrubs (Post 2013a). Reindeer may, however, have little impact on established thickets of very tall shrubs (above the 'browsing line') (Forbes *et al.* 2010).

Other non-mammalian herbivores may contribute to controlling the growth of shrubs. Tape *et al.* (2010), for example, provided evidence of substantial impacts of willow ptarmigan on shrub growth and shoot patterns. While insect folivores are usually considered to be unimportant compared with vertebrates in Arctic tundra (Callaghan *et al.* 2004b), recent studies have demonstrated impacts of lepidopteran population outbreaks on deciduous shrubs that, at least occasionally and locally, can outpace the impact of vertebrate folivores (Post & Pedersen 2008, Jepsen *et al.* 2013). The role of boreal and Arctic insects in controlling woody vegetation may become substantially more important in a warming climate, because of their often non-linear responses to increasing temperature (Hagen *et al.* 2008, Jepsen *et al.* 2011).

Evidence for vegetation-state shifts from moss-rich tundra heaths to more productive grasslands caused by reindeer grazing, according to the framework of Van der Wal (2006; see Fig. 12.7), comes from sites in high Arctic Svalbard (van der Wal & Brooker 2004) and sub-Arctic northern Fennoscandia (Olofsson *et al.* 2004). However, Bråthen *et al.* (2007) suspected that the finding regarding semi-domestic reindeer in northern Fennoscandia (Olofsson *et al.* 2004) was confounded by local effects of trampling close to fences separating herding districts (see Forbes *et al.* (2009) for similar local effects close to Nenets camp sites). Using a spatially extensive sampling design, Bråthen *et al.* (2007) found that abundant reindeer on the contrary depressed biomass of palatable grasses. However, in accordance with the EEH they noted that abundant semi-domestic reindeer were able to homogenize biomass of palatable forage plants across landscape-scale productivity gradients. Although

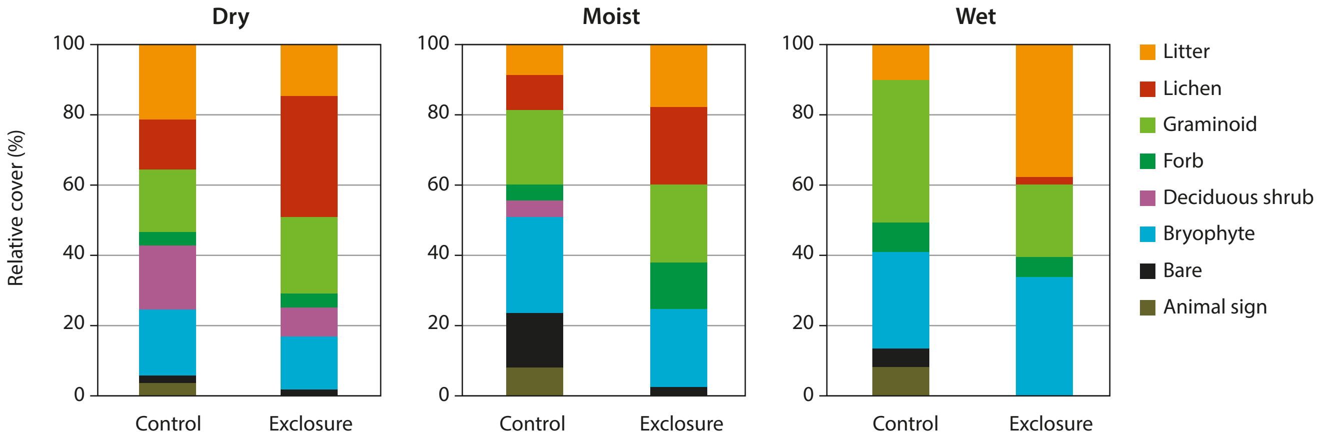


**Figure 12.9.** Long-term effects of lemming grazing on tundra vegetation composition. The plots show the mean relative cover of plant functional types and animal signs in control plots and exclosures from which lemmings had been excluded over 50 years in three tundra types on the Arctic coastal plain near Barrow, high Arctic Alaska, in 2010 (from Johnson *et al.* 2011).

abundant reindeer are known to be able to deplete their lichen resources on winter pastures (Johansen & Karlsen 2005) to the extent that this may cause population crashes and economically unsustainable management (Hausner *et al.* 2011), there is at present little evidence to substantiate use of terms such as 'habitat degradation' or 'ecological disasters' (e.g. as suggested by Moen & Danell 2003) to characterize reindeer-caribou grazing systems (van der Wal 2006).

A relatively high resilience of Arctic vegetation to herbivory is expected (van der Wal 2006, Oksanen *et al.* 2008), both owing to the fact that some Arctic plants are adapted to tolerate high levels of grazing (e.g palatable grasses; Zimov 2005), while others are generally unpalatable and thus resistant to herbivores. One typical grazing-resistant species is the black crowberry *Empetrum nigrum* that often dominates low Arctic tundra heath vegetation and has a retarding effect on ecosystem productivity (Bråthen *et al.* 2010). Crowberry does not appear to respond to changed abundance of vertebrate herbivores (Bråthen *et al.* 2007, Ravolainen *et al.* 2010), but may be severely impacted by emergent climate change-induced outbreaks of insects and pathogens (see Section 12.2.2.3). Conversely, grasses with high concentrations of silica – considered to be a defense against herbivory – decreased rapidly in response to experimental exclusion of mammalian herbivores, indicating that herbivores maintain their dominance (Ravolainen *et al.* 2011). Herbivory may also facilitate certain Arctic vegetation types. Arctic steppes are promoted by trampling and grazing by large mammalian herbivores (Zimov *et al.* 1995, Zimov 2005), while intense pulsed lemming grazing on mosses in snow beds (Virtanen 2000, Virtanen *et al.* 2002a) appears to stimulate growth of vascular plants and to promote higher species richness in such habitats (Oksanen *et al.* 2008). Examining the vegetation in 50-year-old lemming exclosures near Barrow in high Arctic Alaska also suggested that sustained lemming activity promotes growth of vascular plants in some habitats at the expense of lichen (Johnson *et al.* 2011; Fig. 12.9). However, other Arctic habitats appear to have little resilience to certain forms of herbivory. A prime example of apparently irreversible habitat degradation caused by herbivore overabundance is the locally devastating impact of lesser snow goose populations in salt marshes in northern Canada (Jefferies *et al.* 2006). Grubbing for underground plant roots and rhizomes by geese is also a form of herbivory that has been found to have locally destructive effects on other types of Arctic vegetation, such as wet tundra, as well as drier tundra on Svalbard (van der Wal *et al.* 2007, Pedersen *et al.* 2013).

Explicit consideration of spatial scale is important in any studies concerned with trophic interactions (Post *et al.* 2009), because resource availability varies in space (habitat heterogeneity, patch dynamics) and time (successional processes, seasons). Jefferies (1999) emphasized that herbivores, because of their mobility, can exploit high quality forage, in a landscape context, when and where it occurs. Marell *et al.* (2006) studied nutrient dynamics of reindeer forage species across regional and local snowmelt regimes and found that the greatest spatial and temporal variability in nutrient concentrations occurred early in the thaw period, at the time of highest nutrient requirements by reindeer (including calves). Landscape-level heterogeneity in forage availability may decline in the future with earlier and faster melt-out of snow beds and snow patches (Bjork & Molau 2007, Post *et al.* 2008) leading to mismatched timing of herbivore reproduction relative to peak quality of their forage plants (Miller-Rushing *et al.* 2010).

### Predator-prey interactions

Contrary to the predictions of the EEH, empirical evidence reveals that predators play an important role for the functioning of even high Arctic tundra food webs (Gauthier *et al.* 2011). Predators are present nearly everywhere in the terrestrial Arctic (Krebs *et al.* 2003). The guild of small- or meso-sized predators has been shown to depress lemming populations (Reid *et al.* 1995, Wilson *et al.* 1999), and it has been suggested that specialist predators can drive the lemming cycle (see below). Applying a mass balance model to data from 12 sites located throughout the Canadian Arctic, Krebs *et al*. (2003) provided evidence that top-down regulation is more prevalent than bottom-up regulation, at least for small herbivores. This approach was further developed by Legagneux *et al.* (2012), who show that on Bylot Island only < 10% of the annual primary production is consumed by herbivores, whereas up to 100% of the herbivore production can be consumed by predators. Predator populations, which are larger than expected based on local terrestrial primary production, can be maintained mainly because of subsidies from marine ecosystems (Leroux & Loreau 2008, Gauthier *et al.* 2011). Marine resources are important for Arctic fox populations in many areas (Roth 2003, Eide *et al.* 2012, Tarroux *et al.* 2012), illustrating the 'coastal' aspect of the Arctic tundra biome. Inuit residents of Pond Inlet on Baffin Island, Nunavut report Arctic fox movements on the sea ice, particularly in spring when seals have newborn pups (Gagnon & Berteaux 2009). Allochthonous resources subsidizing predators can also originate from southern ecosystems. Geese and other birds breeding in the tundra in large numbers every summer, and whose eggs and chicks are heavily predated by tundra predators, are prominent examples (Gauthier *et al.* 2004, Jefferies & Drent 2006). For the large Arctic herbivores (reindeer and muskoxen), regulation by predators within the Arctic region has not been reported and seems improbable given the very low densities of large predators such as wolves (Reid *et al.*, Chapter 3).

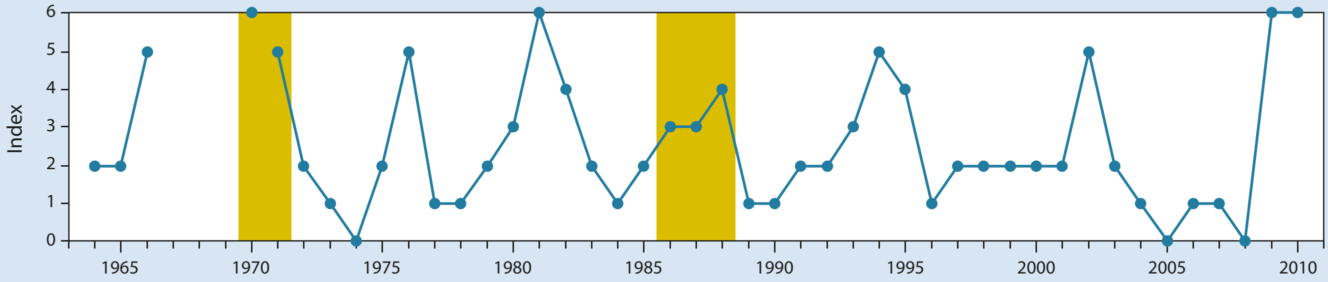
Despite the fact that keystone predators have not been explicitly described from Arctic tundra ecosystems, predators may have indirect effects on vegetation primarily though their effect on small rodents. The characteristic small rodent cycles (voles and lemmings; Reid *et al.*, Chapter 3) have been attributed to many hypothetical causes, but currently the main focus is on trophic interactions. According to classical models, specialist predators are dynamically strongly coupled to their prey. In particular, year-round resident specialist predators can cause population cycles in their small rodent prey, whereas generalist or nomadic predators stabilize the prey's population dynamics (Hanski *et al.* 1991, Hanski *et al.* 2001). In the Arctic, small mustelids are resident specialist predators (Andersson & Erlinge 1977) and have been attributed a keystone role in generating the small rodent cycles (Hanski *et al.* 1991, Gilg *et al.* 2003; see Box 12.2).

## Box 12.2. Lemming cycles in the unique food web of Wrangel Island

Wrangel Island is situated 140 km north of the Chukotka peninsula in bioclimate subzone B (Russia; 70.8° N, 179° W). Biodiversity on Wrangel is uniquely high for the Arctic (e.g. Daniëls *et al.*, Chapter 9 for plants), due to both historical stability (it has not been glaciated during at least two last major glaciations, was part of the extensive Beringian land area, and was not fully flooded by ocean transgressions; Bauch *et al.* 2001, Stauch & Gualtieri 2008) and the high diversity of landscapes. The Wrangel Island State Nature Reserve was established in 1976 and covers the whole island together with surrounding sea areas.

Systematic research on the island's fauna and flora started in 1970-1980. Since 1990, systematic monitoring of key species has been carried out by the scientific staff of the reserve using standard protocols. Two lemming species (Wrangel Island collared lemming *Dicrostonyx vinogradovi* and Wrangel Island brown lemming *Lemmus portenkoi*) are present together with a predator guild typical for this bioclimatic subzone, with the notable exception of small mustelids (stoat and least weasel). Despite the lack of small mustelids, the lemming populations exhibit cyclic fluctuations. The period of the cycle was 5-7-years in 1970-1980 (Chernyavsky & Tkachev 1982). During the last decades, however, the cycles have been less pronounced, with more years with intermediate abundances and periods increasing to 8-9 years (Box 12.2 Fig. 1; Menyushina *et al.* 2012). Changes in snow conditions and repeated ground icing in winter are most likely causing these changes.

**Box 12.2 Figure 1.** Qualitative time series of lemming dynamics on Wrangel Island using an index ranging from 0 to 6. This series depicts the dynamics of both species together and combines information from all available sources of data (cf. Menyushina *et al.* 2012). The yellow boxes mark years where there were discrepancies between the different sources.



Other researchers, referring to EEH, propose that plant-herbivore interactions cause the lemming cycles (Turchin *et al.* 2000, Oksanen *et al.* 2008). Resolving the controversy regarding whether bottom-up vs. top-down processes cause Arctic small rodent cycles is at present hampered by limited time series data from few monitoring sites (Oksanen *et al.* 2008, Gauthier *et al.* 2009, Krebs 2011). Nevertheless it is important for understanding the functioning of tundra ecosystems.

A major difference between high Arctic lemming cycles and low Arctic vole cycles is their seasonal dynamic. Whereas lemmings typically reach peak densities before snow melt, because they breed under the snow, the exclusively summer-breeding voles usually reach their peaks in the fall (Ims & Fuglei 2005). High densities in spring, when predators reproduce, make lemmings a particularly important resource for specialized Arctic predators. Recent results suggest that lemming peaks are limited by snow conditions and winter climate (Kausrud *et al.* 2008, Gilg *et al.* 2009, Ims *et al.* 2011), setting a southern border for lemming-dominated small rodent communities and their associated predator guild (Section 12.2.1.1, Fig. 12.3). An alternative explanation could be that southern species of voles competitively exclude lemmings at their southern border.

#### Competition, facilitation and indirect interactions

Besides the trophic interactions reviewed above, other types of inter-specific interactions also structure tundra food webs. Their effects can be mutually negative (competition) or positive (facilitation) and be mediated by direct or indirect ('apparent') interactions. Cases of influential direct competitive interactions in tundra ecosystems have been found between predators (e.g. between the Arctic and the red fox; Tannerfeldt *et al.* 2002), herbivores (i.e. between lemming species; Morris *et al.* 2000) and plants (e.g. shading effects of tall shrubs; Totland *et al.* 2004). However, for plants in particular it has been noted that positive interactions ('facilitation') may be prominent and even dominate towards the climatically most extreme high Arctic subzones (Svoboda & Henry 1987, Callaway & Walker 1997). Facilitation may also take place among tundra herbivores as indicated by the positive association between reindeer and lemmings in snow-bed habitats (Ims *et al.* 2007). In the latter case, the underlying mechanism was thought to be a positive engineering effect of lemming moss grazing on growth of palatable herbaceous plants (Fig. 12.7; see also Oksanen *et al.* 2008). Conversely, abundant semi-domestic reindeer may have both habitat engineering and trophic effects that impact biodiversity negatively (see Section 12.3.3.4).

An influential indirect facilitation effect in tundra food webs is the well-documented link between the lemming cycle and the breeding success of ground nesting birds (Bety *et al.* 2001, 2002). In lemming peak years, predators concentrate on lemming prey, and, as a consequence, predator pressure on geese and shorebirds relaxes, and they breed successfully. In contrast, in subsequent years, when the lemming population crashes, predators such as Arctic foxes, which have become numerous during the lemming peak, switch to prey on the eggs and chicks of ground nesting birds. As a result, the reproductive success of geese and shorebirds drops dramatically (e.g. Summers 1986). It has been suggested that the shorebird species most sensitive to predation by Arctic foxes are limited in their distribution to areas with regular lemming peaks (Gilg & Yoccoz 2010), because they are only able to maintain viable populations due to years when the predation pressure imposed by Arctic foxes is released by high lemming abundance. This assumption is supported by the fact that the highest diversity of *Calidris* species is found to coincide with the distribution area of lemmings, although alternative interpretations of such distribution patterns are possible.

### 12.2.2.2. Ecosystem functions

#### Above- and below-ground linkages

There is growing evidence that plant functional traits (PFT) (Lavorel & Garnier 2002) might have parallel implications both for herbivores and for decomposers (Cornelissen *et al.* 2004, Diaz *et al.* 2004, Cornwell *et al.* 2008, De Deyn *et al.* 2008, Fortunel *et al.* 2009). Thus, shifts in plant community composition will likely have important cascading effects above and below ground (Wookey *et al.* 2009). Conversely, soil microbes (the 'unseen majority', as described by van der Heijden *et al.* (2008)) may have important effects on Arctic plant diversity and productivity (Wallenstein *et al.* 2007). Furthermore, in spite of the major research emphasis on above-ground plant biomass, it is clear that below-ground plant biomass generally substantially exceeds above-ground in tundra (Jackson *et al.* 1996, Chapin & Ruess 2001, Mokany *et al.* 2006, Hollister & Flaherty 2010) with root:shoot ratios of ~ 4.8-6.6.

Undoubtedly, any analysis of the structure and function of Arctic ecosystems must therefore give appropriate emphasis to below-ground biota, even where the 'functional role' of the organisms themselves is not clearly known. Microbial communities do not necessarily respond to abiotic environmental factors in the same way as 'macro-organisms'; the latter show well-established declines in diversity with increasing latitude and altitude, but this is not apparent for soil microorganisms (Neufeld & Mohn 2005, Fierer & Jackson 2006, Bjorbaekmo *et al.* 2010, Chu *et al.* 2010, Fierer *et al.* 2011, but see Geml *et al.* 2009). However, such generalizations mask potentially important specific links between plants and microbes in the form, for example, of mycorrhizal associations (see Bjorbaekmo *et al.* 2010, Timling & Taylor 2012), endophyte/endorhizal fungi (Newsham *et al.* 2009, Peters *et al.* 2011) or symbiotic nitrogen-fixers; even here, though, the diversity of Arctic mycobionts appears high (Gardes & Dahlberg 1996, Peters *et al.* 2011) and not substantially constrained by large-scale (i.e. open ocean) dispersal barriers (Geml *et al.* 2012). Host-specificity of mycorrhizal fungi in the Arctic appears to be low (Walker *et al.* 2011c, Timling & Taylor 2012; see also Dahlberg & Bültmann, Chapter 10). The dominant ectomycorrhizal (ECM) fungi also show wide ecological, and host, amplitude (Ryberg *et al.* 2009, 2011). Such 'cosmopolitan' strategies are likely clues to the success of these taxa in the Arctic.

Quantifying and understanding the links between soil biodiversity and ecosystem processes and functions remain a grand challenge globally, as well as for Arctic ecosystems. For the remainder of this section, we present examples of above- and below-ground linkages and processes in Arctic ecosystems, with specific emphasis on both C and nutrient cycling, and on energy fluxes, with their broader implications for biogeochemical and biophysical processes that link to the climate system. Examples include changes in net fluxes of GHGs, such as carbon dioxide ($CO_2$) and methane ($CH_4$), and alterations in surface roughness and albedo.

**Effects of shifts in plant communities on net fluxes of GHGs**

Global change drivers may operate directly on individual ecosystem components (e.g. producers, consumers and decomposers, and their component species), but also indirectly via responses in the other components. The timescales of responses may vary between ecosystem components (Shaver *et al.* 2000), and the question emerges whether traditional concepts of 'climax' ecosystems, or above- and below-ground processes and state variables being in equilibria, still apply. Indeed in the Arctic, where below-ground C and nutrient stocks are massive (Schuur *et al.* 2008, Tarnocai *et al.* 2009, Hugelius 2012) and have been accumulating over millennia, the potential exists for very substantial shifts in GHG budgets, with global implications in terms of the C cycle, $CO_2$ and $CH_4$ concentrations in the atmosphere, and thus the climate system. Shifts in plant communities (including treeline species, as well as the increasingly robustly documented 'shrub expansion' (see Section 12.3.3.1) and changes associated with disturbance (e.g. thermokarst or tundra fire) will lead to mismatches in above- and below-ground C stocks and fluxes. Thus the 'dynamic disequilibria' paradigm (Luo & Weng 2011) may now be a more useful framework for understanding ecosystem dynamics and coupling to the Earth System. Expressed very succinctly, however, "climate-induced ecological shifts in the plant community will affect the transfer of carbon-dioxide between biological and atmospheric pools" (Natali *et al.* 2012); in specific cases, the same assertion applies to net $CH_4$ fluxes.

Examples involving named species are few, especially from the Arctic, but changes in plant traits, with associated mycorrhizal shifts, have the potential to alter the magnitude, as well as the direction, of net $CO_2$ fluxes. Hartley *et al.* (2012) demonstrated that colonization of ericaceous heath (dominated by crowberry) by mountain birch *Betula pubescens* in the mountain birch forest-tundra heath ecotone in sub-Arctic Fennoscandia would likely result in a net loss of C to the atmosphere, even though the mountain birch forest is more productive than the heath (Fig. 12.10). It was thought that high plant (tree) activity in mid-season stimulates the decomposition of older soil organic matter (SOM) through so-called rhizosphere 'priming' (Kuzyakov 2002), and that this may relate to a shift from the ericoid mycorrhizal status of the heath, toward ECM dominance beneath birch; the latter resulting in more efficient decomposition of SOM. The net result of these changes in C stock might be a release of $CO_2$ to the atmosphere, possibly resulting in a positive contribution to global warming. The study supports the assertion of Read *et al.* (2004) that symbioses control nutrient cycles, productivity, species composition and functioning of heathland and boreal ecosystems. In a related study, Ryberg *et al.* (2009) concluded that the low host-specificity of ECMs in alpine cliff locations (c. 300-490 m in elevation above the previous study, but in the same region) is "likely to be able to facilitate the succession of the alpine tundra to subalpine forest by serving as mycorrhizal partners for establishing pioneer trees." This illustrates the potential interdependence of plants and their symbionts when individual species or communities are shifting, and the potential consequences for ecosystem C balance (see Hogberg & Read 2006). However, much more research is needed in order to understand and model the processes robustly, as well as to identify the microbial 'actors' involved, and whether ECMs are associated with specific rhizobacteria (see e.g. Courty *et al.* 2010, Hrynkiewicz *et al.* 2010), including 'mycorrhization helper bacteria' (Aspray *et al.* 2006).

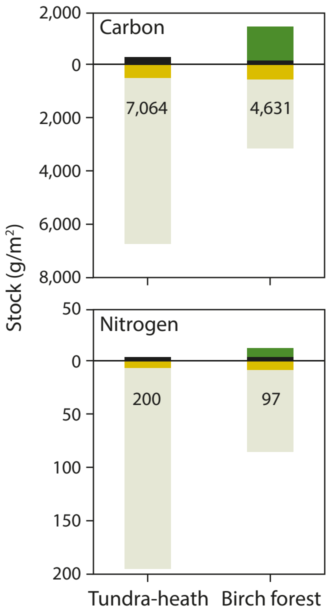


**Figure 12.10.** C and N storage in two ecosystems. The stocks are divided into above-ground tree biomass (green fill), above-ground shrub biomass (black fill), roots (yellow fill) and soils down to the underlying parent material (white fill). Above-ground stocks are shown above the x-axis; below-ground stocks are shown below the x-axis (from Hartley *et al.* 2012).

The on-going Arctic greening, with its apparently strong component of increasing deciduous shrub abundance and height (Section 12.3.3.1), also raises the prospect of complex cascading effects on physical environment, biotic processes and interactions, and links with the broader earth system (Fig. 12.11). Our understanding of these cascades and their feedback implications for energy budget and climate relies heavily on a few local- to regional-scale field campaigns (Thompson *et al.* 2004, Beringer *et al.* 2005, Sturm *et al.* 2005a, 2005b) and modelling studies (McFadden *et al.* 2001, Loranty *et al.* 2011, Bonfils *et al.* 2012, Pearson *et al.* 2013).

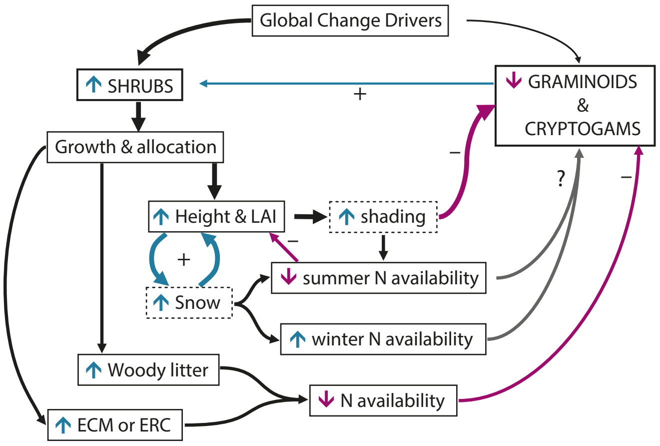


**Figure 12.11.** Ecosystem cascades and feedbacks resulting in an increase in deciduous shrubs and a decline in both graminoids and cryptogams (mosses and lichens) in response to increasing warmth and duration of the growing season in Arctic tundra. Note that stronger responses to climate drivers among deciduous shrub species result in a positive feedback between increasing height and leaf area index (LAI) and increased trapping of snow. Changes in the depth, duration and both physical properties and chemical composition of the snowpack can have either positive or negative impacts on N availability through altering soil thermal and moisture regime. Increased height and LAI of shrubs will likely have a negative impact on graminoids and cryptogams through shading effects. Furthermore, increased prevalence of species with ectomycorrhizas (ECM) or ericoid mycorrhizas (ERC) will likely decrease nutrient availability to other species, with further negative consequences. Increases in the proportion of low-N, but high lignin woody litter (leaf and stem litter of woody species associated with increasing shrub dominance) will also tend to reduce N availability (from Wookey *et al.* 2009). For clarity, the figure does not address herbivory directly; this is discussed in the text.

Although increasing shrub height and canopy density is likely to trap more snow and reduce sublimation losses, this process depends on regional snow availability and distribution patterns in the landscape, as well as on vegetation structure (McFadden *et al.* 2001, Liston *et al.* 2002). The implications for surface energy budget and the partitioning of net radiation into ground, latent and sensible heat fluxes (particularly during late winter and spring) also depend on whether snow entirely covers the vegetation, or whether branches protrude substantially above the snow. Using an Earth System Model, Bonfils *et al.* (2012) determined that taller and aerodynamically rougher shrubs lower the albedo (reflectance) earlier in the spring than short shrubs, and they also transpire more ($H_2O$ vapor) following bud-burst; both factors contribute to regional warming. Indeed, the shrub expansion can accentuate the 'polar amplification' of climate change (Serreze *et al.* 2000, Chapin *et al.* 2005, Bhatt *et al.* 2010).

Although still challenging to quantify and model, albedo effects are relatively well-understood compared with the implications of increased 'shrubiness' in terms of regional snow depth and duration and soil thermal regimes throughout the year (Blok *et al.* 2010, Lawrence & Swenson 2011, Bonfils *et al.* 2012). These are, however, critical factors influencing ecosystem C balance through their influence on soil biological activity (Sturm *et al.* 2005b, Cahoon *et al.* 2012a). Sturm *et al.* (2005b) highlighted that shrub expansion on the low Arctic North Slope of Alaska, with associated increases in depth of winter snow, would increase substantially the days when soils beneath the snow remain warm enough (down to -6 °C, or even lower) to support continued biological activity; this has the potential to increase plant-available nitrogen (N) during the thaw period (Fig. 12.11), further supporting shrub growth. Further, Weintraub & Schimel (2005) hypothesized that the interplay between N and C cycling and shrub expansion has the potential to increase C sequestration because wood has the highest C:N ratio of any plant tissue and decomposes slowly. Cornelissen *et al.* (2007) concur that "the ongoing warming-induced expansion of shrubs with recalcitrant leaf litter across cold biomes would constitute a negative feedback to global warming", although they caution that this negative feedback has to be evaluated against any direct warming-related increases in decomposition rate (and therefore, potentially, nutrient availability), a phenomenon that is well-documented (Rustad *et al.* 2001). Whether 'shrubification' alters the fire-susceptibility of plant communities also warrants serious attention (Higuera *et al.* 2008, 2011), especially as wild-fires have profound ecological consequences not just for vegetation and wildlife, but also for surface energy budget, permafrost and C cycling, as dramatically illustrated by the Anaktuvuk River tundra fire of 2007 in low Arctic Alaska (Jones *et al.* 2009, Mack *et al.* 2011, Rocha & Shaver 2011b).

'Shrub-related' changes in soil physical conditions, as well as mycorrhizal status, have major implications for soil microbial communities and their functioning, and these will be superimposed upon the direct responses of soil microbes to climate change drivers. Wallenstein *et al.* (2007) compared the bacterial and fungal community structure of tussock, intertussock and shrub organic and mineral soils at Toolik Lake, low Arctic Alaska. They found that shrub soils were consistently dominated by Proteobacteria, while tussock and intertussock soils were dominated by Acidobacteria. It was concluded that shrub soils contained an active, bioavailable C fraction, while tussock and inter-tussock soils were dominated by more recalcitrant substrates for microbes. This result might appear at odds with Weintraub & Schimel's (2005) and Cornelissen *et al.*'s (2007) suggestion that shrub litter is recalcitrant, but subtler rhizosphere and mycorrhizal processes, such as rhizosphere 'priming' (see above and Hartley *et al.* 2012) may also be at play (as noted by Clemmensen *et al.* 2006). Thus, several shrub species, with their associated ECMs, may function similarly to mountain birch in 'priming' organic matter decomposition (see Hartley *et al.* 2012, as discussed above) and accelerate C release from soils. The net effect on ecosystem $CO_2$ fluxes will depend on both rates of primary production and decomposition (De Deyn *et al.*

2008, Cahoon *et al.* 2012a), and the results of a long-term nutrient addition experiment in low Arctic Alaskan tussock tundra (Mack *et al.* 2004) caution against the assumption that increased plant productivity necessarily means greater ecosystem-level C sequestration.

The actual species involved in the shrub expansion will likely also play a significant role. The key genera are *Betula* (birch), *Salix* (willow) and *Alnus* (alder), and there are regional contrasts in the way the shrub expansion is expressed (Myers-Smith *et al.* 2011a). Although these are all deciduous shrubs, their stature varies both within and among genera, as, potentially, does their interaction with snow (Sturm *et al.* 2005a). A key functional contrast may also exist between *Alnus* and the other shrub genera; the former is able to fix N in symbiosis with the actinomycetous genus *Frankia* (Huss-Danell 1997), and is likely also strongly dependent on ECM symbionts to meet the increased phosphorus (P) demands of nodule formation (Gentili & Huss-Danell 2003). This tripartite symbiosis undoubtedly has major implications for ecosystem nutrient recycling and C fluxes, but has not been explicitly addressed in the context of the pan-Arctic shrub expansion.

#### Effects of plant community shifts on biophysical processes

Several studies indicate that the Arctic 'shrubification' will likely have negative consequences for cryptogams (mosses, lichens, liverworts and hornworts; Cornelissen *et al.* 2001, van Wijk *et al.* 2004, Stewart *et al.* 2011, Elmendorf *et al.* 2012, Lang *et al.* 2012; see also Daniëls *et al.*, Chapter 9 and Dahlberg & Bültmann, Chapter 10). The broader consequences of a shift in plant community composition for ecosystem physical properties (e.g. soil temperature and moisture status, and active layer depth) and function (i.e. nutrient cycling, N fixation and trace gas fluxes) remain unclear (Cornelissen *et al.* 2007, Stewart *et al.* 2011, Street *et al.* 2012). However, we do know that key bryophyte genera (e.g. *Sphagnum*) are 'peat-forming' and play a key role in C balance (Cornelissen *et al.* 2007). For example "*Sphagnum*-dominated peatlands head the list of ecosystems with the largest known reservoirs of organic carbon" (Hajek *et al.* 2011). Van Breemen (1995) refers to *Sphagnum* as an 'ecosystem engineer' through its ability to outcompete vascular plants for light, through its influence on peat moisture content and thermal status, and because of its resistance to decay. The explanation for the latter remains the subject of active research, but the synthesis of both recalcitrant polyphenols and cell-wall pectin-like polysaccharides ('sphagnan'), as well as the strong acidification of the environment, are implicated (Hajek *et al.* 2011). Clearly, the decay resistance of *Sphagnum* litter has profound implications for C sequestration, soil thermal and moisture regimes, and interactions with vascular plants (Keuper *et al.* 2011). The role of bryophytes, more generally, as modifiers of soil thermal regime (and biological processes) and surface energy budget has been modeled by Beringer *et al.* (2001) and demonstrated experimentally by Gornall *et al.* (2007). Furthermore, both bryophytes and lichens are associated with cyanobacterial N-fixing communities (Gavazov *et al.* 2010), but their broader role as the main pathway for new N supplies to tundra ecosystems is often overlooked. Turetsky *et al.* (2012) emphasize the functional role of mosses more generally in northern ecosystems, noting the need for studies that increase our understanding of slow ecosystem processes that "play out over centuries – permafrost formation and thaw, peat accumulation, development of microtopography." Generally, cryptogam functional ecology merits much more research attention in the Arctic (see Daniëls *et al.*, Chapter 9).

#### Effects of permafrost thaw

Permafrost thaw (through both active-layer deepening and thermokarst) has the potential for far-reaching consequences for ecosystem structure and function, as well as for down-stream processes in surface waters (see Wrona & Reist, Chapter 13). Tarnocai *et al.* (2009) estimate that permafrost soils contain ~ 50% of the estimated total global below-ground organic C pool. This C is not sequestered in a stable or safe site: deepening of the active layer will alter ecosystem net C flux (both for $CO_2$ and for $CH_4$), both by bringing 'old' soil organic matter into contact with actively metabolising microbial communities, and also through direct effects of changes in the thermal and moisture regimes in the active layer itself (Christensen *et al.* 2003, Schuur *et al.* 2008, 2009). In a recent modeling study, Koven *et al.* (2011) report that inclusion of permafrost in coupled models changes both the magnitude and direction of net C flux – from sink to source – at high latitudes (> 60° N). They emphasize that a major constraint for modeling is quantifying and understanding fine-scale controls on hydrological processes (at plot, hillslope and headwater catchment scale) that strongly modulate $CO_2$ and $CH_4$ emissions from soils (Fig. 12.12).

Permafrost thaw will influence emissions of $CO_2$ and $CH_4$ from soils and sediments directly through changes in temperature, oxygen status and the amount of organic material available for decomposition or fermentation, and also indirectly. Changes in microbial communities (Mackelprang *et al.* 2011) and vegetation in areas affected by permafrost thaw (due often to changes in hydrological status and the mixing of mineral and organic soils) will also influence net GHG fluxes. In a 'natural gradient' study in the sub-Arctic alpine tundra of the northern foothills of the Alaska Range, three sites were used to represent stages in the process of permafrost thawing and thermokarst over several decades (Schuur *et al.* 2007, 2009). The study recorded substantial shifts in plant community composition, from graminoid-dominated tundra in the least disturbed (and cold) site to shrub-dominated tundra at the most subsided (and warm) site (a feature also noted in Yamal, Russia; Walker *et al.* 2009). In spite of demonstrating the highest productivity, the shrub-dominated site showed a net loss of $CO_2$ to the atmosphere. Further studies are required on the consequences of permafrost thaw for net GHG emissions to the atmosphere, but it is logical to assume that a net release is likely, at least until net primary productivity 'catches up'.

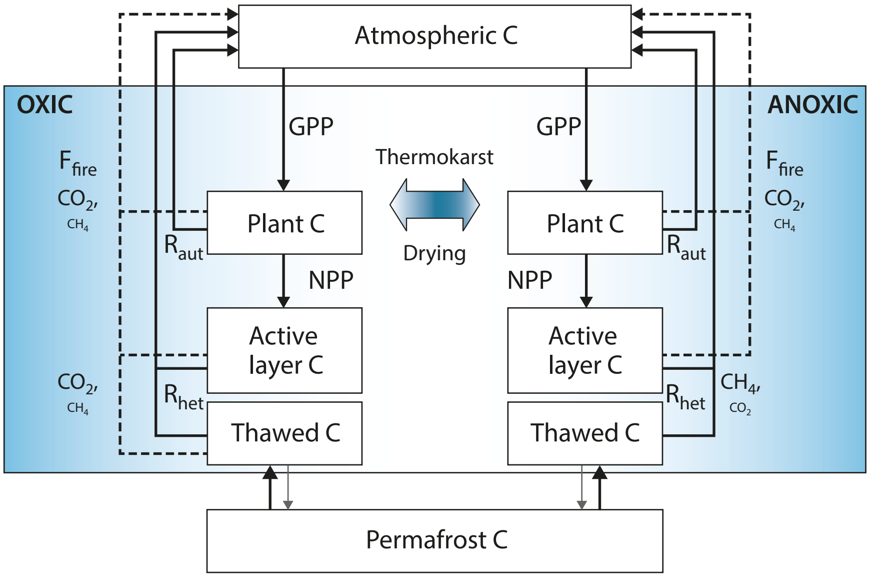


**Figure 12.12.** Conceptual diagram of the effect of permafrost thawing on climate. Permafrost C, once thawed, can enter ecosystems that have either predominantly oxic (oxygen present) or predominantly anoxic (oxygen limited) soil conditions. There is a gradient of water saturation on the landscape that ranges from fully oxic to fully anoxic, and ecosystems can become drier as permafrost thaws (shrinking lake area, drying wetland/peatlands), or wetter (thermokarst lakes). Soil oxygen status is a key determinant of the rate and form of C loss to the atmosphere. Decomposition in oxic soils releases primarily $CO_2$, whereas anoxic decomposition produces both $CH_4$ and $CO_2$, but at a lower total emission rate. Fire releases mostly $CO_2$, but also some $CH_4$, and can burn upland and wetland ecosystems, although burning of organic soils at depth is restricted in wetter environments unless there is a severe drought. These emissions of C through decomposition are offset by gross and net primary productivity (photosynthesis and net plant growth). Under some local conditions, it is possible that C will enter the permafrost pool (grey arrows), although this total amount is small relative to C that is expected to thaw from permafrost as a result of climate change. Abbreviations: C = carbon, $CH_4$ = methane, $CO_2$ = carbon dioxide, F = fire, carbon flux from fire, GPP = gross primary productivity, NPP = net primary productivity, $R_{aut}$ = autotrophic respiration, $R_{het}$ = heterotrophic respiration (from Schuur *et al.* 2008).

Shifts in hydrological conditions, and associated shifts in plant communities, can also have substantial consequences for $CH_4$ emissions, as $CH_4$ formation and emissions are modulated by individual plant species. In high Arctic NE Greenland (Zackenberg) Ström *et al.* (2003) found the sedges Arctic cotton-grass *Eriophorum scheuchzeri* and outspread tundra grass *Dupontia psilosantha* differed in release rates of acetate, which was hypothesized to be a precursor of $CH_4$ formation. The overall message is that key processes in the global C cycle (and the climate system) are not independent of the specific species involved.

### 12.2.2.3. Linking trophic interactions and ecosystem function

Recent studies have demonstrated an explicit link between trophic interactions and ecosystem function relating to GHG; specifically, they highlight the potential interactions that may arise between climate change drivers and the responses of biota across more than one trophic level (including pathogens). For example, climate and herbivores represent potential dual controls of vegetation communities and major ecotones in Arctic and alpine ecosystems (Section 12.2.2.1). For C cycling, however, major research emphasis on quantifying and understanding the abiotic controls on primary production and decomposition has resulted in a systematic neglect of the ecological role of biotic factors, including trophic interactions, consumers and pathogens.

For invertebrate and vertebrate (mammalian and avian) herbivores, there is growing evidence of links between trophic interactions and ecosystem-level processes such as net $CO_2$ exchange. In a factorial warming × herbivore (muskox and caribou) exclusion experiment in low Arctic W Greenland, Cahoon *et al.* (2012b) showed that removal of the herbivores resulted in dramatic increases in shrub cover, ecosystem photosynthesis and a c. threefold increase in net C uptake. Warming accentuated these responses, but only when herbivores were absent. Concurrently, there was no clear indication of a change in soil respiration, so the conclusion is that herbivory constrains shrub productivity and limits C sequestration in this region. Similarly, Sjögersten *et al.* (2011) found that excluding grazing barnacle geese *Branta leucopsis* turned plots from sources to sinks of $CO_2$ at a high Arctic wet moss meadow in Svalbard, with associated changes in above-ground biomass and the proportion of vascular plants to bryophytes, but no effects on $CH_4$ fluxes, the total litter C pool or the soil C concentration. A related study (Sjogersten *et al.* 2012), with both grazing manipulation and experimental warming, revealed that high grazing intensity combined with warming reduced C storage and promoted decomposition both above and below ground.

Finally, milder winters can have unexpected effects on trophic interactions, with implications for ecosystem functions such as C cycling. The well-documented link between geometrid moth (*Operophtera brumata* and *Epirrita autumnata*) outbreaks and mild winters (Tenow & Bylund 2000, Jepsen *et al.* 2008, 2009, 2011), and the dramatic defoliation of mountain birch and corresponding shifts in the understory vegetation at the forest-tundra ecotone in northern Fennoscandia (Jepsen *et al.* 2013), has recently been shown to have major consequences for ecosystem C balance (Heliasz *et al.* 2011). Another scenario of winter warming in the Arctic might involve increases in depth (and possibly duration) of winter snow-pack. Olofsson *et al.* (2011), using snow fences to increase snow cover in sub-Arctic Swedish Lapland, found that plant biomass actually decreased owing to an outbreak of a host-specific parasitic fungus, *Arwidssonia empetri*, which killed the majority of the shoots of the dominant plant species, crowberry. Thus plant diseases can alter, and even reverse, the effects of a changing climate on tundra C balance. Outbreaks of both defoliating and parasitic fungi may become more frequent and widespread in the future, also in the Arctic.

## 12.3. TRENDS

In Section 12.2 we reviewed our current understanding of how climate and other abiotic pressures and disturbances interact with the structure and functions of tundra ecosystems as to shape biodiversity based on spatial analogues, experiments and models. In this section, we review observations of temporal trends in tundra ecosystems and the extent to which they can be attributed to specific drivers of change. Both the current status of terrestrial Arctic biodiversity and how it has been recently changing ought to be interpreted in light of its historical context and long-term trends (Section 12.3.1). Thus, even though our main purpose is to assess recent trends in ecosystem structure and function relative to contemporary anthropogenic drivers (Sections 12.3.2 and 12.3.3), it is generally important to keep in mind that non-equilibrium processes may also be involved, such as long-term recoveries from historical events. Finally, while we focus on trends in biodiversity at levels of communities or species guild, we also consider individual (keystone) species for which trends are expected to have knock-on effects on many other species, and the overall structure and functions tundra ecosystems.

### 12.3.1. Historical context

#### 12.3.1.1. Environmental history and paleogeography

Present biodiversity patterns of Arctic terrestrial ecosystems became established during the Quaternary period, which spans the past c. 2.4-2.6 million years (see Section 2.3 in Payer *et al.*, Chapter 2). The Quaternary has been characterized by numerous fluctuations between globally cooler and warmer conditions with a periodicity of c. 40,000 years. During the cold intervals, ice sheets accumulated on the northern continents, especially over northwestern Eurasia and northern North America. For the last 0.8-1.0 million years BP these fluctuations have been of larger amplitude than previously and have had a predominant periodicity of c. 100,000 years (Imbrie *et al.* 1984). This period is often referred to as the Quaternary Ice Age, with the cold intervals referred to as glacial stages, and the warmest intervals, with global climatic conditions broadly similar to those of the recent historic past, referred to as interglacial stages. These large climatic fluctuations are linked to major changes in the geography of the Arctic. Because of the accumulation of large volumes of ice in the continental ice sheets, global sea level was lowered by 100-120 m during glacial maxima (Fairbanks 1989), resulting in an extensive area of land in the region of the Bering Sea between Alaska and eastern Siberia, referred to as Beringia (Hopkins 1967, Hopkins *et al.* 1982). This region has been of considerable importance in relation to the history of Arctic biodiversity (Hultén 1937). During the glacial stages, the North Sea basin of NW Europe was also exposed, as well as large areas of additional land north of eastern Siberia. Although the coldest intervals during glacial stages occupy only perhaps 10% of the last 0.8-1.0 million years, glacial stages *sensu lato* account for > 85% of this time, while interglacials occupy < 15%. Thus, for most of the past million or so years, the geography of the Arctic has been very different from that with which we are familiar, with substantial ice sheets over northern North America and the western half of Eurasia, sea level markedly lowered and no connection between the North Pacific and the Arctic Ocean.

As a result, for much of the past one million years the extent of terrestrial ecosystems has been much reduced in the high Arctic and biota have been confined to nunataks during glacial stages. A similar displacement by ice occurred over much of northern continental North America and NW Eurasia, leaving central and eastern Siberia together with Beringia as the only extensive areas at Arctic latitudes supporting terrestrial ecosystems during glacial stages. On the other hand, the much colder climatic conditions of glacial stages have allowed many species that are today restricted to higher latitudes to extend their distributions to much lower latitudes. These same climatic conditions also led to the extension of permafrost to much lower latitudes, especially in Europe (Dawson 1992, van Huissteden *et al.* 2003). It would, therefore, be inappropriate to view the effects of Quaternary history on Arctic biodiversity only from an Arctic perspective. Thus the geographical scope of this discussion includes those areas of the boreal and north temperate zone that supported characteristically Arctic biota during glacial stages.

#### 12.3.1.2. Paleodiversity of Arctic terrestrial ecosystems

The expansion of cold Arctic habitats provided opportunities for the evolution in the Arctic of taxa adapted to these conditions (Lister & Sher 2001, Abbott & Bro-

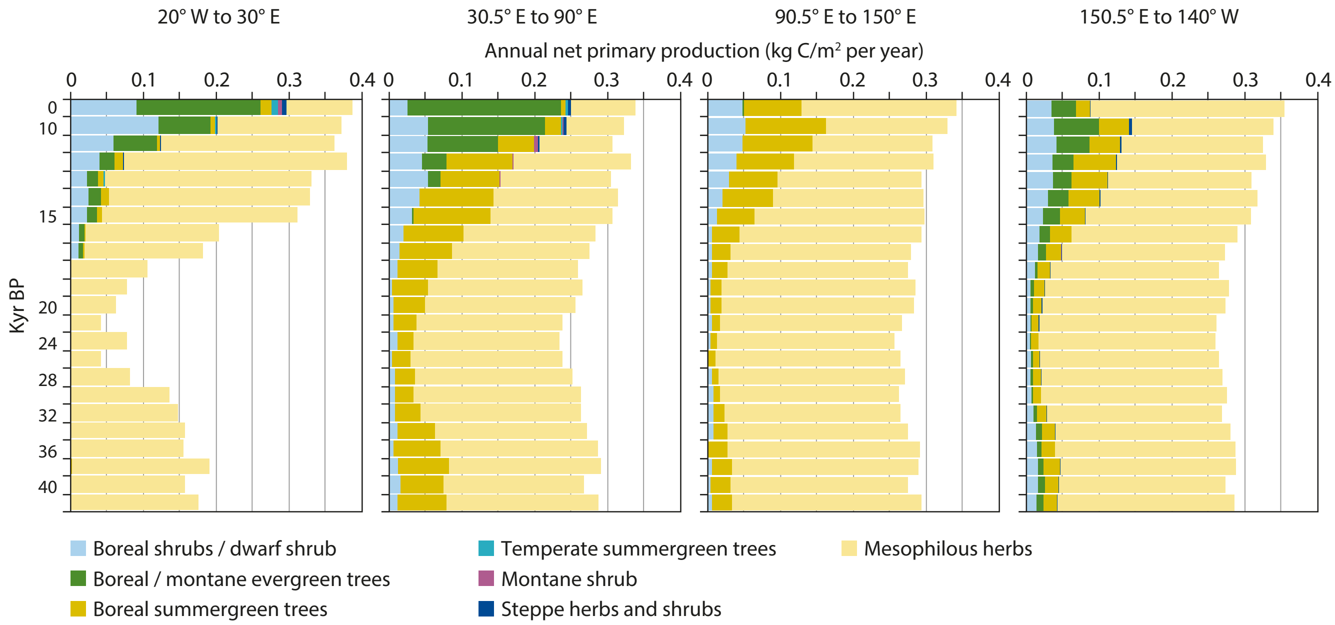


**Figure 12.13.** Simulated annual net primary productivity of 11 aggregate plant functional types during the later part of the last glacial stage and the early Holocene (42,000-10,000 years BP) for northern Eurasia and Beringia. Each panel represents a longitudinal section north of 60.5° N. For details of the methods used to make these simulations, see Allen *et al.* (2010).

chmann 2003, Harington 2008). Plant species evolved from shrubs and herbs that occupied open areas of the northern forest and from alpine species that migrated northward along mountain ranges (Murray 1995). Newly evolved mammalian species contributed to a long-term increase in biodiversity in the region (Lister 2004). Recently, this trend has reversed. Iconic species like woolly mammoth *Mammuthus primigenius*, woolly rhinoceros *Coelodonta antiquitatis* and other 'megafauna' are now extinct (Lister & Sher 1995, Stuart *et al.* 2004, Stuart 2005), having failed to survive rapid environmental changes during the transition to the Holocene (Lister & Stuart 2008). While the underlying causes of these extinctions, and especially the extent to which humans played a part, remain a matter of debate (Barnosky *et al.* 2004, Stuart 2005, Guthrie 2006, Nogués-Bravo *et al.* 2008), the loss of these species represents a (geologically) highly recent decrease in Arctic biodiversity. Furthermore, the extinction of these and other large herbivores may have had long-term impacts upon many other components of Arctic ecosystems (Zimov 2005, Johnson 2009).

These cold-adapted large vertebrates had maximum distributional extents during glacial stages (Stuart *et al.* 2004). Extant Arctic and sub-Arctic species, such as reindeer/caribou, muskox and Arctic fox, were also present in the faunas characterized by the now extinct species. So too were species that today are associated with steppe or prairie ecosystems, notably saiga antelope *Saiga tatarica* and horse *Equus ferus*. Paleovegetation evidence indicates that these extensive ecosystems of glacial stages were composed of mixtures of plant species principally found today either in tundra or steppe ecosystems, often with a predominance of grasses Poaceae and sedges Cyperaceae accompanied by a wide variety of mesic forbs (Edwards *et al.* 2000, Anderson *et al.* 2004). The macrofossil evidence that so far has been studied indicates that these ecosystems likely comprised a mosaic of tundra-like and more steppic communities, related to topographic and climatic gradients, and that these communities also were relatively diverse compared with many contemporary tundra communities (Edwards & Armbruster 1989, Goetcheus & Birks 2001, Kienast *et al.* 2005, Zazula *et al.* 2006a, 2006b).

The presence of a large biomass of herbivores in the glacial stage ecosystem raises the so-called productivity paradox: how could there have been enough primary production to have supported such a diverse fauna? A recent study using a dynamic vegetation model (Smith *et al.* 2001, Miller *et al.* 2008) to simulate the past vegetation cover of northern Eurasia and Beringia, north of 35° N and for the period 42,000-10,000 years BP, shows a higher productivity of mesic herbs in treeless northern regions during much of the last glacial stage than in modern tundra, but a reduced productivity of shrubs and dwarf shrubs (Fig. 12.13; Allen *et al.* 2010). These findings are in broad agreement with the observation that ecosystems dominated by palatable forbs and grasses are able to support more grazers than are those dominated by woody plants, such as modern shrub-tundra (Guthrie 1982). These glacial ecosystems represent a distinct biome that does not exist today, except for potential small-scale analogues in the continental interiors of Alaska, Yukon and Siberia (Edwards & Armbruster 1989, Zazula *et al.* 2006a), but that was often extensive during the Quaternary period, reaching its greatest extent during glacial stages and most probably being restricted to eastern Siberia during interglacial stages prior to the Holocene (Sher 1997). This biome is most often referred to as 'steppe-tundra', reflecting the mixed composition of its biota: steppe and tundra biomes would have become contiguous over large areas with the virtual disappearance of boreal forest under the dry, cold glacial conditions (Edwards & Armbruster 1989, Guthrie 2001, Walker *et al.* 2001b, Elias & Crocker 2008).

Whereas the steppe-tundra biome may often have been extensive in the past, it seems likely that some components of the modern tundra biome are more extensive today than they have been during most of the past 0.8-1.0 million years. Discontinuously-vegetated tundra and polar desert are inferred to have occupied some drier regions of the high Arctic during glacial stages, and also to have occurred on nunataks, but their extent nonetheless was less than today. Tussock-tundra (dominated by cotton grasses *Eriophorum* spp.) and shrub-tundra communities that are today characteristic of more mesic, continuously-vegetated areas were not important components of the glacial-stage biomes. Pollen data show these communities expanding to replace steppe-tundra with the onset of interglacial conditions in Beringia (Oswald *et al.* 2003, Anderson *et al.* 2004).

Many species considered today to be typical dry tundra species were components of the very different steppe-tundra biome for most of their evolutionary history. Whereas, for much of the Quaternary, plant species requiring more mesic conditions (e.g. dwarf birch, shrub birch *Betula glandulosa* and cotton grass) would have been restricted to locally favorable habitats, species that are adapted to dry, steppic habitats (e.g. saiga antelope) and Arctic steppe plants are geographically much more limited today than during glacial stages (Murray *et al.* 1983, Edwards & Armbruster 1989). The niches of other species, however, are such that they were widely distributed in both glacial and interglacial ecosystems (e.g. reindeer/caribou). Thus, over the past 0.8-1.0 million years, many species' geographical distributions and populations are likely to have been reduced and/or fragmented during interglacial stages, whilst for other taxa the reverse is probable.

The early Holocene (c. 11,400-8,000 years BP) may have been an interval of extreme range reduction for Arctic terrestrial taxa with tundra affinities (e.g. Kraaijeveld & Nieboer 2000). In many regions, although not all, boreal forests extended to higher latitudes than today (MacDonald *et al.* 2000, Payette *et al.* 2002), responding to and also amplifying the warmer climatic conditions (Gallimore *et al.* 2005). Globally the area of tundra has been estimated to have been reduced by ~ 20% compared to the present (Callaghan *et al.* 2005). This is likely to have represented significant bottlenecks for some taxa, reducing Arctic biodiversity at least regionally, and perhaps even globally, especially at the intra-specific level. For example, a marked reduction in genetic diversity in muskoxen is dated to between c. 21,000 and 5,000 years BP (MacPhee *et al.* 2005). This reduction in genetic diversity is associated with regional extinction of the species across much of Eurasia during this interval. A well-documented global extinction of an essentially Arctic species during the middle Holocene is that of woolly mammoth, the last known population of which went extinct on Wrangel Island ~ 4,000 years BP (Vartanyan *et al.* 1993). On the other hand, the more favorable mid-Holocene climatic conditions are also likely to be implicated in greater productivity at very high latitudes, as reflected in the colonization of high Arctic islands by reindeer/caribou (Gravlund *et al.* 1998) and the extension of the range of muskoxen to N and NE Greenland (Bennike & Andreasen 2005, Campos *et al.* 2010), both of which apparently date from the middle Holocene.

Thus, in the context of recent geological history, the present biodiversity of the Arctic and its ecosystems is relatively low. Cold-adapted biota, including many species that today are restricted to the Arctic, were more widely distributed during much of the Pleistocene. The repeated changes between glacial and interglacial periods may have promoted an increase in Arctic biodiversity through allopatric[3] speciation, promoted by range fragmentation and dispersal-related founder effects. The nature of the climatic transition to the Holocene, and of the warmer climatic conditions in high northern latitudes during the early and middle Holocene, however, appears to have been uniquely deleterious in its impacts upon Arctic biota, leading to regional and even global extinctions of some Arctic taxa. Seen against this background, current global climatic warming poses a severe threat to the maintenance of the present, already impoverished, biodiversity of the cold-adapted Arctic biota.

## 12.3.2. Contemporary trends in drivers of change

### 12.3.2.1. Climate change

Climate in the Arctic is currently warming rapidly. In the five years following the Arctic Climate Impact Assessment (ACIA 2005) the annual temperature anomalies averaged over a pan-Arctic domain (60-90° N) exceeded values measured since 1880 and were the warmest five years in the entire record (Walsh *et al.* 2011). Considering a wider time frame, four of the five warmest decades of a reconstruction of the climate for the last 2000 years occurred between 1950 and 2000 (Kaufman *et al.* 2009). There is, however, considerable spatial and temporal variability in the present Arctic warming (Walsh *et al.* 2011). Warming is greatest in autumn and winter over the Arctic Ocean and adjacent areas, consistent with the recent loss of Arctic sea ice (Serreze *et al.* 2009). Summer warming is particularly strong in eastern Eurasia, the Canadian high Arctic and Greenland (IPCC 2007, NASA-GISS 2010). Some of the key manifestations of a warmer climate in terrestrial areas include: (1) later freeze-up and onset of snow cover in autumn, (2) earlier snow melt in spring (Derksen &

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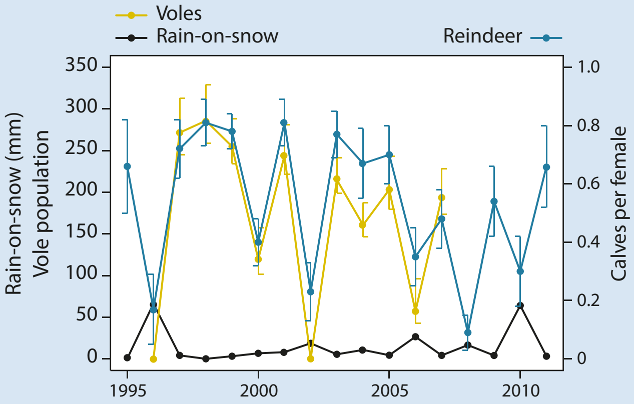
[3] Allopatric speciation is speciation that occurs when biological populations of the same species become isolated from each other to an extent that prevents genetic interchange.

## Box 12.3. Rain-on-snow (ROS) events on Svalbard

The high Arctic Svalbard archipelago harbours one of the northernmost terrestrial ecosystems of the world (74°-81° N, 10°-35° E). However, a branch of the North Atlantic Current that runs to the west of the archipelago causes mean winter temperatures to be up to 20 °C warmer than found at similar northern latitudes elsewhere.

A main climatic driver in the Svalbard ecosystem is ROS events in winter, which occur regularly due to the oceanic climate and cause icing and inaccessible pastures. Icing events have a strong impact on the population dynamics of Svalbard reindeer *Rangifer tarandus platyrhynchus* and sibling vole *Microtus levis* (Box 12.3 Fig. 1; Hansen *et al.* 2011, Stien *et al.* 2012), as well as the two other resident vertebrates, the Svalbard rock ptarmigan *Lagopus muta hyperborea* and the Arctic fox. Thus the ROS events synchronize the dynamics of the entire herbivore guild (reindeer, vole and ptarmigan) and the only predator (Arctic fox), the latter with a one year lag (Hansen *et al.* 2013). The population dynamics of the Arctic fox seem to be driven mainly by fluctuations in the density of Svalbard reindeer carcasses in late winter (Fuglei *et al.* 2003, Eide *et al.* 2012), and this causes a delayed response in the Arctic fox population dynamics to the ROS driven fluctuations observed in the reindeer population (Hansen *et al.* 2013). Variations in the Arctic fox population size have knock-on effects on the breeding success of geese (Tombre *et al.* 1998, Fuglei *et al.* 2003). Furthermore, icing is also found to impact the soil invertebrate community (Coulson *et al.* 2000).



**Box 12.3 Figure 1.** Rain-on-snow events (mm) synchronize annual estimates of sibling vole population sizes and calves per female of Svalbard reindeer (from Stien *et al.* 2012).

Brown 2012), (3) warming and thawing of permafrost, (4) increase in the frequency and severity of extreme weather events, and (5) increase in the frequency of tundra fires (IPCC 2007, Bartsch *et al.* 2010, Bhatt *et al.* 2010, Hu *et al.* 2010, Xu *et al.* 2013).

In addition to decadal temperature trends, there is widespread concern over changing patterns of precipitation (Walsh *et al.* 2011). Snow is a dominant feature of Arctic terrestrial landscapes. Snow has low thermal conductivity, which allows it to insulate the surface from large heat losses in winter, and at the same time its high albedo contributes to keeping the Arctic cold. In addition to the duration of snow cover and snow depth, the quality of the snow is an important determinant of ecosystem functioning. Over the pan-Arctic terrestrial region (excluding Greenland) snow cover duration decreased by 3.4 days per decade between 1972 and 2009 (Callaghan *et al.* 2011a). At the same time, however, snow depth has increased in some areas, notably in Eurasia. Mild spells in winter inducing freeze-thaw cycles and sometimes heavy precipitation in the form of rain-on-snow (ROS) (Rennert *et al.* 2009, Bartsch *et al.* 2010, Hansen *et al.* 2011, 2013) create either very ice-crusted snow packs or sometimes even layers of pure ice on the ground (Box 12.3). While ROS is a sufficiently regular phenomenon in the oceanic parts of the Arctic not to be defined as an extreme event, it is considered extreme for the continental parts of the Eurasian Arctic (AMAP 2011).

While climate has always fluctuated dramatically in the northern high latitudes, the warming phase underway is important in several respects. First, it is taking place at a time when the Arctic is host to large numbers of human residents (Larsen *et al.* 2010). Second, pressures for strategic access to the region, for resource exploitation and geopolitical purposes, are at an all-time high, with major implications for future energy supplies and governance regimes (AMAP 2007, AGP 2010, Smith 2010). Finally, the current warming trend began from a higher baseline mean temperature than was the case for the most recent previous warming trend at the end of the Pleistocene approximately 11,000 years BP.

### 12.3.2.2. Land-use, natural resource management and industrial development

There is no crop agriculture in the Arctic, and the major form of land-use is reindeer herding by indigenous people, mostly in Eurasia. The tundra areas in Eurasia occupied at least seasonally by semi-domestic reindeer herds are immense, even if many regions are shared with wild herds. Trends in the herding industry including changes in the size of herds have recently been reviewed elsewhere (Forbes & Kumpula 2009, Forbes 2010, Hausner *et al.* 2011, Huntington, Chapter 18) and will be mentioned only very briefly here. Reindeer management is important because the animals lie at the center of a complex web of ecosystem goods and services.

Herds constitute a critical renewable resource upon which people and wildlife depend, including predators vital to regional biodiversity (e.g. lynx *Lynx* spp., wolf, wolverine, bears and eagles). Strong predator control is often an integral part of the reindeer management regime that ultimately may result in regional extermination of top predators such as wolf (Tveraa *et al.* 2007). Due to their large numbers, reindeer exert a number of important controls on ecosystem structure and function, through their effects on vegetation and the associated guild of scavengers (see Section 12.2.2.1 and Box 12.6). Herd sizes in the Nordic countries and the Nenets portions of northern Russia have increased considerably during the last decades and are at or near historic highs (Forbes & Kumpula 2009, Forbes *et al.* 2009). In other areas of Russia, herd sizes have on the contrary declined (Vors & Boyce 2009, Huntington, Chapter 18). The best ways to manage herds and pastures is subject to political discussion (Hausner *et al.* 2011). Some authors write about overabundance of reindeer, and concerns about the sustainability of pasture use are arising (e.g. Moen & Danell 2003).

Wild ungulates such as caribou/wild reindeer, muskoxen or Eurasian elk/moose are important hunting resources for people living in tundra areas, and as such they are managed in many parts of the Arctic (see Reid *et al.*, Chapter 3 and Huntington, Chapter 18). Although wild populations usually do not reach as high densities as the semi-domestic reindeer herds, management decisions may have consequences for the ecosystem. Muskoxen have been reintroduced in several areas in Alaska and the Russian Arctic, notably on the Taimyr Peninsula, as well as in W Greenland. On Wrangel Island both muskoxen and reindeer have been introduced during the 20th century (1975 and 1950 respectively, Gruzdev & Sipko 2007a, 2007b).

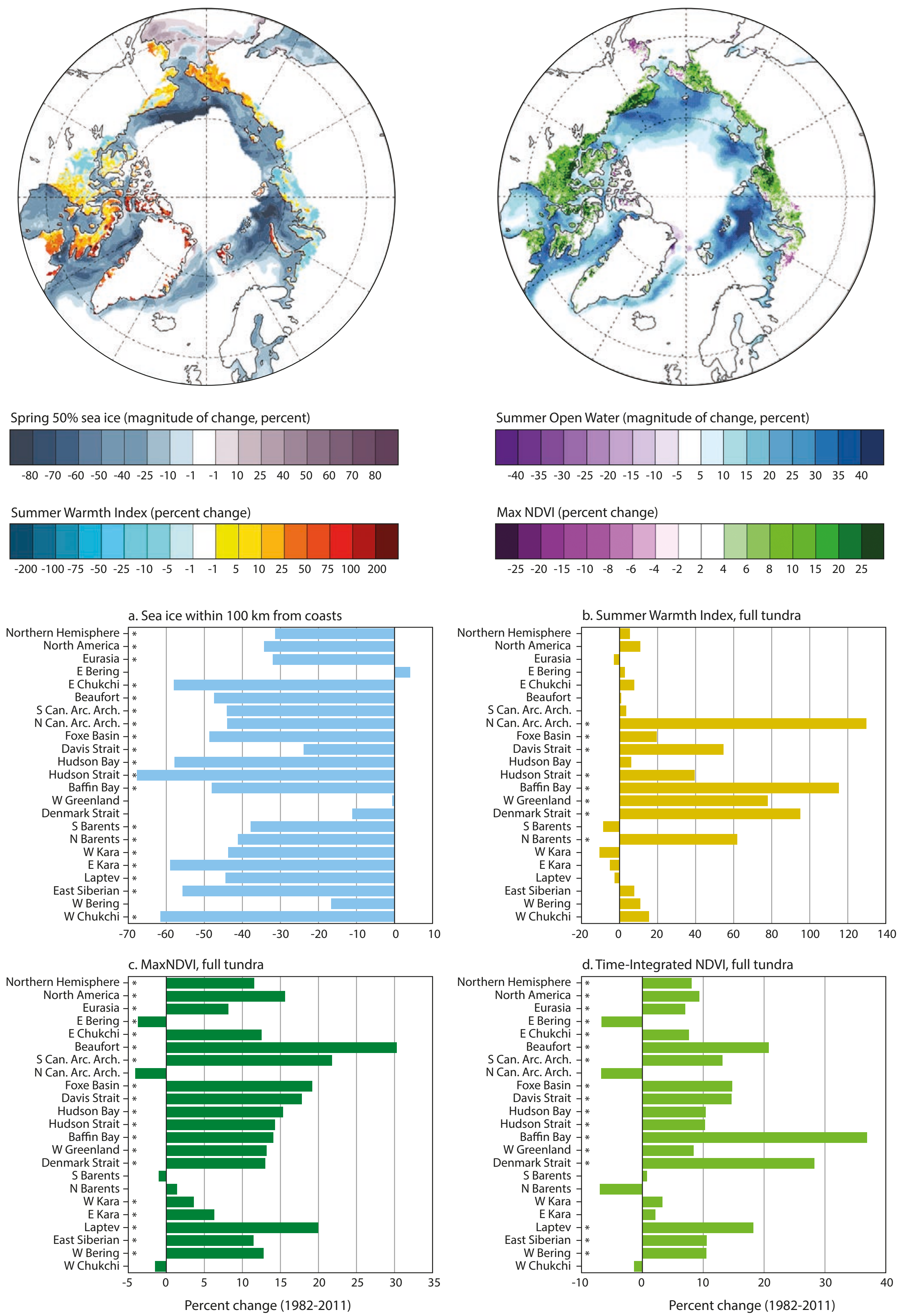
The present distribution of large-scale industrial developments is very localized (AMAP 2007, Kumpula *et al.* 2011, 2012). Onshore oil and gas extraction is concentrated on the North Slope of Alaska, Canada's Mackenzie River valley and delta regions, and in Russia within the Timan-Pechora and W Siberian basins (Nuttall & Wessendorf 2006). However, industrial development is spreading rapidly across many sectors of the circumpolar North (Walker *et al.* 1987, NRC 2003, Rasmussen & Koroleva 2003, AMAP 2007, Mikkelsen & Langhelle 2008, Kumpula *et al.* 2011). This trend is expected to continue in conjunction with a warmer climate, as existing resources become potentially easier to access and new sources become more economically viable (IPCC 2007, Smith 2010). In terrestrial ecosystems, the chief concerns surrounding industrial development are that (1) most types of human impact invariably reduce species richness in tundra vegetation and may induce vegetation transitions, and (2) the results of these impacts can persist for many decades, if not centuries (Vilchek *et al.* 1996, Forbes *et al.* 2001). However, to some extent anthropogenic mechanical disturbances resemble those resulting from natural phenomena, such as land-slides or cryoturbation, which are inherent parts of the functioning of the tundra that stimulate ecosystems dynamics (Walker 1996; see Section 12.2.1.2).

## 12.3.3. Contemporary trends in ecosystem structure and function

### 12.3.3.1. Climate change and trends in vegetation

Remote sensing studies show that the NDVI (see Box 12.1) has increased across much of the Arctic between 1982 and 2008 (Fig. 12.14; Bhatt *et al.* 2010), indicating increased productivity (Raynolds *et al.* 2006). The latest and most robust NDVI dataset shows that between 1982 and 2012 about a third of the Pan-Arctic has substantially greened, < 4% browned and > 57% did not change significantly (Xu *et al.* 2013). The greatest changes occurred in N Alaska and on the Beaufort Sea coast, whereas some regions along the Bering Sea and Chukchi Sea coasts show a decrease in NDVI. The increase in NDVI was correlated with sea ice declines and warmer summer temperatures (Raynolds *et al.* 2008, Bhatt *et al.* 2010), as well as with a prolongation of the growing season (Xu *et al.* 2013). Vegetation seasonality in the Arctic region has had a 7° latitudinal shift equatorward during the last 30 years (Xu *et al.* 2013). The observed changes in NDVI are attributed to increased growth of shrubs, as evidenced in Alaska, and to increased plant density in the high Arctic (Bhatt *et al.* 2010). Using a newly developed regression model between NDVI and above-ground tundra plant biomass (Epstein *et al.* 2012), Raynolds *et al.* (2012) show that biomass has increased most in southern bioclimate subzones (E to C). Results also showed that heterogeneity was high across regions and vegetation types. Changes in NDVI, and thus in plant biomass and phenology, are however not caused by climate alone but are a result of multiple ecological and social factors that affect primary tundra productivity (Walker *et al.* 2009). For example, studies on the Yamal Peninsula in Russia showed no strong spatial correlation between summer warmth and NDVI. In fact, much of Yamal has greener vegetation than expected based on the circumpolar correlation of temperature and NDVI, and much intra-regional variation in NDVI was associated to landscape structure and land-slides (Walker *et al.* 2009).

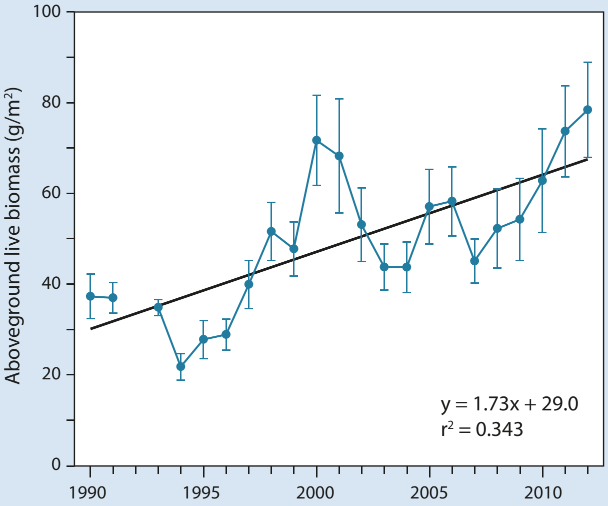
Increased plant productivity with climate warming has been documented at high latitudes, notably for a high Arctic heath and wet sedge tundra on high Arctic Ellesmere Island, Canada (Hudson & Henry 2009) between 1981 and 2008. On high Arctic Bylot Island, Canada, plant biomass in wetlands at the peak of summer production has increased by 123% over the last 23 years (Box 12.4; Gauthier *et al.* 2013). Changes in productivity are often associated with changes in plant community composition. Hence, on Herschel Island, the cover of grasses and dwarf shrubs increased at the expense of lichens in some upland habitats (Kennedy *et al.* 2001). In the tundra heath of Ellesmere Island, the productivity of evergreen shrubs and mosses increased, whereas deciduous shrubs,


Spring 50% sea ice (magnitude of change, percent)
-80 -70 -60 -50 -40 -25 -10 -1 -1 10 25 40 50 60 70 80
Summer Open Water (magnitude of change, percent)
-40 -35 -30 -25 -20 -15 -10 -5 5 10 15 20 25 30 35 40
Summer Warmth Index (percent change)
-200 -100 -75 -50 -25 -10 -5 -1 -1 5 10 25 50 75 100 200
Max NDVI (percent change)
-25 -20 -15 -10 -8 -6 -4 -2 2 4 6 8 10 15 20 25
a. Sea ice within 100 km from coasts
b. Summer Warmth Index, full tundra
c. MaxNDVI, full tundra
d. Time-Integrated NDVI, full tundra
Northern Hemisphere
North America
Eurasia
E Bering
E Chukchi
Beaufort
S Can. Arc. Arch.
N Can. Arc. Arch.
Foxe Basin
Davis Strait
Hudson Bay
Hudson Strait
Baffin Bay
W Greenland
Denmark Strait
S Barents
N Barents
W Kara
E Kara
Laptev
East Siberian
W Bering
W Chukchi
*
-70 -60 -50 -40 -30 -20 -10 0 10
-20 0 20 40 60 80 100 120 140
-5 0 5 10 15 20 25 30 35
-10 0 10 20 30 40
Percent change (1982-2011)
Percent change (1982-2011)

## Box 12.4 Increased primary production under climatic warming on Bylot Island

Bylot Island is located in the Canadian Arctic Archipelago, at 73° N, 80° W (subzone C). From 1976 to 2010, the area has experienced a strong warming trend in the fall (+4.3 °C over a 35-year period) and in spring and summer (+2.8 °C) but not in winter (December to February; Gauthier *et al.* 2011).

Two 100 km$^2$ study areas centered on glacial valleys have been the focus of continuous monitoring and intensive observational and experimental studies since 1989. Monitoring at Bylot aims to obtain quantitative data on all important ecosystem components. The strongest temporal trend detected on Bylot is a more than doubling (123% increase) of annual above-ground graminoid production (mostly tundra grass *Dupontia fisheri* and Arctic cotton-grass *Eriophorum scheuchzeri*) in wetlands over a 23-year period (Box 12.4 Fig. 1). This is largely due to an increase in summer temperature, because the sum of thawing degree-days explains a significant proportion of the annual variation in plant growth (Gauthier *et al.* 2013). The proportion of the primary production consumed by herbivores also shows a decreasing trend over time. A trophic balance model showed that < 10% of the total annual primary production is consumed by herbivores, whereas 20-100% of the herbivore production is consumed by predators (Legagneux *et al.* 2012). This suggests that predation plays a key role in the functioning of this ecosystem, and that increased plant production has little effect on higher trophic levels in this top-down regulated food web. Allochthonous subsidies may be important to maintain high predator populations. For instance, high goose populations may help to sustain fox populations, especially in low lemming years (Giroux *et al.* 2012). In winter, predators like snowy owls and Arctic foxes use the sea ice for extensive periods of time (though this may be variable among years for foxes; Tarroux *et al.* 2010, Therrien *et al.* 2011), and thus they may depend upon the marine environment for their survival.



**Box 12.4 Figure 1.** Annual above ground production of wetland graminoid plants on Bylot Island, 1990-2012. Mean ± SE (n = 12 samples per year; trend equation based on individual samples). From Gauthier *et al.* (2013).

**Figure 12.14.** Trends in sea ice, open water, land temperature and NDVI for the circumpolar Arctic.

Top: The left panel shows the magnitude of changes in sea ice break-up (as represented by 50% sea ice concentration) and percent change for Summer Warmth Index for land area. The right panel panel shows the magnitude of changes in summer (May-Aug) open water and percent change in tundra MaxNDVI (annual maximum NDVI, usually reached in early August). Magnitude of change is the slope of the simple linear regression trend line multiplied by the number of years of record (30 years: 1982–2011). The sea ice concentration and open water data were derived from SMMR and SSM/I passive microwave records. Ice concentration time series were assembled using data averaged over a three-week period centered on the week when mean concentrations were 50%; the more negative the value on the scale, the earlier 50% ice concentration, or break-up, occurs. Open water indicates the integrated summer open water amount. NDVI and land surface temperatures (SWI) information were derived from AVHRR data and the NDVI is from the Global Inventory, Modeling and Mapping Studies (GIMMS) dataset.

Bottom: Percentage change for northern hemisphere, North America, Eurasia and major Arctic seas and adjacent land for (a) Open water, (b) Summer Warmth Index calculated as the sum of monthly mean temperatures on land exceeding 0 °C, (c) MaxNDVI, and (d) Time-Integrated NDVI (based on Bhatt *et al.* 2010, updated to 2011). Stars denote statistically significant changes.

forbs, graminoids and lichens did not change (Hudson & Henry 2009). A strong increase in above- and below-ground biomass was also documented over the past 25 years in wet sedge tundra on Ellesmere Island (Hill & Henry 2011). This increase in productivity is most likely due to indirect effects of increased temperature on mineralization and nutrient availability.

One of the best documented trends of change in the tundra ecosystem is increased growth of tall shrubs in the low Arctic tundra subzones (see Myers-Smith *et al.* 2011a for a review). Sturm *et al.* (2001) and Tape *et al.* (2006) compared aerial photographs from 1945-1955 with equivalent photos taken in 1990-2002 in N Alaska and documented a significant expansion of shrubs. Myers-Smith *et al.* (2011b) reported an increase in canopy cover and height of dominant willows on low Arctic Herschel Island, Canada, and Forbes *et al.* (2010) documented that a warming trend over the last six decades in the NW Russian Arctic was accompanied by a significant increase in growth of tall willow. Climate warming may also indirectly promote shrub growth. For example, Lantz & Kokelj (2008) show that retrogressive thaw slump activity resulting from permafrost thaw has increased in recent decades in western Canada. Such disturbances lead to increased nutrient availability and active layer thickness which in turn create opportunities for increased growth of shrubs, notably alder, and overall change in plant community composition (Lantz *et al.* 2009). Apart from vegetation succession that follows from the abrupt disturbance effect of thawing permafrost, the changed hydrology (either drying out or paludification) associated with lost permafrost or changed depth of active layers is expected to cause large-scale vegetation changes. Fire is another source of disturbance, which may promote shrub growth in the low Arctic (Lantz *et al.* 2010). The expansion of tall shrubs in the tundra has been reported as well by indigenous tundra residents such as Nenets in Yamal (Forbes & Stammler 2009, Forbes *et al.* 2010). Kitikmeot Inuit observed that the vegetation in Nunavut, N Canada, became more lush and plentiful in the 1990s, and that in particular shrubs expanded and grew larger (Thorpe *et al.* 2002).

The observed changes in vegetation composition are to some extent in agreement with changes predicted from experimental studies. A meta-analysis of 61 warming experiments carried out over up to 20 years showed that warming led to an overall increase in the growth of deciduous shrubs, while mosses and lichen decreased (Elmendorf *et al.* 2012). There was, however, large variation in the response of different plant groups to warming depending on natural variation in site warmth and moisture. The International Polar Year Project *Back to the Future* (Callaghan *et al.* 2011b) revisited numerous Arctic research sites that were established 15-60 years ago and documented changes in plant community composition. Daniëls *et al.* (2011), for instance, observed a decrease of a number of widely distributed Arctic and middle Arctic species and an increase of several low Arctic and boreal species, by comparing the present day vegetation around Tasiilaq in low Arctic E Greenland with descriptions from 1912. They suggested that climatic change may be triggering a trend towards 'sub-Arctification' of the area.

At the southern border of the Arctic, the treeline is predicted to move northwards with climate warming. Thus processes in the forest-tundra ecotone are pivotal to the future extent of the Arctic tundra. In a recent review, Harsch *et al.* (2009) analyze a large number of reports and conclude that treelines are either advancing or remaining stable. This result is consistent with what might be expected if treelines were responding to increasing global temperature, but were also constrained by other factors. Indeed, treeline dynamics are affected by a complex interaction of abiotic and biotic factors such as changes in hydrology and grazing, which have to be understood to make realistic predictions of forest encroachment in tundra (Aune *et al.* 2011). A global-scale analysis of spatial patterns of boreal tree density that included the forest-tundra ecotone suggested that forest-tundra transitions were likely to be controlled by non-linear (tipping-point) processes (Scheffer *et al.* 2012). In the northern boreal forest zone, there is evidence for a climate change-related impact that is the opposite of the 'greening of the Arctic tundra', that is 'forest browning' (Sturm 2010, Beck & Goetz 2011). Such a browning is believed to result from a combination of droughts, fires and insect outbreaks (Sturm 2010). Such processes are also likely to become involved in the dynamics of the forest-tundra ecotone. Indeed, in the mountain birch forest-tundra in northern Fennoscandia two species of geometrid moths (*Operophtera brumata* and *Epirita autumnata*) have expanded their outbreak range into more northern and alpine areas, causing large-scale devastation of birch forest during the last decade (Hagen *et al.* 2007, Jepsen *et al.* 2008). The expansion of a third defoliating moth species (*Agriopis aurantiaria*) is now promoted by warmer springs (Jepsen *et al.* 2011). The outbreaks of these species have had dramatic cumulative impacts on the forest tundra ecosystem by cascading to the understory vegetation (causing a shift in dominance from ericoid dwarf shrubs to graminoids) and to the herbivores (causing a shift from browsers to grazers; Jepsen *et al.* 2013). At present, irruptive defoliating insects affect primarily sub-Arctic birch forests, but their larvae occur also in dwarf birch in the shrub tundra beyond the tree line (Fig. 12.15; Torp *et al.* 2010, Karlsen *et al.* 2013), indicating that in the future tundra vegetation

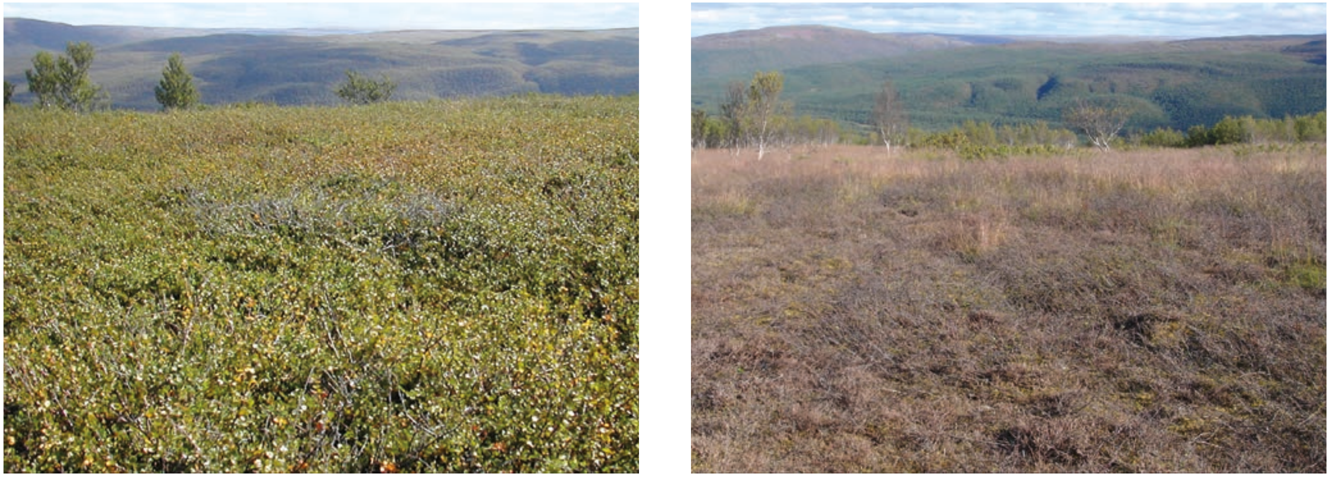


**Figure 12.15.** The devastating impact of an outbreak of the invasive geometrid moth *Operopthera brumata* on dwarf birch *Betula nana* in the shrub tundra above the mountain birch *Betula pubescens* treeline on Varanger Peninsula, NE Fennoscandia (from Karlsen *et al.* 2013).

may also be affected. It is, however, unclear whether these larvae currently are resident tundra populations or whether they spread to these areas from the nearby forest tundra.

The controlling impacts that tundra herbivores exert on several important plant functional groups and vegetation communities are now robustly demonstrated (see Section 12.2.2.1). Therefore, both the current trends in cover of shrubs and positioning of the treeline must be evaluated in light of potentially matching temporal trends in populations of keystone herbivores either due to change in climate (i.e. folivorous insects, caribou and lemmings) or anthropogenic land-use in tundra regions and farther south (semi-domestic reindeer; Section 12.3.3.4 and geese; Section 12.3.3.3).

As reviewed in Section 12.2.2.2, the climate-induced expansion of shrubs into open tundra landscapes is expected to have important feedback effects on global climate by altering fluxes of GHG and heat. However, while there have been many modeling studies and 'mensurative experiments' across spatially contrasting vegetation types, there are few time-series studies that have actually documented trends in such feedback processes. A study of C fluxes over eight years in eastern Siberia showed that primary production increased more with warmer summers than with the length of the growing season, but that it was mostly compensated by higher respiration (Parmentier *et al.* 2011). Net C uptake was highest in the shortest and coldest growing season. A study in high Arctic Svalbard showed that a considerable part of the annual $CO_2$ effluxes (14 to 30%) occurred in winter, and that soil respiration was strongly affected by near-surface soil temperature (Elberling 2007). Experimental increase of snow depth, leading to higher soil temperatures, has also been shown to increase soil respiration in winter (Morgner *et al.* 2010). Results from a circumpolar modeling study (Hayes *et al.* 2011) suggest that whereas the tundra was a sink for C during the 1960s and 1970s, it has become a net source of C since the 1990s.

### 12.3.3.2. Climate change and phenology

Earlier snow melt results in advanced spring and earlier onset of the growing season. June snow cover has decreased by 17.8% per decade since satellite records began in 1979, i.e. more than the concomitant reduction in Arctic summer sea ice (Fig 12.16.; Derksen & Brown 2012). Ecosystem-based monitoring at Zackenberg Research station in high Arctic Greenland revealed how this impacted much of the ecosystem including spring phenology of plants and arthropods (Box 12.5). Tulp *et al.* (2008) modeled the timing of peak insect abundance in high Arctic Taimyr, Russia, as a function of weather, date and cumulative temperature, and 'hindcasted' the timing of this peak using existing weather data. Their simulations showed that the period of high insect abundance may have advanced by seven days between 1973 and 2003.

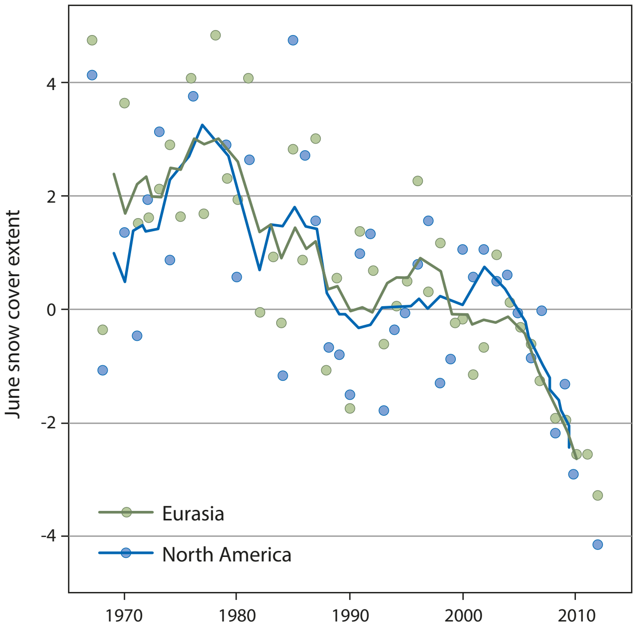


**Figure 12.16.** Trends in terrestrial June snow cover 1967-2012 based on averages for the North American and Eurasian continents, virtually all of it in the Arctic. Values are standardized anomalies with respect to the 1988-2007 mean. Solid lines are five-year running means (adapted from Derksen & Brown 2012).

Trophic mismatch is the temporal mismatch between herbivores and food plants or predators and prey which may result from the phenological responses of species to climate change (e.g. Visser *et al.* 1998, Miller-Rushing *et al.* 2010). Large phenological shifts make it likely that trophic mismatch, notably between migrating and local species, could become a serious problem. In the future, chicks of long-distance migrants such as shorebirds and passerines risk hatching after the peak of insect abundance, on which they depend to survive and grow, if the timing of migration is based on clues which do not change correspondingly (Tulp & Schekkerman 2008). At present, however, there are no data to assess whether this is already a problem for Arctic breeding birds, although years with early springs have been found to be associated with reduced gosling growth (Dickey *et al.* 2008). Post & Forchhammer (2008) reported that the advancement of plant phenology in W Greenland over a period of 13 years created a trophic mismatch with caribou, whose reproductive cycle follows the seasonal changes in daylight. As calving date is thus rather fixed, the peak demand for resources by reproductive females now falls later than the peak of nutritional value in their food plants, shortly after their emergence. This trophic mismatch was closely related to early caribou calf mortality. Interestingly, studies on semi-domestic reindeer in sub-Arctic northern Norway showed an opposite trend and documented a positive effect of earlier onset of spring on calf weight in fall, which is related to survival probability over the first winter (Pettorelli *et al.* 2005, Tveraa *et al.* 2013).

## Box 12. 5. Change in spring phenology at Zackenberg

Zackenberg Research Station is located in central NE Greenland in bioclimate subzone C. The concept of ecosystem monitoring applied at Zackenberg follows the recommendations of the Arctic Climate Impact Assessment (ACIA 2005), and at present the integrated monitoring program Zackenberg Basic is the only program that addresses these recommendations within a single ecosystem (Forchhammer *et al.* 2008). Since its implementation in 1995, Zackenberg Basic annually includes more than 1,500 parameters from the biological and geophysical environments (Meltofte *et al.* 2008a).

Through the monitoring period, climatic conditions have changed markedly: some have exhibited trends, while others have, just as importantly, exhibited large inter-annual variability (Hansen *et al.* 2008). The most dramatic increase in temperature has been registered during the summer months (June through August) with rates as high as 1.4-2.2 °C per decade (Schmidt *et al.* 2012b). Snow and ice are the primary drivers of ecosystem changes at Zackenberg (Box 12.5 Table 1; Forchhammer *et al.* 2008). Inter-annual changes in timing of snow and ice melt not only affect most species directly, but these drivers have significant indirect, cascading effects through species interaction within and across trophic levels. Some of the most significant changes are related to spring phenology. The timing of clearance of snow and ice cover together with spring temperature is pivotal for the onset of production plant communities and the emergence of arthropods (Høye *et al.* 2007a, 2007b). There are, however, indications of some plant species approaching their limit of phenological change (Iler *et al*. 2013). The affected arthropods include those that act as pollinators (Olesen *et al.* 2008) and food base for several avian species (Klaassen *et al.* 2001). A narrow phenological range together with host and predator specialization could make these species particularly vulnerable to trophic mismatch (Høye & Forchhammer 2008). In addition, a shortening of the flowering season in a warmer Arctic has been observed, with negative consequences for flower-visiting arthropods (Høye *et al.* 2013) as temperatures increase. Hence, in addition to its direct effect on the reproductive phenology of shorebirds (available nest sites; Pellissier *et al*. 2013), variability in the timing of snow clearance has an indirect impact on shorebirds through shorebird-arthropod interactions (Meltofte *et al.* 2007). Change in snow cover is also the likely primary driver of the observed lemming collapse at Zackenberg (Schmidt *et al.* 2012a).

**Box 12.5 Table 1.** Key ecological changes observed in the ecosystem monitoring program at Zackenberg since 1995.

| Observed changes | | Likely physical driver | References |
|---|---|---|---|
| **Active layer** | Increased active layer depths | Timing of snow melt, temperature | Christiansen *et al.* 2008,<br>Sigsgaard *et al.* 2010) |
| **Vegetation** | Advanced flowering phenology across multiple species | Timing of snow melt, temperature | Høye *et al.* 2007b,<br>Ellebjerg *et al.* 2008 |
| | Marked changes in plant composition and biodiversity in some vegetation types | Snow (water availability), temperature | Schmidt *et al.* 2012b,<br>Elberling *et al.* 2008 |
| **Growing season** | Earlier growing season initiation | Timing of snow melt, temperature | Grøndahl *et al.* 2008,<br>Sigsgaard *et al.* 2010 |
| | Longer growing season | Timing of snow melt, temperature | Grøndahl *et al.* 2008,<br>Sigsgaard *et al.* 2010 |
| | Initial increase in heath carbon uptake, but recently apparently levelling off | Timing of snow melt, temperature | Grøndahl *et al.* 2008,<br>Sigsgaard *et al.* 2010,<br>Lund *et al.* 2012 |
| | Increased primary productivity in fen areas | Temperature, $CO_2$ fertilization | Tagesson *et al.* 2012 |
| **Invertebrate community** | Advanced emergence phenology of multiple taxa | Timing of snow melt, temperature | Høye & Forchhammer 2008 |
| | Shorter flowering season and declining flower visitors | Timing of snow melt, temperature | Høye *et al.* 2013 |
| | Climate-driven phenotypic variation in spiders | Timing of snow melt | Høye *et al.* 2009 |
| **Vertebrate community** | Collapse of lemming cycles with negative cascading effects on the entire predator guild | Snow | Schmidt *et al.* 2008,<br>Gilg *et al.* 2009,<br>Schmidt *et al.* 2012a |
| | Varying nest initiation in shorebirds | Timing of snow melt | Meltofte *et al.* 2007,<br>Meltofte *et al.* 2008b |
| | Initial increase in musk oxen numbers, but with recent decline | Timing of snow melt, temperature (plant productivity) | Hansen *et al.* 2009 |

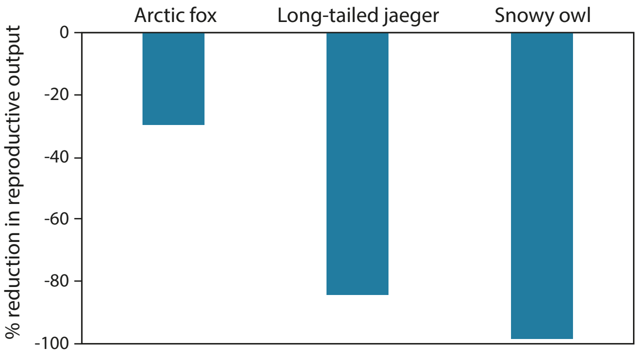


**Figure 12.17.** The impact of a collapse of the lemming cycle on the reproductive performance of three Arctic predator species with different degrees of specialization to lemming prey. The percent reduction in reproductive output is based on a comparison of yearly mean number of predator young produced during two periods with presence (1998-2000) and absence (2000-2011) of regular peak years of the population of collared lemmings at Trail Island, NE Greenland. Data were derived from Table 12.1 in Schmidt *et al.* (2012a).

### 12.3.3.3. Cascading impacts of trends in keystone animal species

#### Changed small rodent population dynamics

Small rodent population cycles are a keystone process of the tundra ecosystem with strong impacts both for the vegetation and the predator community (Ims & Fuglei 2005). In recent decades, a fading out or collapse of lemming population cycles has been reported from several Arctic regions (Gilg *et al.* 2009, Ims *et al.* 2011, Nolet *et al.* 2013) and has been attributed to increased frequency of melting-freezing events leading to ground ice-crust formation (Ims *et al.* 2008, Kausrud *et al.* 2008, Stien *et al.* 2012) as well as a to a longer snow-free season (Gilg *et al.* 2009, Nolet *et al.* 2013).

Changes in dynamics and community composition of small rodents affect predator guild composition (Ims & Fuglei 2005). The guild of small and medium-sized terrestrial Arctic predators is composed of species with different degrees of diet specialization (Fig. 12.3). Data from high Arctic NE Greenland show that snowy owl fledgling production declined by 98% after the collapse of the collared lemming cycle (Fig. 12.17), and no lemming nests with signs of predation from stoat have been found since then (Schmidt *et al.* 2012a). Breeding of long-tailed jaeger and Arctic fox was affected as well, but these species were the least negatively affected, probably because they are more able to switch to other resources than are the other predators in the guild (cf. Elmhagen *et al.* 2000, Gauthier & Berteaux 2011). Snowy owls (Jacobsen 2005) and Arctic foxes (cf. Box 12.6) have been declining in sub- and low Arctic northern Fennoscandia during the last century, and this decline in recent decades coincided with a dampening of the small rodent cycle (Ims & Fuglei 2005). In a modeling study, Henden *et al.* (2008) showed that whereas cycle length (periodicity) had relatively little impact on the growth rate of the fox population, the mean of small rodent abundance had a substantial effect, supporting the causal link between climate-induced changes in small rodent dynamics and the decline of the Arctic fox.

Finally, as expected from the indirect facilitation provided by lemmings on breeding success of ground nesting birds (i.e. mediated by relaxed predation pressures during lemming highs; see Section 12.2.2.1), recent time series analyses have indicated that growth rates of brant geese *Branta bernicla* in high Arctic Taimyr (Nolet *et al.* 2013) have become negatively impacted by dampened lemming cycles. Unfortunately, data on predator dynamics was missing in this study, so the connection could not be confirmed. In general, long-term, simultaneous monitoring data on linked herbivore species, predator guilds and direct climatic drivers in the Arctic are very scarce and seriously limit our knowledge of food-web-level changes.

#### Increasing species

Human-induced passive or active transfer of species (exotics/invasives) appears to have increased in the Arctic (see Lassuy & Lewis, Chapter 16), but there is still no evidence for this to have had cascading effects on other component of tundra ecosystems. Natural range expansion of species following climate warming is starting to be observed, especially among insects (e.g. Leung & Reid 2013), some of which may have strong ecosystem impacts (Section 12.3.3.1; Jepsen *et al.* 2013), whereas others may not. Finally, there are some species with a long-term presence within the tundra biome that have increased substantially in abundance to the extent that knock-on effects now are evident.

The red fox is a wide-spread generalist predator, which has expanded its range northwards during the last century (Reid *et al.*, Chapter 3), an increase that has been attributed to climate warming-induced increased secondary productivity (Hersteinsson & Macdonald 1992). More generally, increased abundance of medium-sized generalist predators (meso-predators) often results from human intervention in ecosystems, and the impacts on biodiversity can be severe both through increased competition with other predators and through their impact on prey populations (see Prugh *et al.* 2009 and Ritchie & Johnson 2009 for reviews). Interspecific competition from the red fox in conjunction with dampened and/or irregular lemming cycles is likely to be one of the main causes of the depressed populations of the Arctic foxes in some sub- and low Arctic areas (Tannerfeldt *et al.* 2002, Angerbjorn *et al.* 2013). Killengreen *et al.* (2007) showed that Arctic foxes on low Arctic Varanger Peninsula had ceased to use their traditional breeding dens in the most productive habitats where red foxes currently are very abundant. In this region, the abundant red fox population appears to be subsidized by an increased herd size of semi-domestic reindeer that provides carrion resources during the winter (Killengreen *et al.* 2011; Box 12.6). In other areas of the Arctic, such as in north Yukon, there is however no indication of an increase of

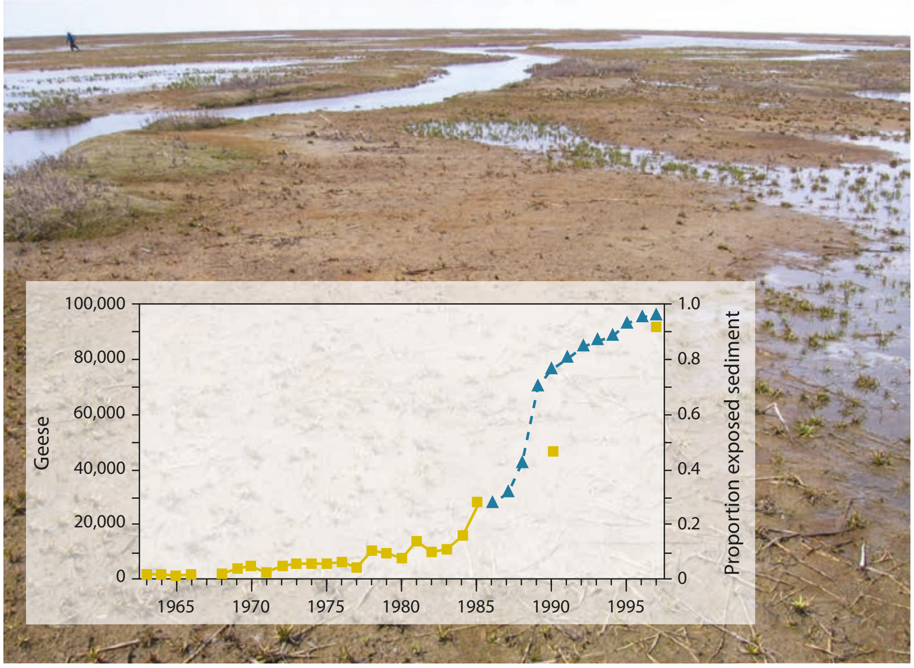


**Figure 12.18.** Numbers of nesting geese from 1963 to 1997 (solid squares) and the proportion of total area of salt-marsh as exposed sediment from 1986 to 1997 (blue triangles) at La Pérouse Bay, Manitoba, low Arctic Canada (from Jefferies *et al.* 2006). The background picture shows a salt marsh degraded after intense grazing by geese. Photo: Ken Abraham.

red foxes although climate warming has been substantial there (Gallant *et al.* 2012).

Northwards expanding and generally more abundant and stable populations of red foxes and other generalist boreal predators are likely to have detrimental consequences for many potential prey species, notably ground-nesting birds. Using artificial nests, McKinnon *et al.* (2010) showed that nest predation declined more than two-fold along a gradient from the sub-Arctic to the high Arctic in Canada. This gradient may be explained by a corresponding gradient in the abundance of generalist predators such as red foxes or corvids (crow *Corvus corone* and raven *C. corax*). In particular, corvids are known to prey on eggs and young of ground-nesting birds such as ptarmigans (Watson & Moss 2004, Stoen *et al.* 2010), waterfowl (Stien *et al.* 2010) and shorebirds (Parr 1993, Wallander *et al.* 2006). Both species abundance and richness within generalist predator guilds have recently been demonstrated to be closely linked to ecosystem productivity gradients in low Arctic tundra (Killengreen *et al.* 2012). The impact of an increasing population of generalist predators has also been suggested as an explanation for the decline of the willow ptarmigan in Norway during the last decade (Ehrich *et al.* 2012). The increase of the red fox population in northern Scandinavia has sparked drastic actions to control their numbers in the context of conservation of both the Arctic fox (Angerbjorn *et al.* 2013) and the lesser white-fronted goose *Anser erythropus* (DN 2011). However, apart from studies on red fox in Fennoscandia (Elmhagen & Rushton 2007, Selås & Vik 2007) there is no solid information about temporal trends in important generalist predators such as eagles and corvids (Ganter & Gaston, Chapter 4); although in particular the corvids may be favored by increasing human land use. Thus, among 16 local hunters and fishermen interviewed in Khatanga and Novaya (sub-Arctic eastern Taimyr) in fall 2012, 14 said that there were more ravens now than earlier and nine had observed an increase in the presence of crows. Ravens were now observed close to Lake Labaz and Lake Taimyr, two large tundra lakes, whereas this was not the case earlier (D. Ehrich unpubl.).

Populations of some species of geese breeding in the Arctic have increased strongly in abundance during the last decades (Ganter & Gaston, Chapter 4). This increase, which may primarily be due to causes outside the Arctic such as increased food supplied by changes in agriculture and decreased hunting during migration and in wintering areas, has a significant local impact on several components of the tundra ecosystem. Thus, the tremendous increase of lesser snow geese in the Hudson Bay area has caused persistent degradation of salt marshes (Fig. 12.18; Jefferies & Drent 2006). The resulting loss of vegetation triggers profound changes in sediment properties, including the development of hypersalinity and aridification. Re-establishment of vegetation on the hypersaline sediments is very slow (Abraham *et al.* 2005). This habitat degradation has been shown to have negative fitness consequences for the geese (Williams *et al.* 1993), and degraded patches are gradually abandoned, as the geese move to other areas (Jefferies & Drent 2006). Plant community alterations and vegetation damage resulting from increasing goose populations have also been reported with varying degrees of severity from other areas in the Canadian Arctic such as the low Arctic Karrak Lake, Nunavut (Alisauskas *et al.* 2006) and high Arctic Svalbard (van der Wal *et al.* 2007). On high Arctic Bylot Island, Canada, a decrease in plant primary production has been documented in the goose colony (Valery *et al.* 2010). In Jameson Land, high Arctic NE Greenland, an increase in primary plant production related to climate change allowed for a threefold increase in the number of molting geese from 1982-84 to 2008 (Madsen *et al.* 2011). Goose grazing impacted species composition, but did not lead to serious habitat degradation, possibly because molting geese feed only on the above-ground parts of plants. Apart from local disturbance effects (van der Wal *et al.* 2007, Pedersen *et al.* 2013), there is at present no evidence for severe goose-driven habitat degradation in the Eurasian Arctic, although goose populations have been increasing considerably in several areas (Jefferies & Drent 2006).

Vegetation degradation caused by overabundant geese in Canada has also been shown to have consequences for other components of the tundra ecosystem. Thus, Milakovic & Jefferies (2003) showed that the abundance of both spiders and beetles decreased in salt marshes degraded by overgrazing. The population of savannah sparrows *Passerculus sandwichensis* in the area declined by 77% over a period of 25 years (Rockwell *et al.* 2003). At the same time, the goose increase did not lead to any overall decrease in most other groups of breeding birds over a period of 16 years at Cape Churchill, low Arctic Canada, although at the habitat patch scale most species were less abundant in the degraded habitats (Sammler *et al.* 2008). Herring gulls *Larus argentatus*, however, exhibited an increase in numbers probably due to increased prey availability, possibly leading to enhanced predator pressure on eggs and chicks of large ground nesting birds such as willow ptarmigan (Sammler *et al.* 2008). At Karrak Lake, there was a strong negative correlation between habitat alteration by geese and local abundance of lemmings and voles (Samelius & Alisauskas 2009). This negative impact of geese on small rodents was attributed to a reduction in both food availability and protective cover.

### 12.3.3.4. Trends related to land-use changes

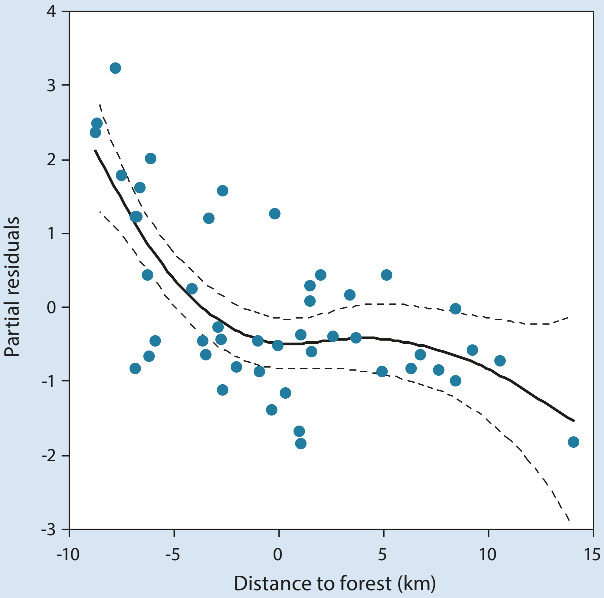
Increased grazing by reindeer in the tundra has been predicted to lead to transitions between vegetation states (Fig. 12.19; van der Wal 2006), although the propensity for such transitions is likely to differ between regions as reviewed in Section 12.2.2.1. Rees *et al.* (2003) documented a transition from dwarf shrub to graminoid dominated tundra over a 12 year period in an area where reindeer numbers increased locally in the low Arctic Nenetsky district of NW Russia. Nenets reindeer herders, who were involved in this study, confirmed that such a transition was the usual consequence of intense grazing. In Yamal, Russia, vegetation shifts from lichen, dwarf shrub and *Sphagnum* mosses to more grasses, sedges and ruderal bryophytes have been observed locally in areas where reindeer concentrate, such as around camp sites

**Figure 12.19.** While avoiding the sorts of negative impacts of herbivore overabundance that have been documented in some regions, an appropriately high density of semi-domestic reindeer appears to be able to keep shrub tundra in almost an open savannah-like grassland state by preventing recruitment of willow saplings between patches of tall shrubs. Here from a low Arctic riparian landscape on Varanger Peninsula, NE Norway. Photo: L.A. Støvern.

## Box 12.6. Issues of ungulate management in Varanger Peninsula

Varanger Peninsula in NE Norway harbors the westernmost fringe of the Eurasian Arctic tundra at 70-71° N, 30° E and belongs to subzone E. The Arctic tree-line (mountain birch) runs across the peninsula. Since 2004, research has focused on semi-domestic reindeer management as a potential driver of vegetation states and other components of the food web.

The abundance of semi-domestic reindeer has more than tripled over the last four decades. Reindeer herders have experienced that warmer falls (cf. Karlsen *et al.* 2009) interfere with reindeer migration, so that an increasing number of deer reside on Varanger Peninsula during winter. This provides carrion subsidies to a species-rich guild of scavengers that spills over from the adjacent forest-tundra zone (Box 12.6 Fig. 1; Killengreen *et al.* 2012), where the population of moose is also growing (Ims *et al.* 2013). In particular, the competitively dominant red fox is maintained in high numbers in the tundra even in the low-phase of the rodent cycle (Killengreen *et al.* 2011). This increase and less lemming prey appear to be the main causes of the decline of the Arctic fox in this area (Killengreen *et al.* 2007, Angerbjorn *et al.* 2013, Hamel *et al.* 2013). Adaptive management attempting to actively control the red fox has been run since 2005 with promising results so far (Angerbjorn *et al.* 2013, Hamel *et al.* 2013).



**Box 12.6 Figure 1.** Species richness of vertebrate scavengers recorded by camera traps at reindeer carrion as a function of distance from sub-Arctic birch forest on Varanger Peninsula in winter 2006. The graph shows the predicted species richness (whole line) with standard error envelopes (dotted lines) and partial residuals (dots) from a general additive model. The distance from the forest is 0.1-23.5 km. Adapted from Killengreen *et al.* (2012).

(Forbes *et al.* 2009). These lush habitats constitute nutrient-rich and easily digestible forage attractive for further grazing by reindeer. The somewhat contrasting results for Russia and northern Fennoscandia (Bråthen *et al.* 2007 cf. Section 12.2.2.1) may be due to different scales of investigation, as notably the increased productivity documented by Forbes *et al.* (2009) was very local, or possibly to different bedrock qualities (higher fertility in Russia where large sediment plains dominate). A profound reduction in lichen cover resulting from increased abundance of semi-domestic reindeer has been reported from sub-Arctic northern Fennoscandia (Suominen & Olofsson 2000, Moen & Danell 2003, Forbes & Kumpula 2009) and from Yamal in Russia (Podkorytov 1995). Recently, Tømmervik *et al.* (2012) showed that this change was reversible, as lichens recovered rather rapidly on plots from which reindeer were excluded over seven years.

Owing to a combination of governmental policies and social factors (Hausner *et al.* 2011, 2012) some semi-domestic reindeer herds in sub-Arctic northern Fennoscandia have risen in size to become likely the most densely stocked herds worldwide (Ims *et al.* 2007). Apart from the effect on lichens on the winter pastures, reindeer impacts on tall willow shrubs in summer pastures are the most robustly demonstrated impact of reindeer herding on tundra ecosystems. Intense reindeer browsing leads to reduced vertical growth (den Herder *et al.* 2004, 2008, Kitti *et al.* 2009) as well as areal fragmentation or shredding of willow thickets (Ravolainen *et al.* 2013), thus supporting the suggestion arising from studies based on small-scale experiments (Post & Pedersen 2008, Olofsson *et al.* 2009, Ravolainen *et al.* 2011) that large ungulates may counteract the climate driven expansion of shrubs. The herbaceous vegetation may be locally dominated by the unpalatable grass *Deschampsia cespitosa* (tussock grass; Ravolainen *et al.* 2013, Soininen *et al.* 2013). Presently, the impact of semi-domestic reindeer on tall willow shrubs and associated vegetation in riparian habitats in low Arctic Fennoscandia is regionally so severe that wildlife species are negatively affected. Such negative impacts have been documented for willow ptarmigan (Henden *et al.* 2011a, Ehrich *et al.* 2012) and more generally for the community of land birds (Ims & Henden 2012). On riparian sediment plains on the Varanger Peninsula, species richness of land birds was reduced by 50% in areas where tall willows had been entirely eliminated by heavy reindeer browsing. However, tundra voles appear to be unaffected by these changes in vegetation state (Henden *et al.* 2011b).

High reindeer abundances together with a practice of leaving some reindeer on summer pastures in winter have led to increased availability of reindeer carcasses for

Images of scavenger species involved as they were obtained from the camera trap placed on tundra and baited with reindeer carrion. From the top left: Arctic fox, hooded crow *Corvus cornix*, wolverine, white-tailed eagle *Haliaeetus albicilla*, red fox, golden eagle *Aquila chrysaetos* and common raven *Corvus corax*.

predators/scavengers in winter. This additional resource has been shown to contribute to maintaining a high abundance of boreal generalist predators (Box 12.6).

### 12.3.3.5. Impact of industrial development

Industrial development in the Arctic implies construction of roads and other infrastructure, oil-drilling, seismic exploration, tracks from vehicles, increased human presence and in some cases severe pollution, factors which all either lead to local destruction of the ecosystem or to different degrees of disturbance causing habitat and vegetation transformation. The area affected by habitat transformation around industrial development sites varies considerably and often increases over time. The area visibly affected was estimated to be 67 km$^2$ around the Toravei oil field in 2005 (Nenetsky Autonomous Okrug, Russia; Kumpula *et al.* 2011) and 836 km$^2$ around the Bovanenkovo gas field in 2011 (Yamalo-Nenets Autonomous Okrug, Russia; Kumpula *et al.* 2012), while 70 km$^2$ were covered by infrastructure in the North Slope oil fields in Alaska (NRC 2003; see Tab. 19.1 in Huntington, Chapter 19). Off-road vehicle tracks, in particular those left by the heavy Russian all-terrain tracked vehicles, remain visible for decades on satellite images. Traffic of vehicles used for seismic exploration during winter has been shown to cause long-term (20 years) changes to plant communities and permafrost stability in the coastal plain of Alaska (Jorgenson *et al.* 2010). Indirect impacts on tundra landscapes, such as thermokarst, may develop with a lag of many years (Walker *et al.* 1987). The number of vascular and non-vascular plant species adapted to grow on disturbed ground surfaces tends to decrease with latitude, in part because the set of colonists is derived mainly from local floras, so temperate ruderal taxa are largely absent (Chernov & Matveyeva 1997). In sub-Arctic and low Arctic ecosystems, the colonizers easily spreading and persisting on anthropogenically disturbed terrain are low shrubs, graminoids (grasses and sedges), composite forbs and ruderal bryophytes (Vilchek *et al.* 1996, Sumina 1998, Forbes *et al.* 2001).

Plant communities recolonizing disturbed ground differ from natural communities by a lower cover of most plant groups and lower total species diversity, but an increased cover of graminoids (Forbes *et al.* 2009, Jorgenson *et al.* 2010, Kumpula *et al.* 2011). Willows, in particular, are active colonizers of disturbed sites in moist habitats in sub-Arctic and low Arctic regions (Cooper & van Haveren 1994, Densmore 1994). Lichens are the most easily removed component of tundra communities, and on disturbed sites they regenerate even more slowly than vascular plants and bryophytes. Only a few of the most widespread lichen species of *Stereocaulon*, *Peltigera* or *Cladonia* are found on disturbed habitats. Despite a general trend toward graminoid-dominated tundra, vegetation changes on disturbed surfaces vary considerably depending on substrate, humidity and the nature of the disturbance (Forbes *et al.* 2001). Another effect of infrastructure is caused by dust from gravel roads. In both Russia and Alaska, calcareous dust has been shown to increase soil pH in initially acidic tundra, to reduce species richness and biomass, and to increase graminoid and cloud berry *Rubus chamaemorus* cover at the expense of *Sphagnum* mosses, lichen and dwarf shrubs (Forbes 1995, Auerbach *et al.* 1997, Myers-Smith *et al.* 2006).

Pollution has a strong local impact on the vegetation surrounding mining sites in Russia such as the nickel smelters in sub-Arctic Norilsk and Nikel or the coal mine complex in low Arctic Vorkuta. Virtanen *et al.* (2002b) observed an increase in graminoid coverage in sites impacted by industrial activity in Vorkuta. Willow cover increased at the expense of dwarf birch with increasing pollution levels, and lichen were absent from sites with major pollution. The area around Norilsk is characterized by the most intense sulphur deposition in the sub-Arctic (Forsius *et al.* 2010) as well as high heavy-metal contamination. Soils in the vicinity of the smelter are acidic, and the microbial community is affected both regarding species composition and reduced functional activity (Bogorodskaya *et al.* 2012). Whereas the vegetation is destroyed or severely disturbed in the immediate surroundings of the industrial area (Tutubalina & Rees 2001, Zubareva *et al.* 2003, Bogorodskaya *et al.* 2012), direct pronounced effects of Norilsk industrial activities are absent from the tundra region on the Taimyr Peninsula (Zhulidov *et al.* 2011).

Whereas impacts of industrial development on tundra vegetation have been thoroughly documented, not much is known about impacts on animals. Kevan *et al.* (1995) showed that abundance of soil arthropods was reduced on old tractor tracks on high Arctic Ellesmere Island, Canada, but diversity was not. Whether such very local changes in abundance have an impact on ecosystem processes is at present unclear. In the vicinity of Prudhoe Bay, low Arctic Alaska, the density of calving caribou declined exponentially with road density and the main calving grounds were moved to inland areas with lower forage biomass (Cameron *et al.* 2005). On the low Arctic Varanger peninsula, the likelihood of presence of the endangered Arctic fox declined with decreasing distance from roads (Hamel *et al.* 2013). One reason suggested for this was increased presence of the competitively dominant red fox. Indeed, generalist predators such as the red fox and corvids are favored by human presence (Restani *et al.* 2001, Liebezeit *et al.* 2009, Stoen *et al.* 2010). Feral dogs around settlements (Kumpula *et al.* 2011) can also act as generalist predators with serious negative impacts notably on local populations of ground nesting birds.

## 12.4. KEY FINDINGS

### 12.4.1. How the structure and functioning of tundra ecosystems are determined

#### 12.4.1.1. Abiotic controls on ecosystem structure

The Arctic tundra is a bioclimatically defined biome that geographically is restricted to a band around the margins of the Arctic Ocean. Hence, large parts of the tundra are subject to neighborhood effects both from marine and boreal forest ecosystems. Within its domain, the Arctic tundra biome has a zonal structure as described by bioclimate subzones A-E of the Circumpolar Arctic Vegetation Map (CAVM Team 2003), which provides a framework for describing the structure of tundra ecosystems. A key structuring force is the bottom-up effect of decreased vegetation productivity and complexity with increasing environmental severity. Accordingly, there are trends of decreasing food-web complexity in terms of diversity within and among trophic guilds of consumers with increasing latitudes. However, the four trophic levels of producer-plants, consumer-herbivores, consumer-carnivores and decomposers are present, even at high Arctic sites with very low terrestrial primary productivity, likely due to available resource subsidies from the adjacent marine food webs. Low food-web complexity in the most northern subzones (i.e. subzones A and B) may also partially be attributed to island biogeographic features (area size and isolation), as large parts of these subzones are located on islands in the Arctic Ocean and Nordic seas. Similarly, a substantial proportion of the high biodiversity of low Arctic subzones (D and E) stems partly from the close neighborhood and 'spillover effects' from sub-Arctic forested ecosystems. Microbial and plant communities, being less constrained by dispersal ability and area size requirements than animals, appear to be less influenced by such geographical constraints.

Besides latitudinal zonation there are other large-scale and long-term structuring forces such as present and past climates (including glaciation history), substrates and topography that have shaped unique communities. One notable case is steppe-tundra, which constituted very extensive, productive and species-rich ecosystems during past climates (Pleistocene), but which is currently found only as small remnant communities in the oldest regions of the terrestrial Arctic and with distinct continental climates.

At sub-regional scales, the terrestrial Arctic harbors diverse mosaics of communities that are structured by gradients in climate, substrate and hydrology often associated with topography and disturbance factors. Unique within- (alpha-) and among-community (beta-) diversity is shaped by the cryosphere (above-ground snow and below-ground permafrost). Examples are topographic (hill-slope) communities shaped by snow-depth and soil-moisture related processes along gradients from ridge to snow-bed communities, and the micro-scale patterning of tundra vegetation and below-ground biota due to the action of permafrost. Thus, hot spots of high regional (gamma) diversity are currently found in topographically and geologically complex regions.

#### 12.4.1.2. Biotic processes shaping biodiversity and tundra ecosystem functioning

The architecture of tundra food webs is modulated by direct and indirect inter-specific interactions within and between trophic levels. Although there is still no scientific consensus about the relative importance of bottom-up and top-down trophic controls in Arctic food webs, some generalizations can be made:

- Herbivores can regionally exert strong top-down controls on the state of tundra vegetation. Notable cases are (1) elimination of lichens from tundra heaths and tall shrubs from low Arctic riparian plains by abundant reindeer, (2) the ameliorating impact of lemming grazing on primary productivity in mesic tundra and snow beds, (3) outbreaks of insect defoliators impacting tundra-forest ecotone dynamics, and (4) over-abundant goose populations causing degradation of wetland plant communities.
- The consumption by predators controls at least regionally (1) the abundance of small mammal herbivores and (2) the reproductive success of ground nesting birds. The strength of this control can be enhanced by marine or anthropogenic subsidies.
- Trophic cascades and other indirect effects in food webs affecting biodiversity include (1) negative impacts of abundant reindeer on riparian bird communities and (2) positive impacts of cyclic lemming peaks on breeding success in ground nesting birds.
- Multi-annual, cascading interaction cycles mediated by fluctuating small rodent populations are crucial for the maintenance of terrestrial Arctic biodiversity in

many tundra ecosystems, including species endemic to the Arctic. In particular, lemmings appear to be keystone species in tundra ecosystems.

Terrestrial Arctic biota play essential roles in the regional-global climate system. They are involved in both biogeochemical processes that control the fluxes of GHG and biophysical processes that control heat fluxes between the earth surface and the atmosphere. A wealth of recent research indicates that the actual composition of terrestrial biodiversity may determine whether the Arctic will become a source or a sink for GHGs in a warming climate and whether the Arctic amplification will become stronger or weaker. Indeed, knowledge of the composition and the functions of Arctic biodiversity appears to be crucial for our ability to predict future climate. Key findings are related to which plant functional traits (PFTs) dominate in tundra vegetation and how these functional traits link to biophysical and biogeochemical processes and biotic interactions:

- PFTs have 'engineering' influences on biophysical processes. Notable cases are (1) increase of tall shrubs and trees, resulting in reduced albedo and accentuating the Arctic amplification of climate change, and (2) decline of mosses accentuating permafrost thaw and causing a cascade of geophysical and biogeochemical processes that leads to GHG release from the massive below-ground stocks of C in frozen Arctic soils.
- PFTs are linked to below-ground biological processes that influence the transfer of C between biological and atmospheric pools. For instance, vegetation shifts from ericoid dwarf-shrub heaths to forest-tundra may induce a net loss of C to the atmosphere via mycorrhizal activity that increases the rate of decomposition of soil organic matter. Indeed, the complexity of soil-plant interactions cautions against the assumption that increased plant productivity necessarily means greater ecosystem-level C sequestration.
- Ecosystem functioning depends also on the traits of the consumers that are involved. Notable cases are (1) the ability of mammalian herbivores to control tall shrubs and thereby albedo and net GHG fluxes, (2) the capacity of geese, lemmings and ungulates to shift tundra plant communities from moss to graminoid dominance, with implications for GHG fluxes, (3) the gross vegetation state shifts in tundra-forest ecotones caused by outbreaks of insect defoliators turning the ecosystem from sink to source of C, and (4) plant fungal pathogens altering the C balance of tundra heaths.

## 12.4.2. Trends attributed to drivers of change

### 12.4.2.1. Climate change

The Arctic tundra biome has been subject to dramatic changes driven by large fluctuations in past climates. In particular, the climatic transition to the warmer climate during the Holocene appears to have been uniquely deleterious in its impacts upon cold-adapted terrestrial Arctic biota, leading to extinctions of some taxa. Seen against this background, future climatic warming, expected to be more rapid than ever, poses severe threats to the maintenance of the present, already impoverished Arctic biodiversity. Conversely, in light of their persistence over episodes of climate change in the past, extant Arctic biota could be expected to show some resilience to at least the incipient stages of contemporary warming.

Climate warming is expected to relax critical climate-related constraints on plant growth. Current trends in vegetation are mostly consistent with this expectation:

- Vegetation seasonality in the Arctic region has had a 7° latitudinal shift equatorwards during the last 30 years. Remote sensing has shown that the Arctic tundra has become greener over vast stretches of the circumpolar Arctic. As verified by both observations and experiments on the ground, this is due to increasing vascular plant biomass.
- Increase of deciduous shrubs in the low Arctic subzones is particularly well demonstrated, sometimes associated with changes in disturbance factors such as permafrost thaw and tundra fires and ecosystem functions such as net C fluxes and albedo.
- The increase of vascular plants occurs at the expense of cold-adapted mosses and lichens. Permafrost-thaw and changed hydrology also impact these cryptogams directly.
- Cascading impacts of changed tundra vegetation dynamics have begun to become demonstrated in terms of (1) phenological mismatches and novel matches between herbivores and their food plants, and (2) changed net ecosystem C fluxes associated with shifts in dominant plant functional traits and related below-ground biota.

Trophic interactions within the tundra food web appear to be notoriously climate-sensitive. In particular those involving keystone species are expected to mediate cascading climate impacts on a host of other species and functions in the ecosystem:

- Climate-induced collapses or dampening of lemming population cycles have caused reduced reproductive success in lemming predators and ground nesting Arctic birds in Greenland and Eurasia. Arctic predators such as the Arctic fox and the snowy owl have been placed on national red lists in regions where lemming populations have exhibited irregular and/or dampened cycles for many decades.
- Climate-induced outbreaks of insect defoliators and fungal plant pathogens have just begun to emerge at the southern border of the Arctic, causing transitions between vegetation states across the tundra-forest ecotone and as a consequence the net release of C to the atmosphere.

None of the trends in Arctic tundra ecosystems are spatially uniform. A large spatial heterogeneity is due to the fact that climate change itself is spatially heterogeneous and that there is also considerable spatial variation in other important controlling processes.

#### 12.4.2.2. Land-use, resource management and industrial development

Change in human population, land-use and resource management practices have resulted in the increased abundance of certain species that may have pervasive impacts on ecosystem structure and functioning. Recent research in the terrestrial Arctic has highlighted three notable cases:

- Reindeer herding, which is the most spatially extensive form of land-use in the Arctic, has been subject to changing policies and/or socio-economic regimes that regionally have given rise to abnormally dense reindeer stocks. This in turn has caused (1) reduced areal extent of low erect shrubs with cascading negative impacts on the shrub-associated fauna and (2) changes in the associated predator guilds due to active control (persecution) of large predators and/or increase of meso-predators that are subsidized by reindeer carrion.
- The increase of boreal meso-predators in the low Arctic, best demonstrated for the red fox, most likely results from increased anthropogenic resource subsidies. Negative impacts of northwards red fox expansion on endemic Arctic species has been demonstrated (Arctic fox), or suspected (willow ptarmigan and lesser-white fronted goose), to the extent that red fox control is currently implemented as a conservation measure in sub- and low Arctic Fennoscandia.
- The increase of populations of Arctic breeding geese results mainly from changed land-use or hunting practices on wintering and staging grounds farther south. Overabundant geese have local ecosystem impacts ranging in severity from apparently irreversible habitat degradation of wetlands to moderate changes in plant community composition.

The distribution of industrial developments in the terrestrial Arctic and their associated anthropogenic pressures is currently patchy but expanding. Impacts on local ecosystems include:

- Increase of plants that are resilient to, or facilitated by, mechanically disturbed ground surfaces; mostly grasses and deciduous shrubs, but including the notable perennial herb, fire-weed *Chamerion angustifolium*.
- Declines in pollution-sensitive growth forms such as lichens around mining sites.
- Local declines of disturbance sensitive (shy) animals such as caribou as a response to the presence of human infrastructure, but increases in human commensal species like the red fox and corvids.

## 12.5. CONCLUSIONS AND RECOMMENDATIONS

### 12.5.1. Status and trends: Implications for the future

The Arctic tundra biome is a bio-climatically defined zone, the integrity of which is ultimately conditional on cold climates. Based on an extensive peer-reviewed literature, the present assessment testifies to the fact that all aspects of tundra ecosystems and their embedded biodiversity are shaped by past and current climates, although in conjunction with other environmental factors. This also means that future climate warming – in combination with other drivers of change – will fundamentally alter Arctic biodiversity. Indeed, our review of contemporary trends demonstrates that the tundra ecosystems have already changed as a result of recent climate warming as well as by intensified human land-use, including industrial development in certain areas.

Concerning the impacts of drivers of change in general and those related to climate warming in particular, the present assessment arrives at the following conclusions:

- Impacts of change are often indirect, both in the abiotic and biotic domains of tundra ecosystems.
- In the abiotic domain, climate warming exerts some of its most profound impacts through second-order disturbances in the cryosphere, such as ground surface icing (ROS) and permafrost thaw, or through drought-related increase of tundra fires.
- In the biotic domain, pervasive driver-impacts are mediated both by bottom-up and top-down cascades in trophic webs. Both types of cascades have recently been found ultimately to harm species endemic to the Arctic such as lemming-dependent predators and grazing-sensitive cryptogams.

Concerning the functioning of tundra ecosystems, new insights have emerged about the essential but complex roles of terrestrial Arctic biota in the evolution of regional-global climates:

- Ecosystem structure in terms of the composition of species guilds, communities and trophic webs may determine whether the terrestrial Arctic will become a future sink or source for GHGs, and whether it will strengthen or weaken the Arctic amplification of climate warming.
- The set of species traits that dominate in an ecological community is important for overall ecosystem functionality, implying that the processes involved in the global C cycle are not independent of the species (and functional traits) involved.
- An important overall message is that 'the Devil is in the details' regarding how terrestrial Arctic biodiversity interacts with climate change, which is indeed an argument for emphasizing Arctic biodiversity in climate research.

The tundra biome's geographic configuration alone, as an irregular and in places very narrow strip of low-lands squeezed in between boreal forest and the Arctic marine environment, implies that the whole biome is vulnerable to climate change-related 'edge effects'; i.e. species-invasions from sub-Arctic ecosystems (e.g. northward expansion of forests) and marine encroachment (erosion of coastlines and rising sea levels). Considering paleo-ecology, the whole biome can already be considered a refugium. Moreover, certain tundra subzones and regions may be particularly sensitive and vulnerable:

- The high arctic subzone A should be considered to be endangered. It is currently restricted to a very small area, about 2% of the non-glaciated terrestrial Arctic, mostly islands surrounded by perennial sea ice. An increase in July mean temperature of only 1-2 °C will permit the introduction of prostrate shrubs, sedges and other temperature-limited species. Disappearing sea ice may also change the levels of marine nutrient and production subsidies to the otherwise extremely nutrient/production limited high Arctic terrestrial food webs.
- The low Arctic subzones (D and E) are particularly vulnerable to increased pressures from range-expanding species with current strongholds in the sub-Arctic. Reported cases include boreal shrubs and trees, outbreaks of insect defoliators and meso-predators. 'Human commensal' meso-predators may also be synergistically enhanced by intensified land-use and expanding infrastructure/industries.
- Steppe-tundras that currently are confined to a few regions with continental climate and calcareous substrate are expected to be strongly affected by increased humidification of the climate and acidification of the substrate.

## 12.5.2. Conservation and management actions

The Arctic tundra biome is still characterized by relatively pristine ecosystems over large areas compared with other biomes on Earth. However, the impact of ongoing and future climate change is expected to be huge and represents the single most severe threat to terrestrial Arctic ecosystems. Moreover, there is significant spatial overlap with other stressors indicating that we must pay special attention to potential synergies. Area protection (reserves and national parks) will be an important means for preserving Arctic biodiversity in the era of climate change, especially since it will act to diminish synergistic impacts of local anthropogenic stressors and climatic warming. With regards to climate warming, there are certain biogeographical features that will make some areas particularly valuable for protection:

- Topographically diverse areas with mountain ranges that include landscape-scale climatic gradients may have 'buffer-capacity' to maintain cold refuges in a warmer climate.
- Remote high Arctic islands that are far north of southern bioclimate subzones and boreal ecosystems, and where Arctic marine waters will serve at least as a partial barrier ('filter') to invasions from the south.

However, regardless of how remote and well-protected, no Arctic reserves or national parks will be immune to the impact of climate change. To conserve Arctic biodiversity it may be necessary to implement active management actions especially within protected areas:

- Encroachment of tall shrubs and trees into tundra can be counteracted, with the added benefit that plant community diversity can be maintained under future warming, by management of large herbivores as shown by recent research in Fennoscandia and Greenland. Such management needs to consider both the positive and negative effects of increasing grazing pressures, other ecological effects of high herbivore densities (e.g. subsidies to meso-predators) and the economies of local people (see Huntington, Chapter 18).
- Certain boreal species expanding their range northwards and anthropogenically introduced invasive species may be controlled locally in the manner currently attempted with meso-predators in northern Fennoscandia.
- Increasing populations of human commensal species should be counteracted, for instance by effective waste management associated with human settlements or encouragement of hunting.

Indeed, in a much warmer climate, a network of 'Arctic parks' which are actively managed to maintain ecosystem processes that are representative of the main geographic regions and subzones of the tundra biome may be the only way to conserve terrestrial Arctic biodiversity in the future.

## 12.5.3. Research and monitoring

As evident from the present assessment, there is a wealth of research and monitoring conducted over recent decades that has provided crucial new insights regarding the structure and functioning of Arctic terrestrial ecosystems, as well as estimates of recent trends. However, this science has also revealed big challenges that remain to be met before we can answer critical questions about contemporary and future states of tundra ecosystems and their biodiversity.

### 12.5.3.1. Needs for area- and ecosystem-representative measurements

Over most of the Arctic, it will continue to be easier (and cheaper) to detect changes from space than on the ground. Thus, remote sensing and technological advances to improve it will undoubtedly be important for monitoring the terrestrial Arctic, and Arctic ecologists ought to be in the forefront of the application of such technologies. However, although we may be able to detect changes in gross ecosystem properties from space, we need to be on the ground to explain and manage those changes. Moreover, most of the biodiversity and many of the factors that drive its dynamics will remain unseen from space regardless of future improvements in remote sensing technologies.

Ground-based measurements currently have very poor geographical coverage considering the vast spatial extent of the tundra biome and the large spatial heterogeneity in its habitats and biota. This heterogeneity must be accounted for, if we are to obtain robust estimates of status and trends, for instance by means of meta-analysis (e.g. Elmendorf *et al.* 2012). To do this, research and monitoring efforts need to become much more area-representative than is now the case. This means that many more long-term sites ought to be established, with the demand that sampling design, measurement methods and criteria for classifications are harmonized among sites.

Those processes that exceed the spatial scale of small plots or include ecosystem components dominated by microbial communities and invertebrates are currently underrepresented in terrestrial Arctic research and monitoring. Both of them are, however, critically important for understanding the important biogeochemical and biophysical processes coupling the tundra ecosystem to the climate system. These problems of lack of area- and ecosystem-representativeness are acute challenges that need to be addressed in the upcoming CBMP (see Box 1.4 in Meltofte *et al.*, Chapter 1).

#### 12.5.3.2. Needs for ecosystem-based approaches

A key message emerging from this assessment is that essential attributes of Arctic biodiversity, some of which have global repercussions, are ultimately dependent on how interactions within ecological communities and trophic webs are impacted by external drivers. This provides a compelling argument for research, monitoring and management of Arctic terrestrial biodiversity to adopt ecosystem-based approaches. At present, however, there are very few sites in the Arctic where long-term projects are explicitly ecosystem-based. This state of affairs must be improved, and CBMP ought to play a key role by helping to orchestrate an area-representative, circumpolar network of ecosystem-based monitoring sites.

The planning of a future network of ecosystem-based programs should strive to harmonize monitoring design and measurement protocols and to accommodate a common set of ‘essential biodiversity variables’ (Pereira *et al.* 2013). However, the fact that the ecosystems are structurally and functionally heterogeneous across subzones and regions of the tundra biome, as well as partly subjected to different external drivers of change, implies also a need for site-specific efforts to focus on site-specific processes and components of the ecosystem. Ecosystem-based monitoring should be guided by the best empirical knowledge and most plausible hypotheses regarding key drivers, processes and trends in the focal ecosystem (Lindenmayer & Likens 2009). In order to be relevant to stakeholders, managers and policy makers, those drivers and components of the ecosystem that actually can be amenable to actions in ecosystem-based management ought to be given particular attention in monitoring programs (Westgate *et al.* 2013).

The magnitude of climate warming in the Arctic during the present century may become as extreme as 10 °C. However, the projected temperatures and precipitation patterns vary so much between different models and geographic regions (Overland *et al.* 2011, Xu *et al.* 2013) that one may question the value of the many attempts now taken to derive explicit model-based predictions about how Arctic species and ecosystems will respond. Moreover, the combination of unprecedented rates of climate change, abnormal levels of other stressors, evolution of novel climates (Williams *et al.* 2007) and ecosystem structures (Macias-Fauria *et al.* 2012) accentuate the possibility that present knowledge about past changes, contemporary ecosystems states and trends may have little bearing on what will become the future states of terrestrial high latitude ecosystems (Post 2013b). In such a dire situation it becomes crucial to establish flexible observation systems to enable real-time detection, documentation and understanding of cause-effect relations (Ims *et al.* 2013). The framework of adaptive monitoring as proposed by Lindenmayer *et al.* (2010) may be particularly suitable in the context of ecosystems as likely to be prone to uncertainties and surprises as those currently located in the terrestrial Arctic.

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## LIST OF ACRONYMS

C: carbon
$CH_4$: methane
$CO_2$: carbon dioxide
GHG: greenhouse gasses
NDVI: Normalized Difference Vegetation Index (see Box 12.1)
GLORIA: Global Observation Research Initiative in Alpine Environments
SOM: soil organic matter
ECM: ectomycorrhiza
ROS: rain-on-snow
PFT: plant functional traits

The Arctic is richer in wetlands than most other biomes on Earth.
Photo: Patrick J. Endres/AlaskaPhotoGraphics.com

*Chapter 13*

# Freshwater Ecosystems

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> » **There have been changes to the permafrost: In the past ten years several lakes have disappeared both from the taiga and tundra area where we have our reindeer migration. Lakes have become rivers and drained out. You can see this in the tundra, but even more in forested areas. This impacts the fishing for sure. One of the lakes drained, and the fish got stuck on the bottom and died of course. Wetlands and marshes are deeper or are not so solid. Close to the rivers like Chukatsha, there are depression faults and holes in the ground. The marshlands cannot be used for reindeer travelling anymore.**
>
> Dmitri Nikolayevich Begunov, a Chukchi reindeer herder from the Cherski town in Lower Kolyma in northeastern Siberia (Mustonen 2009).

## SUMMARY

The Arctic contains an abundant and wide range of freshwater ecosystems, including lakes, ponds, rivers and streams and a complex array of wetlands and deltas. This broad range of freshwater ecosystem types contains a multitude of habitats of varying ecological complexity and supports a diversity of permanent and transitory organisms adapted to living in an often highly variable and extreme environment. Moreover, these habitats and species provide important ecological and economic services to northern peoples through the provision of subsistence foods (fish, aquatic birds and mammals), serve as seasonally important transportation corridors (e.g. ice roads), and are ecologically and culturally important habitat for resident and migratory aquatic species.

The Arctic region is currently undergoing significant and rapid environmental and socio-economic change, which in turn will have profound effects on the distribution, abundance and quality of freshwater ecosystems, their associated habitats and related biological and functional diversity. Climate change has been identified as the prominent environmental driver affecting Arctic freshwater ecosystems and their related biological and functional diversity, although other significant drivers and environmental stressors are increasing in relevance (e.g. point and non-point pollution, increased impoundment/diversion of freshwater, enhanced mining and oil and gas activities and anthropogenic introduction of invasive species).

As a result, biodiversity within Arctic freshwater ecosystems is being rapidly altered by natural and anthropogenic drivers. Hence, a parallel understanding of functional diversity (food web structure and complexity, productivity, carbon and nutrient dynamics) is required to develop and implement appropriate conservation and management measures to ensure healthy and functioning ecosystems. Together these observations also contribute to understanding of the factors promoting services provided by freshwater ecosystems.

Currently, knowledge of Arctic freshwater ecosystems and related biodiversity is limited with large spatial gaps particularly in remote areas. The development of appropriate knowledge of reference states is critical to assess the variability and significance of change. Significant knowledge gaps remain in our understanding of how biodiversity contributes to, and how changes affect, freshwater ecosystem function and services. More systematic process-based studies are required to better understand the abiotic and biotic controls on ecosystem properties and to obtain a predictive understanding of how ecological communities are structured in response to changing anthropogenic and environmental drivers.

Future conservation and protection of Arctic freshwater ecosystems and their associated biodiversity requires appropriate long-term monitoring and associated process-based research across relevant spatial and temporal scales. Actions taken must be adaptive and responsive to new information in a rapidly changing Arctic.

## 13.1. INTRODUCTION

Freshwater ecosystems are abundant and diverse throughout the circumpolar region and include lakes, ponds, rivers, streams and a wide range of wetland complexes (Usher *et al.* 2005, Wrona *et al.* 2005, 2006a, Vincent & Laybourn-Parry 2008). The Arctic contains some of the world's largest rivers and associated deltas (e.g. the Lena, Ob, Yenisei, Mackenzie), largest and deepest lakes (e.g. Great Bear Lake, Great Slave Lake, Lake Inarijärvi and Lake Taymyr), numerous permanent and intermittent streams and rivers draining mountains, highlands and glaciated areas, and a myriad of smaller permanent and semi-permanent lakes, ponds and wetlands. In some regions of the Arctic, lake, pond and wetland complexes can cover > 80% of the total land area (Wrona *et al.* 2005, 2006a, Pienitz *et al.* 2008, Rautio *et al.* 2011).

This broad range of freshwater ecosystem types contains a multitude of habitats of varying complexity, which in turn support a diversity of permanent and transitory organisms adapted to living in an often highly variable and extreme environment (Rouse *et al.* 1997, Usher *et al.* 2005, Wrona *et al.* 2005, Prowse *et al.* 2006b, Rautio *et al.* 2008, Heino *et al.* 2009, Moss *et al.* 2009, Schindler & Lee 2010). In addition, high-latitude freshwater systems are of regional and global significance by serving as important tele-connections and providing feedbacks with climate and ocean systems, being critical habitat and/or refugia for unique species and communities, acting as significant sources and/or sinks of $CO_2$ and methane, and serving as trans-ecosystem integrators and links of nutrient, organic matter and freshwater transport and flux between the terrestrial and marine systems (Wrona *et al.* 2005, AMAP 2011b, Prowse *et al.* 2011c).

The Arctic region is currently in a period of major and rapid environmental and socio-economic change, which in turn will have profound effects on the distribution, abundance and quality of freshwater ecosystems and their associated habitats and biological and ecological diversity (Wrona *et al.* 2005, CAFF 2010, AMAP 2011b). While climate change is a key environmental driver affecting freshwater ecosystems and associated biota in the Arctic region and has received a significant amount of attention (ACIA 2005a, 2005b, IPCC 2007, Heino *et al.* 2009, AMAP 2011b, Rautio *et al.* 2011, Culp *et al.* 2012), a number of other significant drivers and environmental stressors are also increasing in relevance in their potential for affecting freshwater ecosystems and related biodiversity. These include, for example, point and non-point pollution (e.g. long-range aerial transport of contaminants; AMAP 2003, 2011a, Macdonald *et al.* 2005, Wrona *et al.* 2006b), altered hydrologic regimes related to increased impoundment/diversion of freshwater (Prowse *et al.* 2006a), water quality changes from landscape alterations (e.g. mining, oil and gas exploration) (AMAP 2008) and biological resource exploitation (e.g. subsistence and commercial fisheries). Furthermore, increased access to the north via land and sea transport including for example, the proliferation of roads in northern Canada and Russia, opens up efficient new dissemination pathways for invasive species (AMAP 2011b; see also Lassuy & Lewis, Chapter 16). Collectively, these drivers/stressors will often synergistically contribute to the alteration and/or degradation of biological diversity at the species, genetic and habitat-ecosystem levels (Pimm *et al.* 1995, ACIA 2005, Wrona *et al.* 2005, IPCC 2007, CAFF 2010).

In the following sections we summarize the current state of knowledge on the relative importance of the past, present and projected environmental and anthropogenic drivers in affecting the status, patterns and trends in ecosystem/habitat, structural and functional diversity of Arctic freshwater systems. In some circumstances it is difficult to fully adhere to the strict definition of the Arctic used in this assessment (see Section 2 in Meltofte *et al.*, Introduction), as certain freshwater systems (notably the large rivers that discharge to the Arctic Ocean) cross several ecozones and related latitudinal and temperature gradients given the scale of their contributing drainage area. Such systems are used as key examples of how Arctic freshwater and habitat quality, quantity and related biodiversity can also be significantly affected through direct linkages to environmental and anthropogenic drivers and ecological processes that are extraneous to the Arctic *per se*.

Through the use of pertinent case studies and examples, we will provide an ecosystem-based, community or food web perspective on how key environmental and anthropogenic drivers in the Arctic, operating singly or in combination, affect the distribution and abundance of freshwater ecosystem types, their related habitats, and structural and functional ecological properties.

In the final section of the chapter we provide perspectives on current and proposed approaches for the conservation and protection of Arctic freshwater biodiversity, identify knowledge gaps and challenges, and forward recommendations on the future directions of monitoring and assessment of aquatic biodiversity in a rapidly changing Arctic.

## 13.2. NATURAL AND ANTHROPOGENIC DRIVERS

### 13.2.1. Effects of latitude and climate

The terrestrial Arctic is largely an extension of the continental land masses, and this has major implications for climate, species colonization and biodiversity. It is characterized by the absence of trees, strong seasonal variations of extreme cold temperature, long durations of ice-cover, continuous and discontinuous permafrost, lack of nutrients and low solar radiation input. In addition to these characteristics, the underlying geology, landscape topography and vegetation as well as the size, water volume and contributing catchment area, all play important roles in shaping freshwater ecosystems and affecting their habitat composition as well as limiting the distribution and abundance patterns of freshwater biota (Wrona *et al.* 2005, 2006a, Prowse *et al.* 2006a, 2006b, Reist *et al.* 2006a, 2006b).

In general, effects of climate on freshwater ecosystems can be assessed in terms of severity (i.e. persistent conditions which are at physiological thresholds thus limit biota), extreme seasonality and high variability both within and among years (ACIA 2005, CAFF 2010, AMAP 2011b). Factors such as ice-cover thickness, duration and quality and precipitation and snow pack conditions influence the hydro-ecology of freshwater environments (Borgström 2001, Schindler & Smol 2006, Christoffersen *et al.* 2008, AMAP 2011b, Prowse *et al.* 2011b). Extreme seasonality combined with low levels of incident radiation also have profound effects for aquatic ecosystems since much of this radiation may be reflected due to high albedo of ice and snow, especially during the critical early portions of the spring and summer. Furthermore, a substantial portion of the total thermal energy input is used to melt ice, rendering it unavailable to biota. The timing of radiation peaks is therefore important with greater than 50% being received prior to the melting of ice-covered aquatic systems. The Arctic also displays generally low levels of precipitation, and most of this falls as snow, resulting in limited and often episodic runoff.

Consequently, Arctic freshwater systems are generally species-poor compared to temperate counterparts, and the overall productivity tends to be low due to low levels of nutrient inputs, low light levels, low temperatures, ice presence and persistence, and short growing seasons (Usher *et al.* 2005, Wrona *et al.* 2005). Lack of nutrients, rather than low temperature or incident radiation, is likely a key factor restricting primary production in freshwater systems in the Arctic. However, based on a study of 12 lakes in sub-Arctic and alpine northern Sweden (64-68° N), Karlsson *et al.* (2009) have shown that within natural variations of nutrient and organic carbon input, unproductive lakes are primarily light limited (through interactions with colored terrestrial organic matter) and not nutrient limited. In general terms, lower productivity of basal components of the food web results in slower growth and longer-lived organisms such as fish and invertebrates (Wrona *et al.* 2005, 2006a, Reist *et al.* 2006a, 2006b). In addition to nutrient/light limitations, changes in freshwater ice cover (duration, thickness and optical quality) has also been proposed by CAFF (2010) as a key ecosystem indicator of climate-change-related impacts on freshwater biodiversity (see Box 13.1).

The annual cyclicity of processes in Arctic aquatic ecosystems is also relatively high, which in turn has resulted in various adaptations in the organisms that thrive there. In animals, such adaptations include high rates of con-

## Box 13.1. Effects of decreased freshwater ice cover duration on biodiversity

Freshwater ice is an integral part of the cryosphere and related hydrologic regimes of cold environments and exerts an enormous influence over key physical and ecological processes in both lentic and lotic systems (CAFF 2010, Prowse & Brown 2010b, 2010c, AMAP 2011b, Prowse *et al.* 2011c). These processes include, for example, the inputs and spectral signature of solar radiation important for photobiological and photochemical processes, ultraviolet radiation, atmosphere-water body gas exchanges, heat budget, stratification and mixing regime, bio-geochemical dynamics and the entrainment of terrestrial inputs, including contaminants (reviewed by Vincent *et al.* 2008). Specific to lotic systems, river ice affects the productivity and diversity of instream and riparian habitat, sediment transport and river morphology and hydrologic extremes such as low flows and floods (Prowse 2001, Prowse & Culp 2003, Prowse *et al.* 2006a).

The duration of freshwater ice cover is strongly controlled by climate (Walsh *et al.* 1998, Prowse *et al.* 2002, 2010a, 2010b, 2010c). In Arctic freshwater systems, the duration of ice cover has decreased by an average of almost two weeks over the last 150 years (Prowse & Brown 2010b, 2010c), with earlier break-ups and later freeze-ups. As the climate warms, longer open-water conditions will prevail. In lentic systems, decreased ice cover is linked to increases in aquatic plant and algae productivity and taxonomic shifts in both algae and invertebrates (Smol *et al.* 2005). The changes in diatom community and abundance resulting from changes in ice cover are pronounced enough that they can be used to reconstruct climate conditions millennia into the past (Smol & Douglas 2007a, 2007b). Changes in productivity and species composition resulting from changes in ice cover are likely to have cascading effects on the entire aquatic ecosystem. Ice cover and related temperature effects are also linked to fish habitat either as preserving habitat for some cold-water species or as a barrier preventing the colonization of cryospherically dominated systems by warm-water species. As such, decreased ice cover will likely lead to reductions in the range of cold-water species while increasing the likelihood of species invasions into northern aquatic ecosystems from the south. In lotic systems, reductions in ice cover will result in fewer ice-dam flood events and reductions in the severity of break-up ice scouring, which are processes that are critical in nutrient and organic matter dynamics, spring water chemistry and the abundance and diversity of river biota (Prowse *et al.* 2006b, 2011c). Lake and river ice are also critical for the transportation routes of northern communities, either as an economical means for the hauling of commercial goods or for travel onto the land as part of traditional subsistence lifestyles.

Given the strong influence of climate on the extent and duration of ice cover on freshwater systems, projected climate warming has raised concern about related changes in freshwater ice. Further study including extensive monitoring of freshwater ice regimes and their related ecosystems is critical to increasing our capacity to understand and therefore predict the changes occurring in these vital systems.

sumption of food when it is available and rapid conversion of food to lipids for storage. Additionally, some groups (e.g. fish, waterfowl) exhibit highly migratory behavior to optimize life-history functions resulting in movements between different habitats triggered by environmental and geophysical cues (e.g. temperature drop, sun height), which usually coincide with transitions between particular seasons (Wrona *et al.* 2005, Reist *et al.* 2006a, 2006b, Power *et al.* 2008).

Although freshwater ecosystems are especially abundant in the Arctic, they do not generally support the levels of biodiversity found in more southerly regions (Wrona *et al.* 2005, Wrona *et al.* 2006b). For example, fish species diversity is low at both regional and local scales in high latitudes (Matthews 1998, Reist *et al.* 2006a, 2006b); however, considerable diversity of the fishes exists below the species level and contributes significantly to the functionality of the ecosystem (see Christiansen & Reist, Chapter 6). Yet, high latitude freshwater ecosystems support both taxonomically and functionally diverse biota (Heino 2008, Erős *et al.* 2009), and differences among northern regions may be considerable (Heino 2001, Heino & Toivonen 2008). In addition, the diversity of microbial communities in certain Arctic freshwater systems has been found to be equivalent to or greater than their counterpart environments in more southerly latitudes (Comeau *et al.* 2012, Charvet *et al.* 2012).

The regional numbers of freshwater species typically decrease sharply poleward even within the boreal-Arctic region alone (Heino & Toivonen 2008, Heino 2009). Due to such strong relationships of freshwater biodiversity to latitude and co-varying climatic factors, the responses of various organism groups to climate change by latitudinal range shifts are likely to be straightforward. This is because the northern range margins of many freshwater species are largely determined by temperature (Chu *et al.* 2005, Sharma *et al.* 2007). However, the rapidity of the range shifts is likely to vary between different species, for example, depending on (1) species' dispersal capability, (2) their ability to colonize local communities in the new areas and produce viable populations there, and (3) their ability to persist during the set-back years with less suitable weather that may occur embedded in the otherwise long-term warming trend (Hellmann *et al.* 2008, Pöyry *et al.* 2009). These responses are likely to be seen not only in increased regional species numbers, but may also have various effects on community structure, food web dynamics and ecosystems characteristics at the local scale (Schindler 1997, Poff *et al.* 2002, Quinlan *et al.* 2005, Wrona *et al.* 2006a, Woodward *et al.* 2010).

### 13.2.2. Environmental stressors

Freshwater systems are in constant transition and are highly vulnerable to global change (Carpenter *et al.* 1992, Allan *et al.* 2005, Dudgeon *et al.* 2006, White *et al.* 2007, Moss *et al.* 2009, Geist 2011). Consequently, the observed patterns of freshwater biodiversity and resulting stability and resilience of ecosystem structure and function are influenced by the magnitudes, rates of change and interactions among key environmental and anthropogenic drivers that can affect physical, geochemical and ultimately biological and ecological properties, processes and interactions. The Millennium Ecosystem Assessment (MEA 2005) defined a 'driver' as any natural or human-induced factor that directly or indirectly causes a change in an ecosystem. Environmental drivers are related to physical, chemical and biological factors, while anthropogenic drivers are associated with human activities that can affect species, their distribution and abundance, and ecological function (Hooper *et al.* 2005, Carpenter *et al.* 2006, Nelson *et al.* 2006).

Fig. 13.1 illustrates the inter-relationships among dominant environmental and anthropogenic drivers and their potential effects on freshwater ecosystems and related ecological services. Freshwater ecosystems provide a variety of ecological goods and services of critical importance to humans at local, regional and global scales, yet they are globally among the most heavily altered ecosystems with a disproportional loss of related biodiversity (Geist 2011). Globally, land use change, invasive species and climate change are considered to be the three main threat factors for these ecosystems (Sala *et al.* 2000). However, the impacts of these drivers are likely to vary globally, with freshwater ecosystems in the Arctic (high latitudes) being more strongly threatened by climate variability and change than other environmental and anthropogenic drivers (ACIA 2005, IPCC 2007, Malmqvist *et al.* 2008, Heino *et al.* 2009, Woodward *et al.* 2010, AMAP 2011b). Understanding the complex interactions among drivers and their combined, cumulative effects on structural and functional biodiversity of freshwater systems remains a key scientific and management challenge, as exemplified by subsequent sections in this and other ABA chapters.

## 13.3. ECOSYSTEM-SPECIFIC PATTERNS IN BIODIVERSITY

A variety of freshwater ecosystem types occur in the Arctic, and these in turn display a significant diversity in associated habitat structure over a wide range of spatial and temporal scales (Huryn *et al.* 2005, Vincent & Laybourne 2008, Moss *et al.* 2009). They often form a continuum, ranging from ephemeral shallow ponds to large lakes, small intermittent streams to permanently flowing large rivers, as well as intricate wetland complexes comprised of fens, bogs and marshes. In northern latitudes, hydrological processes and thus associated freshwater systems are controlled by local and regional

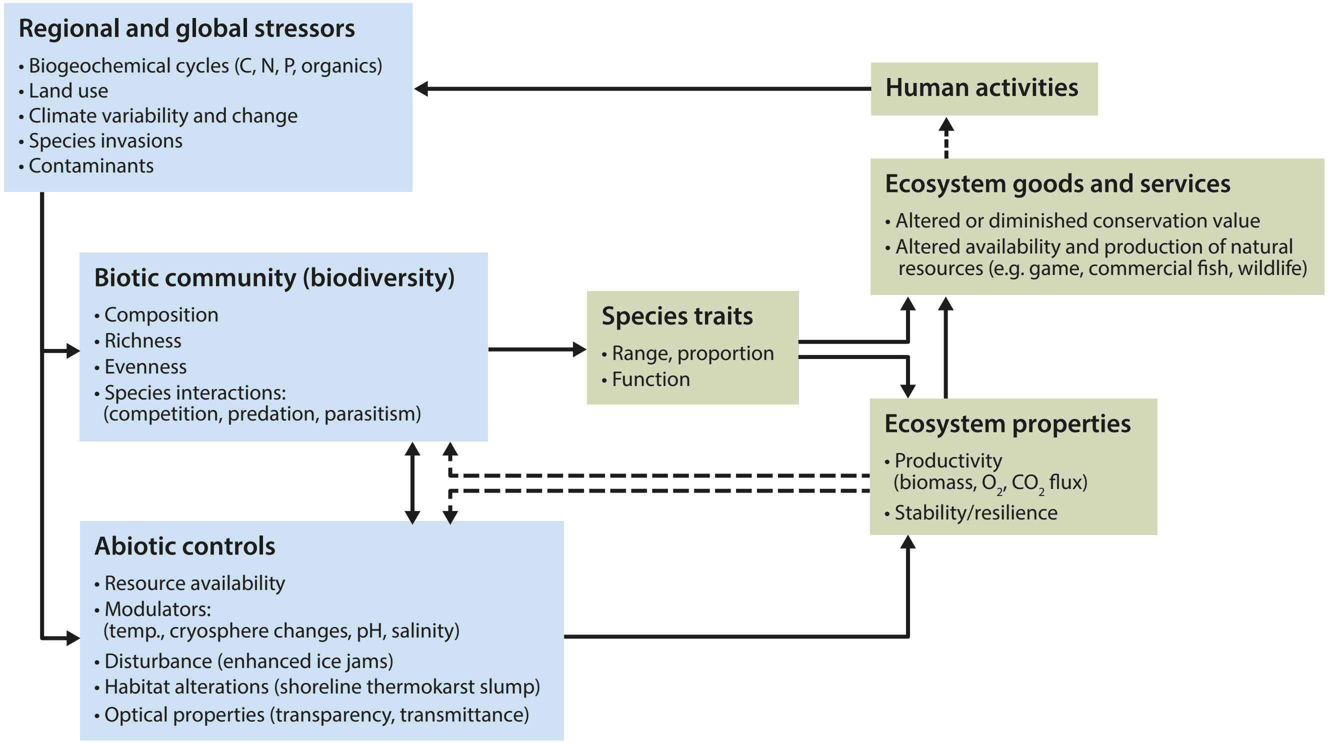


**Figure 13.1.** The inter-relationships among dominant environmental and anthropogenic drivers and their potential effects on freshwater ecosystems and related ecological services. Dashed lines represent the potential feedbacks to the biotic community (either directly or indirectly) via abiotic controls that occur when ecosystem properties are modified by various stressors. Further feedbacks occur as we modify our activities in response to changes (impoverishment) in ecosystem goods and services. (Adapted from Hooper *et al.* 2005).

geology, landscape geomorphology and catchment characteristics such as the associated terrestrial vegetative cover and the presence or absence of permafrost (White *et al.* 2007). Collectively, these attributes affect the physical and geochemical properties of freshwater environments and their related habitat quality and quantity. Since freshwater systems form an often highly interconnected network at the landscape scale, they serve as important integrators of hydrological, atmospheric and terrestrial processes (Williamson *et al.* 2009).

Below, we describe the distribution and key ecological properties of each freshwater ecosystem type and provide an overview of the associated general patterns of structural and functional biological diversity.

### 13.3.1. Lake/pond ecosystems

Many areas of Arctic North America and Eurasia are lake-rich, and in some regions lake/pond complexes can cover > 80% of the total land surface area (Mackay 1992, Yoshikawa & Hinzman 2003, Pienitz *et al.* 2008, Kling 2009, Marsh *et al.* 2009, Rautio *et al.* 2011). The Arctic also contains a multitude of lake types, the most common being post-glacial lakes remaining from the Pleistocene, those that evolved subsequently in the glaciated environment, and thermokarst or 'thaw'-lakes and ponds (Prowse & Brown 2010a, 2010c). Rarer lake types include meteoritic impact crater lakes, stamukhi, epishelf, karst, tectonic and volcanic lakes (McNight *et al.* 2008, Pienitz *et al.* 2008). Lakes are generally more abundant in glaciated, permafrost peatland areas (~ 14.4 lakes/1,000 km$^{2)}$ and least abundant in unglaciated, permafrost-free regions (~ 1.2 lakes/1,000 km$^2$) (Smith *et al.* 2007).

Deep lakes can be defined as those having a mean depth of > 10m. In the high Arctic, they only weakly stratify if at all, whereas deep lakes in the low Arctic usually display seasonal thermal stratification. Shallow lakes with maximum depths of < 10 m typically show no or periodic thermal stratification. There are notable exceptions, however. For example, 2-4 m deep thermokarst ponds in Nunavik, Canada, have been found to stratify through most of the year, resulting in anoxic bottom waters and high rates of methane generation (Laurion *et al.* 2010). Similar to lower latitude lakes, Arctic lakes vary in size and type across the Arctic landscape. Many are sustained by water sources primarily from the local catchments, such as spring melt from snow accumulation and runoff (Wrona *et al.* 2005). The physical and chemical characteristics of lakes vary by location with the associated catchment geomorphology and underlying geology playing important roles in affecting lake morphometry and water quality. Local catchments vary significantly across the Arctic region. For example, catchments with lush vegetation in the forest-tundra zone immediately south of the Arctic are different than those in the sparsely vegetated polar desert zone in the extreme northern part of the Arctic (Vincent & Hobbie 2000, Vincent & Laybourn-Parry 2008).

Arctic lakes are generally low in nutrients and can be broadly classified as ultraoligotrophic to oligotrophic, with smaller shallower lakes typically more oligotrophic than large lakes (Vincent & Hobbie 2000, Vincent & Laybourn-Parry 2008). Depending on latitude and altitude, the abundance (or lack) of vegetation in the surrounding catchment determines the allochthonous inputs to the lakes during spring snowmelt. Autochthonous production is considered low and limited to the ice-free season, although increasing evidence suggests that the extent of winter productivity is underestimated (Vincent & Laybourn-Parry 2008). In large deep lakes, the shallower littoral zones are often the only areas of high primary productivity in the summer months owing to warming water and more light penetration.

Thermokarst lakes and ponds are generally the most abundant and productive lentic ecosystems in the lowland regions of northern Siberia (Hinzman *et al.* 2005), western and northern Alaska (Hinkel *et al.* 2005) and northern Canada (Kokelj *et al.* 2005, Lantz & Kokelj 2008, Marsh *et al.* 2009). They are generally relatively productive and contain abundant and diverse communities of aquatic biota including bacterioplankton, phytoplankton, zooplankton, benthic invertebrates, submerged aquatic plants and associated birds (Vincent *et al.* 2008). Thermokarst lakes often have significant seasonal terrigenous inputs (predominantly during spring melt and with associated overland runoff), often resulting in elevated concentrations of anions/cations, nutrients, dissolved organic carbon and associated high turbitity (Rautio *et al.* 2011). Retrogressive shoreline thaw slumping in these lakes has been shown to produce significant shifts in lake geochemistry and phytoplankton relationships (Thompson *et al.* 2012). Slump-affected thermokarst lakes were found to have elevated levels of major ions but had clearer water than unaffected systems (Kokelj *et al.* 2009). Correspondingly, Mesquita *et al.* (2010) found higher macrophyte species richness and biomass in slump-affected compared with unaffected lakes. Because of their wide Arctic distribution and their apparent sensitivity in geochemical and biological responses to climatic and cryospheric changes, the appearance and disappearance of thermokarst lakes has been identified as a key indicator of ecosystem and related freshwater biodiversity change by CAFF (2010) (see Box 13.1).

Shallow Arctic ponds have maximum depths of < 2 m, contain low water volumes and have higher surface area compared with depth (i.e. a typical tundra pond in the high Arctic is less than 1 ha in area and up to 0.5 m deep; AMAP 1998) and typically freeze to the bottom for up to 10 months out of the year (Wrona *et al.* 2005, Smol & Douglas 2007b). They are subject to high seasonal variation and fluctuations in light, temperature and allochthonous inputs of nutrients and major ions from snow/permafrost melt and atmospheric inputs (Rautio *et al.* 2011). Most shallow ponds are oligotrophic in terms of nutrient concentrations in the water column, although nutrient concentrations within the benthic microbial mats they often contain can be several orders of magnitude higher (Villeneuve *et al.* 2001, Rautio & Vincent 2006). In the many tundra ponds that freeze to the bottom in winter, nutrient limitation results in the detrital food web being an important energy transfer pathway in these systems (Wrona *et al.* 2005). Shallow lakes and ponds are often dominated by macrophytes and benthic bacteria, algae and zooplankton (Hobbie 1980, Wrona *et al.* 2005). Fish are generally absent, often resulting in high zooplankton abundance.

#### 13.3.1.1. Changes in pond/lake distribution and abundance

In permafrost regions of the Arctic, the sequence of pond and lake initiation, development and disappearance are natural landscape processes (Sellmann *et al.* 1975, White *et al.* 2007). More recently, in many regions throughout the Arctic and sub-Arctic alterations in the magnitudes and rates of lake appearance and disappearance have been increasingly linked to a more variable and changing Arctic (Hinzman *et al.* 2005, Prowse & Brown 2010a, 2010c, AMAP 2011b, Smith *et al.* 2005, 2007, Smol & Douglas 2007a, 2007b). Consequently, CAFF (2010) proposed that a key indicator of ecosystem change that has significant regional and circumpolar implications on the status and trends of biodiversity in Arctic lake and pond ecosystems is an alteration in their distribution and associated appearance and disappearance on the landscape (Prowse & Brown 2010a, 2010c; Box 13.2). Both increases and decreases in pond and lake area have been related to climatic processes and related interactions with thawing permafrost and alterations in local and regional precipitation or evaporation regimes (White *et al.* 2007).

Smith *et al.* (2007) conducted a comprehensive geographical analysis of approximately 200,000 lakes to identify possible first-order controls on lake abundance and land-area fraction at the circumpolar scale. Glaciation history and the presence of some form of permafrost were found to be the most important geophysical determinants to the existence of lakes, with lake densities and area fractions averaging ~ 300-350% greater in glaciated (versus unglaciated) terrain, and ~ 100-170% greater in permafrost-influenced (versus permafrost-free) terrain. The presence of peatlands was found to be associated with an additional ~ 40-80% increase in lake density and ~ 10-50% increases in area fraction. Therefore, on average, lakes were found to be most abundant in glaciated, permafrost peatlands and least abundant in unglaciated, permafrost-free terrain.

Spatial distribution, level of persistence and physical connectivity, and regional abundance collectively contribute to the patterns of freshwater biodiversity observed in Arctic lake/pond systems. Smith *et al.* (2007) estimated that for all glaciated/lowland Arctic and sub-Arctic terrain (~ 27 million km$^2$), ~ 48% was in some state of permafrost. They projected that in a possible future 'permafrost-free' Arctic, the number of lakes could be reduced by ~ 46% and their total inundation area reduced by ~ 42%. In a related analysis, Smith *et al.* (2005) found a widespread decline in lake abundance and area in Siberia between 1973 (~ 10,882 lakes > 40 ha) and 1997-98 (9,712 lakes), a loss of ~ 11%. Similarly, Marsh *et al.* (2009), examining the rate of thaw lake drainage in the western Canadian Arctic from 1950 to 2000, found that 41 lakes drained at a rate of slightly less than one lake per year; however, the rate of decadal decline was not constant over the period.

Understanding the complex interactions between climate, landscape geomorphology and the hydrology responsible for this change will be critical to fully understanding and predicting causal mechanisms of changes in corresponding regional and circumpolar aquatic biodiversity patterns.

#### 13.3.1.2. Fish community diversity patterns

Less than 1% of all anadromous and freshwater fish species occur in Arctic freshwater systems, and detailed long-term data on fish community structure for many Arctic and sub-Arctic lakes is lacking (Power 1997, Power *et al.* 2008; see also Christiansen & Reist, Chapter 6). Only a few year-round investigations have ever been conducted on fish communities in high Arctic lakes (Svenning *et al.* 2007, Amundsen & Knudsen 2009). In general, high-latitude lakes display low fish abundance and diversity, with Arctic char *Salvelinus alpinus* often being the most numerically dominant (Power *et al.* 2008). Arctic lakes typically have low productivity, support small fish populations with slow growth rates although biomass may be high (Sierszen *et al.* 2003), and display short, simple food webs dominated by a few species (e.g. Arctic char, lake trout *Salvelinus namaycush*, lake whitefish *Coregonus clupeaformis*; Power *et al.* 2008).

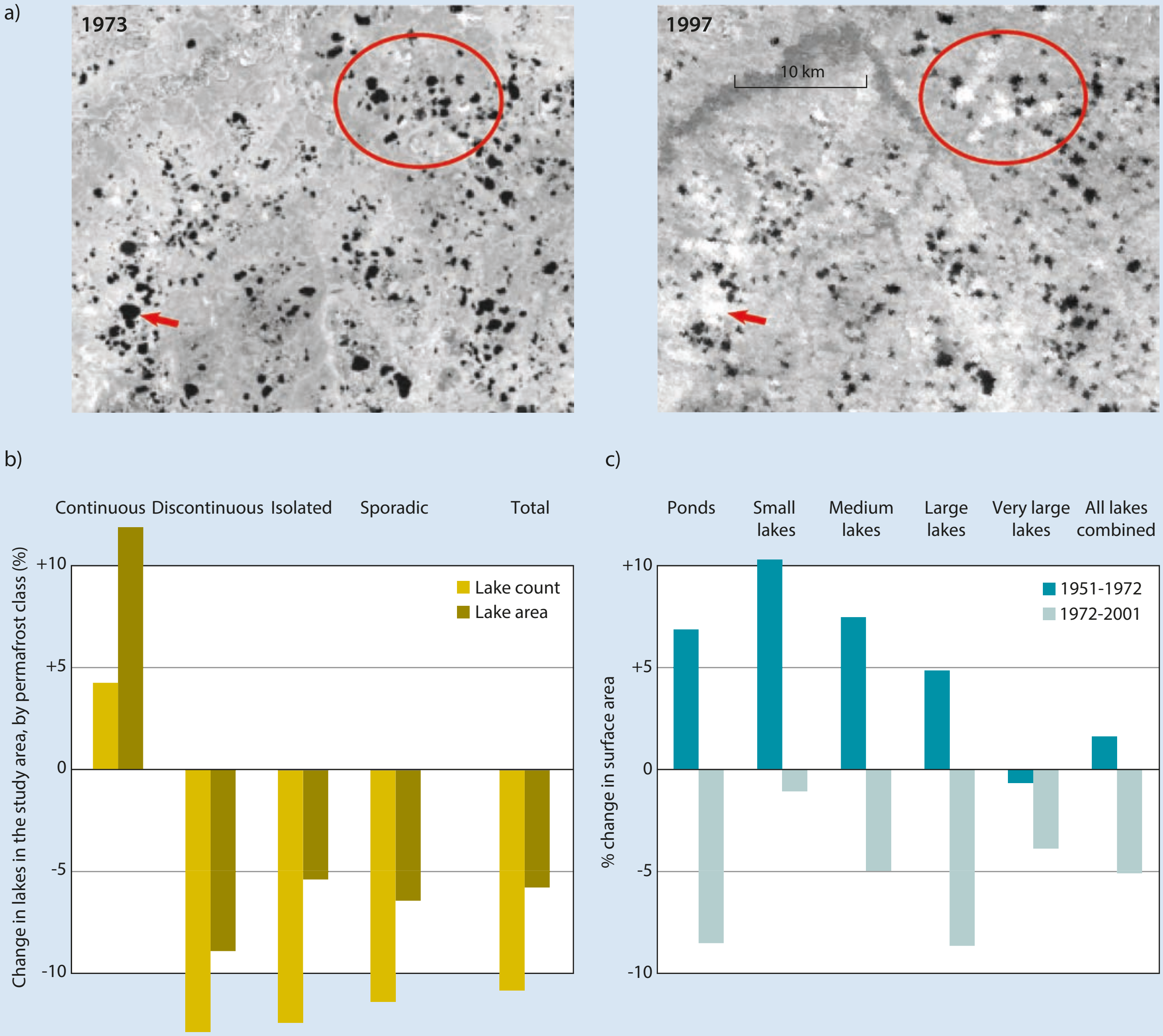
Hershey *et al.* (2006) show that the distribution and related biodiversity of fish species in Arctic lakes is dynamic and influenced primarily by landscape-related features that control species colonization and extinction probabilities. Examining 168 Arctic Alaska lakes, they accurately predicted the presence of fish species in approximately 78% of cases and absence in 75% using physical features such as lake size, depth, outflow gradient, distance to other lakes, lake order, altitude, river connectivity and drainage and age of the glacial surface. Collectively, these factors either affect access of fish to a lake (i.e. colonization potential) or survival in a lake once colonized (i.e. extinction potential).

Ecosystem productivity, food availability and resource partitioning are additional key ecological factors affecting the dietary habits and related structure and biodiversity of fish communities in Arctic lakes (Reist *et al.* 2006a, 2006b, Power *et al.* 2008). For example, Langeland *et al.* (1991) found adult Arctic char and brown trout *Salmo trutta* in sub-Arctic lakes to display similar dietary preferences in allopatry, however when sympatric, brown trout tended to dominate littoral areas and Arctic char were displaced to forage in more open, offshore environments. Svenning *et al.* (2007)

## Box 13.2. Appearing and disappearing lakes and their impacts on biodiversity

The majority of Arctic lakes are thermokarst lakes, formed within depressions left by thawed permafrost (Mackay 1992, CAFF 2010, Prowse & Brown 2010a). These lakes and ponds are the most abundant and productive aquatic ecosystems in the Arctic. The extent of northern latitude lakes is such that they represent a significant portion of global greenhouse gas/carbon budgets (Cole *et al.* 2007). Thermokarst lakes are biological 'hotspots' and critical habitat for abundant microbes, benthic communities, aquatic plants, plankton, fish and birds (Vincent *et al.* 2008). These systems are also vital for Arctic peoples and play a central role in traditional subsistence lifestyles as well as a source of freshwater for communities, especially where groundwater is unavailable (White *et al.* 2007).

Lake drainage and formation events are a significant process in landscape formation in continuous permafrost regions (Frohn *et al.* 2005). For example, it is estimated that thousands of thermokarst lakes have been lost in the western Canadian Arctic through this process since their formation during a post-glacial warm period between 13,000 BP and 8,000 BP (Mackay 1992). With current and projected increases in temperature and climate variability (ACIA 2005, IPCC 2007), there is concern that patterns of lake disappearance and appearance, changes in lake area and the role of lakes in the global climatic system may change. For example, it was recently discovered that some lakes in the high Arctic, which paleolimnological data indicate have been permanent water bodies for millennia, are drying out completely (Smol



**Box 13.2 Figure 1.** (a) Satellite images depicting the decline of total lake abundance in areas of discontinuous permafrost (circled) while lake abundance and surface area increased in areas of continuous permafrost between 1973 and 1997-98, (b) Percent change in lake count and area by permafrost class (from Smith *et al.* 2005) and (c) Change in total lake surface area by lake size in the Old Crow Basin, northern Canada (from Labrecque *et al.* 2009).

& Douglas 2007b). While most studies have found that there is a net decrease in the number of thermokarst lakes over the past fifty years (Frohn *et al.* 2005, Hinkel *et al.* 2005, 2007, Marsh *et al.* 2009), it seems to depend on the extent of the permafrost in the region in question. Smith *et al.* (2005) reported increases in lake surface area and number within regions of Siberia with continuous permafrost, while decreases were observed in areas of discontinuous permafrost (Box 13.2 Fig. 1a, b). Increases are believed to be related to the effects of surface permafrost thawing, while the decreases are linked to taliks completely penetrating the permafrost to the underlying groundwater system causing drainage or, are the result of drying (Smith *et al.* 2005, Smol & Douglas 2007b). Furthermore, patterns of lake abundance and surface area may vary over time and depend on lake size as observed in a study of lakes in the western Canadian Arctic (Box 13.2 Fig. 1c). While most lakes in the early time period (1951 to 1972) gained surface area, the more recent trend (1972-2001) has shown decreasing surface area particularly in ponds and large lakes (Labrecque *et al.* 2009). In a recent study, Vincent *et al.* (2011) also found surface area increases in thermokarst lakes in the eastern Arctic. Often, however, the precise mechanisms, particularly of lake disappearance, are unknown (Hinkel *et al.* 2005, 2007, Marsh *et al.* 2009).

The appearance and disappearance of lakes in the Arctic is likely to be a multi-faceted issue as the effects of climate change intensify, as exemplified by the longest systematic limnological and paleolimnological monitoring records from the Cape Herschel (Ellesmere Island, Nunavut) region in the Canadian high Arctic (e.g. Smol & Douglas 2007b). Given their central role as ecological focal points, both aquatic and terrestrial/transient species including waterfowl are likely to be affected. The traditional practices of indigenous peoples, particularly those involving subsistence fisheries or small mammal harvesting, are also likely to be impacted (Reist *et al.* 2006a, 2006b). Access to water for municipal or industrial use may also become a challenge with further climate change.

However, more research about the processes controlling lake formation and loss in different permafrost regimes is still required to be able to make robust links to changes in climate, especially where the effects of simple air temperature warming can be confounded by other changes, such as in precipitation and the related hydrologic system in which such lakes exist (AMAP 2011b).

found Arctic char in a high Arctic lake in Svalbard to feed at all times of the year, with the diet of smaller size classes (< 15 cm) varying strongly with season, while larger fish (> 15 cm) were mostly cannibalistic over the entire year. L'Abee-Lund *et al.* (1993), studying Arctic char in five boreal Norwegian lakes, found that juveniles foraged mainly in epibenthic habitats but displayed both an ontogenetic and phenological habitat shift by foraging primarily in the pelagic zone in the summer when they reached a body size of > 13 cm. Sierszen *et al.* (2003) highlight the importance of zoobenthic production and consumption, especially in oligotrophic Arctic lakes where nutrient limitation constrains plankton production thus affecting the structure and food energy utilization pathways of resident fish communities. Stable isotope analyses of the fish food web structure in the oligotrophic lake Pulmankijärvi, sub-Arctic Finland, revealed that littoral production dominates the energy flow to most of the resident fish populations. While Arctic char in northern Fennoscandian lakes have also been shown to rely on littoral energy sources in small lakes, there is evidence of them shifting to pelagic energy sources with increasing lake size (Eloranta 2013).

A comprehensive study and census of fish populations in 3,821 boreal Nordic lakes by Tammi *et al.* (2003) further illustrates how anthropogenic drivers such as lake acidification, eutrophication and stocking additionally affect fish community structure and biodiversity (see also Section 13.4). In total, 51 fish species were reported, with the most frequent being perch *Perca fluviatilis*, pike *Esox lucius*, brown trout, roach *Rutilus rutilus* and burbot *Lota lota*. Perch were the most common species in Finland and Sweden, while brown trout occur in ca 50% of lakes in the western part of north Norway arising from stocking over the last 50-70 years. Human-induced acidification was determined to be the most important cause of the observed decline of fish communities in Sweden and southern Norway. In contrast, no general patterns of fish species extinction were found to be directly associated with eutrophication, although cyprinid stocks increased in eutrophic lakes. Interestingly, fish stocking was found to be the primary casual factor affecting observed patterns of fish biodiversity in lakes, although habitat alterations related to climate change were identified as a growing concern.

It is evident that, from an ecosystem perspective, understanding the causal mechanisms producing the present and projected patterns of fish community diversity in Arctic lakes requires comprehensive, long-term fish community information coupled with measurements of pertinent environmental data at appropriate spatial and temporal scales.

#### 13.3.1.3. Diversity of planktonic and benthic organisms

Despite extreme climactic conditions including a winter season that can last up to nine months of the year, planktonic and benthic communities in Arctic lakes can be very productive and, in some Arctic lakes, may even equal the production in lakes at lower latitudes (Vincent & Laybourn-Parry 2008). Reflecting the increasingly harsh conditions, biodiversity decreases with increasing latitude.

Species number of phytoplankton in Arctic lakes ranges from 20 to 150 per lake and has been found to correlate with latitude, altitude or water temperature, while species composition is mainly determined by water chemistry (Moore 1979, Forsström *et al.* 2009). Chrysophytes are often the most dominant algal group (Moore 1979, Forsström *et al.* 2009, Charvet *et al.* 2012), although the most abundant photosynthetic cell type in these waters may be picocyanobacteria (reviewed in Vincent & Quesada 2012). There is not enough uniformly collected and analyzed data to make comparisons between various Arctic regions. At a global scale, phytoplankton species richness is highest in oligotrophic lakes (Dodson *et al.* 2000), which means that Arctic lakes can be expected to have relatively high numbers of species. This is often the case, especially in shallow lakes that include many semi-planktonic species of desmidiales and bacillariales (Forsström *et al.* 2009). However, some Arctic lakes seem to have, at least seasonally, a pronounced dominance pattern where the phytoplankton community is heavily dominated by a few species only (Forsström *et al.* 2009). On the other hand, mass developments such as blooms of harmful blue green algae or nuisance-causing raphidophyte *Gonyostomum semen* do not usually occur in Arctic lakes.

The distribution of zooplankton species in Arctic lakes depends largely on geographic location and in particular correlates with the distance from locations that escaped glaciation in the Pleistocene period (see also Hodkinson, Charpter 7). These locations, roughly corresponding to present-day Alaska and northernmost Greenland, subsequently served as origins of recolonization and hence species richness is greatest close to these areas (Samchyshyna *et al.* 2008, Rautio *et al.* 2011) (Fig. 13.2). Furthermore, species originating from marine populations are also known to contribute to greater species richness in coastal areas (Rautio *et al.* 2008).

Zooplankton density and biomass in shallow Arctic lakes can be considerable despite the typically low concentration of water column nutrients (O'Brien *et al.* 2004, Rautio & Vincent 2006). This may be due to the presence of periphytic microbial mats (discussed in greater detail below) that are common in many Arctic lakes (Rautio & Vincent 2006). In fishless lakes, the abundance of zooplankton is predicated on food supply and the ability to survive cold conditions (Rautio *et al.* 2008), while the zooplankton community in lakes with fish is dependent on the assemblage of fish present (O'Brien *et al.* 2004, Hershey *et al.* 2006). Lakes with fish typically have lower macroinvertebrate species richness and small-sized individuals than fishless lakes (Tate & Hershey 2003, O'Brien *et al.* 2004). Furthermore, in a series of lakes dominated by whitefish *Coregonus* sp. differing in number of gill rakers, it was shown that lakes dominated by species with a high number of gill rakers had a smaller size distribution of zooplankton compared to lakes where the dominant fish species had few gill rakers (Kahilainen *et al.* 2010).

Most Arctic lakes being shallow and oligotrophic with high transparency are favorable for well-developed benthic algal communities, often in the form of microbial mats dominated by cyanobacteria (reviewed in Vincent & Quesada 2012). Algae belonging to Bacillariophyceae, Conjugatophyceae and Chlorophyceae are also common in the mats (Maltais & Vincent 1997). Diversity of periphytic diatoms in the Canadian Arctic has been shown to be inversely related to latitude and explained partly by length of the growing season (Michelutti *et al.* 2003, Douglas & Smol 2010). Diatom assemblages in northern Fennoscandia, Canada and Siberia show high similarity to each other when corresponding ecoregions (e.g. sub-Arctic forest-tundra and Arctic tundra) are compared, and are mainly driven by water chemistry and habitat

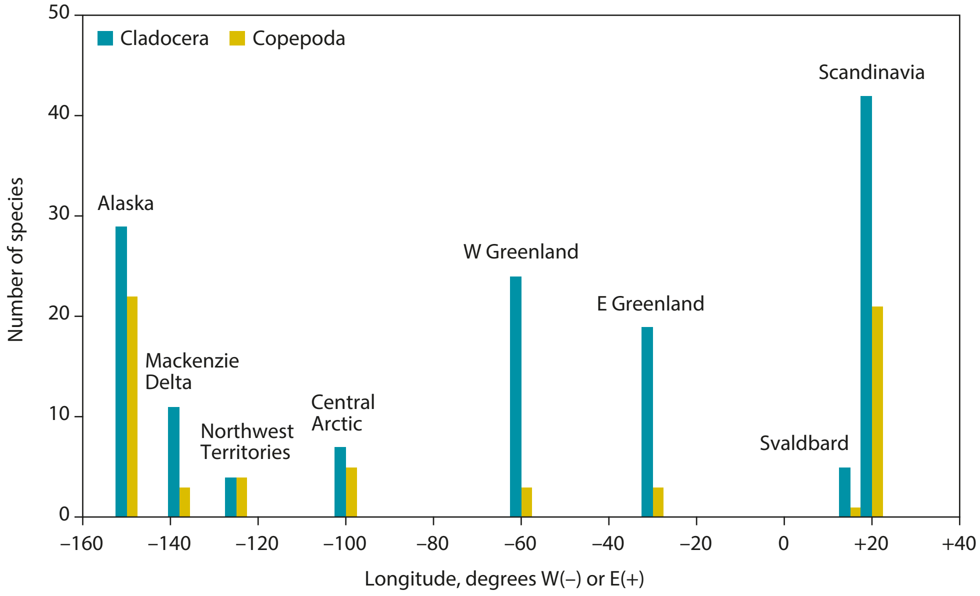


**Figure 13.2.** Species number of water fleas Cladocera and copepods along a longitudinal gradient 68-78° N in different high latitude regions in North America and northern Europe (from Rautio *et al.* 2011).

affinities rather than geographical positioning (Pienitz *et al.* 1995). With the exception of diatoms, studies dealing with benthic algal diversity are extremely rare at high latitudes, and there is not enough information available to make comparisons between various Arctic areas.

The benthic invertebrate community is well-developed and abundant in Arctic lakes although species number is lower than in temperate regions (see also Hodkinson, Charpter 7). The species present are mostly cold stenotherms. The lake littoral areas in the Arctic provide similar habitats for benthos to those of rivers. The oxygen supply is rich, and the detritus accumulation from above is insignificant. Insect larvae, especially midges Chironomidae constitute most of the macrobenthic fauna. Central Canadian Arctic islands including Devon and Cornwallis Islands have the most severe environment for aquatic insect survival and, as a consequence, the lowest diversity. Abiotic conditions largely define the species distribution (Nyman *et al.* 2005).

Climate-change-related permafrost thaw can have significant effects on the geochemistry of Arctic lake and stream systems, and can alter both light and nutrient availability for planktonic and benthic biota. In small tundra lakes in the western Canadian Arctic, permafrost degradation causing large amounts of sediments rich in clays and ions to enter the lacustrine environment has led to a counterintuitive clearing of the water column (Mesquita *et al.* 2008, Thompson *et al.* 2008). The clearing is likely caused by the adsorption and settling of colored dissolved organic carbon to the charged clays and ions entering the lake (Thompson *et al.* 2008, 2012). This mechanism has been postulated to be responsible for the observed significant shifts in light availability and increases in macrophyte and macroinvertebrate biomass in affected lakes (Mesquita *et al.* 2010). A paleolimnological investigation into some of these affected lakes also found an increase in both abundance and diversity of periphytic diatoms coinciding with the timing of historical thaw-slump initiation (Thienpont *et al.* 2013). Studies from NE Greenland have shown that warmer seasons imply higher nutrient concentrations, caused by increased loading of nutrients and humus from the catchment when the active layer melts, and lead to a higher abundance of phytoplankton and zooplankton (crustaceans) and altered species composition (Christoffersen *et al.* 2008). Moreover, in small streams in Alaska a similar type of permafrost degradation led to a detectable but spatially limited nitrate and phosphate enrichment (Bowden *et al.* 2008). Because of the differing mineral content in permafrost *vs.* the overlying active layer, geochemical stream water sampling has even been used to monitor permafrost thaw depth increases over time (Keller 2007). While these effects have implications for freshwater biota, the specific impacts of permafrost thaw depend on the presence or absence of ground ice and water, the geomorphic characteristics of thaw and the permafrost parent material. Ground ice content of permafrost determines in large part the susceptibility of a permafrost landscape to geomorphic change, such as thermokarst development, with rising air temperatures. Permafrost ground ice content varies longitudinally in the circumpolar Arctic. Areas with high ground ice content within thick layers of overburden are found in the western Canadian Arctic, the North Slope of Alaska and parts of northeastern Siberia (Zhang *et al.* 2008). High-ice-content permafrost in thin overburden layers are located over much of the Northwest Territories and Nunavut in Canada together with much of Siberia (Zhang *et al.* 2008).

### 13.3.1.4. Diversity and productivity of aquatic macrophytes

Shallow ponds (< 2 m maximum depth and frozen to the bottom in winter) are often characterized by an encircling fringe of emergent macrophytes (e.g. sedges such as water sedge *Carex aquatilis* but also pendantgrass *Arctophila fulva* and tall cottongrass *Eriophorum angustifolium*; e.g. Hobbie 1984a, Henry 1998) and a central open-water zone. Because of their shallow depth and small volume, ponds thaw earlier than lakes and may achieve water temperatures in excess of air temperature (Douglas *et al.* 1994). These factors contribute to shallow water bodies such as wetlands and ponds being the most productive freshwater habitats in the Arctic.

Arctic lakes (> 5 m maximum depth and a deep central zone, with ice present year round in northerly locations) exhibit a range of growing conditions, largely related to latitude and nutrient supply. Tundra lakes (i.e. lakes usually found on low-lying landscapes such as coastal and interior plains) are typically low in nutrients due to inherently little organic matter in the watershed combined with a low rate of decomposition. Sub-Arctic tundra lakes are typically fringed by emergent macrophytes such as sedges (e.g. water sedge and beaked sedge *Carex rostrata*) and water horsetail *Equisetum fluviatile*. Shallow waters are inhabited by species such as mare's tail *Hippuris vulgaris*, northern bur-reed *Sparganium hyperboreum*, thread-leaved water crowfoot *Ranunculus trichophyllus* and autumn water-starwort *Callitriche hermaphroditica*, while deeper waters are typically colonized by submersed forms such as water milfoil *Myriophyllum* spp., various pondweed species *Potamogeton* spp., quillworts *Isoëtes* spp., muskgrasses *Chara* spp. and mosses (e.g. Jensen & Christensen 2003, Mesquita *et al.* 2010). Lakes that are nutrient rich (because they occur in a river floodplain or receive runoff from enriched soils such as raised marine deposits) show a more diverse macrophyte flora (e.g. lakes in the Mackenzie River Delta, Canada; Squires *et al.* 2002, 2009).

Arctic lakes are typically nutrient poor (oligotrophic) and completely frozen over for nine months of the year or longer, with water temperatures consistently low (i.e. often < 5 °C; Schindler *et al.* 1974). Benthic mosses are usually the only macrophytes present in such lakes, often growing luxuriantly to considerable depths (Bodin & Nauwerck 1968, Welch & Kalff 1974, Priddle 1980, Sand-Jensen *et al.* 1999, Hawes *et al.* 2002). The predominance of mosses in many Arctic lakes may be due to adaption to low temperatures, low light and low nutrients, combined with slow growth and decomposition rates (Bodin & Nauwerck 1968, Grahn *et al.* 1974, Kallio & Kärenlampi 1980, Riis & Sand-Jensen 1997).

The composition of aquatic macrophyte communities in Arctic pond/lake habitats depends largely on four environmental variables: (1) climate, which imposes a major temperature-based zonation, (2) local climates or microclimates, which modify this overall pattern, (3) water clarity, which is determined by proximity to erosional activities (e.g. glaciers, slumps, land clearing activities, etc.) and in-lake productivity (e.g. phytoplankton), and (4) nutrients, which are inherently in limited supply in most Arctic systems.

Aquatic vascular macrophytes show a decline in species richness with increasing latitude, particularly from temperate to polar regions, similar to many other terrestrial and aquatic species. On a finer geographic scale, species richness of vascular macrophytes (but not aquatic mosses) was found to decrease with increasing latitude in boreal Finland (Heino & Toivonen 2008). The result of this decline in species richness of vascular macrophytes with increasing latitude is predominance of bryophytes or charophytes in Arctic lakes. Latitude may be a proxy for climate (e.g. length of growing season, duration of ice cover, summer temperature) or trophic status (southern lakes may be more nutrient rich due to proximity to human activity or to ecozones with more fertile soils), ultimately imposing physiological restraints on the northward extent of many vascular macrophyte (and terrestrial) plant species. The increasing dominance of aquatic mosses at higher latitudes may be due to superior competitive ability under low light and temperature conditions, combined with longevity and low decomposition rates (e.g. Welch & Kalff 1974, Sand-Jensen *et al.* 1999).

Arctic waterscapes are typically viewed as low-nutrient ecosystems where primary productivity is constrained by lack of nutrients and extended ice cover (e.g. Schindler *et al.* 1974, Rigler 1978, Douglas *et al.* 1994, Vézina & Vincent 1997, Douglas & Smol 2000, see Bonilla *et al.* 2005 and 2009 for other references). Although nutrient enrichment experiments on Arctic lakes have shown strong phosphorus control of phytoplankton populations (e.g. Schindler *et al.* 1974, Douglas & Smol 2000), studies on nutrient control of Arctic macrophytes are less common. Controlled experiments on an aquatic moss, floating hookmoss *Warnstorfia fluitans*, from a high Arctic lake in Peary Land, N Greenland showed that growth rate increased with increasing plant phosphorus content (Riis *et al.* 2010). In contrast, bioassays involving nutrient (carbon, nitrogen, phosphorus) enrichment resulted in no growth or photosynthetic response by benthic cyanobacteria in Ward Hunt Lake (83.1° N, 74.1° W) on Ellesmere Island (Bonilla *et al.* 2005, 2009). Few, if any studies have examined nutrient limitation of vascular macrophytes in Arctic freshwaters. However, paleoecological studies have indicated shifts in vascular macrophyte composition in response to oligotrophication (impoverishment in macronutrients and ions) (Fredskild 1992, Eisner *et al.* 1995, Bennike & Funder 1997).

#### 13.3.1.5. Microbial communities

In the majority of shallow, seasonally ice-covered Arctic lakes and ponds, benthic primary (autotrophic) production is the dominant form of biomass accumulation and associated species diversity (Vezina & Vincent 1997, Bonilla *et al.* 2005, Quesada *et al.* 2008). These communities consist primarily of microbial mats, where cyanobacteria are the most abundant taxonomic complex (Villeneuve *et al.* 2001, Quesada *et al.* 2008, Vincent *et al.* 2008, 2009, Vincent 2010). In many shallow lake/pond systems, extreme seasonal and inter-annual variability in temperature, water influx and levels, and light conditions (e.g. in the summer high intensity of light exposure, including UV) preclude the establishment of higher trophic levels such as pelagic and benthic herbivorous and predatory invertebrates and top-down predators such as fish. Moreover, the benthic microbial mats are comprised of complex, vertically-structured communities where the surface layers consist of cyanobacteria taxa adapted to deal with high light radiation regimes (e.g. containing high concentrations of pigments such as carotenoids), while other more photosynthetically active taxa occur in deeper layers within the mat (Quesada *et al.* 2008). Moreover, ice movement and scour during spring melt constrains the development of benthic microbial communities in the littoral zone in some lakes. By contrast, in perennially ice-covered lakes, key limitations for benthic autotrophic production include low light conditions coupled with low temperatures. Highest benthic productivity occurs in the littoral zone, with greatest biomass accumulating at depths where disturbance from ice scour or wave action is minimal (Quesada *et al.* 2008).

A significant research effort occurred as part of the International Polar Year under the project MERGE (Microbiological and Ecological Responses to Global Environmental change in polar regions) in northern Canada, which focused on describing the physical and chemical characteristics of a diverse range of sub-Arctic and Arctic freshwater habitats, and their related microbial biodiversity (Vincent *et al.* 2009). The project has provided new and important datasets (Polar Data Catalogue 2012) and insights into the complexities of freshwater habitats and their associated microbiological complexes.

Understanding the environmental factors affecting the structural and functional diversity and related productivity of pelagic and benthic microbial communities is still a major area of research in Arctic freshwater systems. This rapidly advancing field is benefitting from the application of new molecular techniques such as high throughput DNA pyrosequencing (e.g. Comeau *et al.* 2012) and metagenomic analysis (e.g. Varin *et al.* 2012; see also Lovejoy, Chapter 11).

## 13.3.2. Riverine ecosystems

River and stream ecosystems are common across the Arctic, and include long river systems spanning a large latitudinal range, particularly in the Canadian and Russian Arctic and sub-Arctic regions. The magnitude of seasonal variability in climatic drivers depends, in part, on latitudinal position as climatological extremes increase with increasing latitude. As a result, the period of ice cover can be quite long, limiting light penetration for a large part of the year and reducing the length of the growing season relative to that in temperate systems.

Arctic lotic systems also have highly variable flow, particularly during the spring as solar radiation levels increase and melting of snow and ice begins. Melting of the accumulated snowpack often occurs quickly, resulting in a large influx of water called the spring freshet that may only last a period of days, but may account for the majority of the annual flow in the system (Prowse 2001, Milner *et al.* 2005, Prowse *et al.* 2006a, Prowse *et al.* 2011a). In addition, concurrent dynamic ice breakup in the spring can lead to ice jams that flood the surrounding landscape (Prowse & Culp 2003). The changes in flow that result from these melt events are made more extreme by underlying permafrost that does not allow infiltration (McKnight *et al.* 2008). In northern regions of the Arctic, where precipitation predominantly occurs as snow, stream and river flow may decline sharply during the summer months after surficial snow and ice have melted (Prowse *et al.* 2006a, Prowse *et al.* 2011a). The combined influence of these factors contributes to a harsh physical environment characterized by high variability.

Aquatic biological community structure and function is expected to vary across a gradient in response to latitudinal changes in physical and chemical components of the system (Prowse *et al.* 2006b). However, latitudinal variability in environmental conditions may not be consistent across the full longitudinal range of Arctic systems, as differences in geological composition and geomorphological history may also influence lotic patterns and processes (Prowse *et al.* 2006a). As a result, physical, chemical and biological conditions of lotic systems may vary widely across the extent of the Arctic, resulting in a corresponding complex pattern of related structural and functional biodiversity.

In addition to geographic location, the size of a river or stream and its water source play a large role in determining conditions in the water body. Across the Arctic, lotic systems range in size from small headwater streams to rivers that are among the largest in the world (Prowse *et al.* 2006a, McKnight *et al.* 2008). Small headwater systems in the Arctic experience high seasonal flow variability and most often freeze completely during the winter (McKnight *et al.* 2008). In contrast, the largest Arctic rivers have their headwaters in temperate regions and may experience less of a decline in annual flow than smaller systems as a result of the influx of water from temperate regions (Prowse *et al.* 2006a, 2011b, McKnight *et al.* 2008). Moreover, other physical and chemical aspects of large rivers may differ significantly from smaller systems due to the northward flow of water from warmer regions and the accompanying transfer of nutrients, sediments and contaminants from the headwater system (Prowse *et al.* 2006a, 2006b).

In running water systems that flow entirely within the Arctic, flow variation and physical conditions depend in part on the water source for the system. Arctic streams and rivers are defined based on whether the water source is primarily glacial melt (termed a kryal system), snowmelt (rhithral system), a spring or groundwater (krenal system) (Brittain *et al.* 2009). The coldest temperatures and harshest physical environment are found in glacially fed systems, where conditions deteriorate with increasing proximity to the glacier. Glacially fed systems are characterized by extremely low temperatures, high bed instability and high sediment load close to the water source, though these conditions are highly variable seasonally and diurnally (Brittain & Milner 2001, Milner *et al.* 2005). Lotic systems that are fed in part by glacial melt may continue to have high discharge throughout the summer months (Brittain *et al.* 2009). Annual flow in systems that are primarily fed by snowmelt is much more variable due to the peak in discharge that is driven by the spring freshet. In contrast, springs and groundwater provide a more continuous input of water to a system, resulting in less variable flow and more stable physical conditions (Milner *et al.* 2005). Inputs from springs and groundwater may also be less extreme thermally than glacial melt or snowmelt, resulting in less adverse conditions in the system (Brittain *et al.* 2009). Because of these inherent differences among the water sources, the relative proportion of glacial, snowmelt and spring or groundwater inflows to a system will in part determine the magnitude of seasonal variability within the stream or river.

### 13.3.2.1. Impacts of a shrinking cryosphere

Prowse *et al.* (2006a, 2006b) and AMAP (2011b) provide extensive reviews of the potential interactions between a changing (shrinking) cryosphere (i.e. changes in ice, snow and permafrost) and resulting impacts on riverine geomorphology and related aquatic habitat quantity and quality. For example, changes in river-ice duration, intensity and frequency of ice jams during spring melt, and optical properties of river ice collectively affect riverine habitat persistence and suitability for colonization and utilization by fish, invertebrates and lower trophic levels. McNamara & Kane (2008) showed how changes in permafrost and river-ice regimes can alter the driving and resisting forces responsible for shaping stream and river channel cross sections and magnitudes and duration of sediment transport processes. Syvitski *et al.* (2000, 2002) showed that the magnitude of the sediment load being transported by a river is positively correlated with the temperature of the drainage basin, and estimated that a 2 °C increase in mean annual temperature could result in up to a 30% increase in the sediment load car-

## Box 13.3. The Mackenzie Delta and lakes

Aerial view in May of Mackenzie River and associated delta lakes in the sub-Arctic of Northwest Territories, Canada. Photo: Lance Lesack.

River deltas along the circumpolar Arctic coast are lake-rich and poorly understood ecosystems, set in a region expected to change rapidly. Of these circumpolar Arctic deltas, the Mackenzie Delta is the second largest (after the Lena). The delta forms the outlet of the Mackenzie River into the Beaufort Sea in the western Canadian Arctic and crosses the sub- to low Arctic ecotones. About 90% of the delta's water supply is contributed by the Mackenzie River at Point Separation with minor contributions by the Peel River in the southwest (8%) and others (Burn 1995). The delta is characterized by numerous anastomosing channels, small thermokarst lakes and wetlands that dominate the deltaic plain (Mackay 1963, Marsh *et al.* 1999). The floodplain is composed of permafrost-influenced silt and sand covered by species of spruce, alder, willow, birch, poplar, horsetail *Equisetum* spp. and tundra species north of the tree line (Mackay 1963). Most lakes are shallow enough to support substantial macrophyte growth (species of the common genera pondweed *Potamogeton*, muskgrass *Chara* and hornwort *Ceratophyllum*; Squires *et al.* 2002, 2009).

The surface of the active Mackenzie River Delta (13,135 km$^2$) is comprised of discrete lakes (3,331 km$^2$), channels (1,744 km$^2$), wetlands (1,614 km$^2$) and dry floodplain (6,446 km$^2$) (Emmerton *et al.* 2007). A simple floodplain storage model showed that the total lake volume of this system during the post river-flooding period is 5.4 km$^3$ (Emmerton *et al.* 2007). However, during spring peak flooding, the total floodwater storage in the delta lakes and floodplain is approximately 25.8 km$^3$, a volume equivalent to about 47% of Mackenzie River flow (55.4 km$^3$/yr) during the high-discharge period of spring ice breakup. During this period, the stored river water can be envisioned in the form of a thin layer of water (2.3 m thick on average) spread out over 11,200 km$^2$ of lakes and flooded vegetation and exposed to day and night solar irradiance.

The ~ 45,000 floodplain lakes (Emmerton *et al.* 2007) are generally small and shallow and are mostly of thermokarst origin where heat from standing floodwaters melted ice-rich permafrost and subsidence ensued (Hill *et al.* 2001).

Mackay (1963) classified delta lakes into three basic groups, and Marsh & Hey (1989) quantified the flood frequency of these lakes: no closure lakes are continuously connected to the river, low closure lakes are annually connected during flooding before disconnection, and high closure lakes are connected less than annually. Lake flooding is determined by the sill elevation of the lake and water level of adjacent river channels. These variations in sill elevation, flooding history and distance to nearby main channels result in gradients of turbidity, nutrients, dissolved organic matter, chromophoric water-color, sediment composition and underwater ultraviolet irradiance (Box 13.3 Tab. 1).

Analysis of 40 years of water levels in East Channel of the central delta permitted direct estimation of annual river-to-lake connection times, lake water renewal and inter-annual variability in a representative number of lakes spanning the full range of sill elevations in the delta (Lesack & Marsh 2010). Average river-to-lake connection times varied from > 150 days per year in the lowest elevation lakes to < 4.5 days per year in the highest elevation lakes. Lakes with short and variable connection times plus low and variable river water renewal yield groups of lakes with high degrees of individuality because they are strongly influenced by particular sequences of antecedent years (legacy effects) that may result in lakes simultaneously containing residual waters from multiple river inundation events separated by more than a decade. Lakes with long and less varying connection times plus high river-water renewal with multiple possible river-water resets per year yield lakes with high degrees of similarity. This full combination of lakes arranged in an intermittently connected continuum may be an important mechanism driving the collectively striking productivity, habitat diversity, biodiversity and distinctiveness of aquatic communities in this system and other river floodplains, relative to lakes on the surrounding landscape (Lesack & Marsh 2007).

Following on this work, Lesack & Marsh (2010) postulated that the Mackenzie Delta may generate enhanced biodiversity somewhat similarly to the rain forest refugia hypothesis proposed by Haffer (1969), but where water renewal variability drives divergence of aquatic communities in disconnected lakes located toward the elevational periphery of the system, and episodic interconnection of all lakes during high-magnitude floods disperses and intermixes the aquatic communities. Divergence of communities among lakes may be enhanced by at least four mechanisms that are a consequence of this complex lake connectivity gradient. These include variable nutrients and light, intermittent fish presence, variable predictability of aquatic food supply, and variable UV risk.

Superimposed on this dynamic system is the impact of a changing climate, with warming air temperature, changing river flooding and rising sea level. For example, Lesack & Marsh (2007) showed that over the past 30+ years, annual river-to-lake connection times in the Mackenzie Delta have lengthened (> 30 days) in the lowest elevation lakes and may have shortened in the highest elevation lakes, respectively via sea level rise and declining effects of river-ice breakup. Lengthened connection times indicate that summer low-water levels in the delta have increased by 0.3 m, an amount equivalent to three times local sea level rise over the same period. Such an amplification effect of recent sea level rise has been completely unexpected and may be a result of enhanced storm surges in response to receding Arctic sea ice or coastal backwater effects on the river flow. Shortened connection times are consistent with other work showing a decline in river-ice breakup effects, an important control on annual peak water levels.

**Box 13.3 Table 1.** Summary of gradients in the physical properties, nutrient regimes, and biotic communities as a result of differing river-to-lake connection times among lakes of the Mackenzie Delta (from Lesack & Marsh 2010). TSS = total suspended solids, DOC = dissolved organic carbon, HNAN = heterotrophic nanoflagellates.

| | **Lake-channel connection time** | | |
|---|---|---|---|
| | **>120 to >150 days/year** | **>17 to 120 days/year** | **<4.5 to 17 days/year** |
| **Physical and Chemical Gradients** | | | |
| TSS | High | | Low |
| Transparency | Low-unstable | | High-stable |
| Chromophoric color | High | | Low |
| Total DOC | Low | | High |
| Peroxide | Low | High | Low |
| Inorganic nutrients | High | | Low |
| Lake sediments | Inorganic | | Organic |
| Underwater UVR | Negligible | Low | High |
| River connection | Long | Short | Discontinuous |
| **Gradients in Biota** | | | |
| Bacteria | Low-high | | Low-high |
| HNAN | High | | Low |
| Macrophytes | Low | | High |
| Phytoplankton | Moderate | High | Low |
| Epipelon | Low | High | Low |
| Epiphytes | Low | | High |
| Zooplankton | Low,<br>small bodied | High,<br>small bodied | Low,<br>large bodied |
| Fish | High | Low | None |

ried by rivers in the Arctic. Frey & McClelland (2009) further highlight that significant shifts are projected to occur in Arctic river biogeochemistry as a result of projected warming-induced changes to permafrost and the delivery and transport of organic matter, inorganic nutrients such as nitrogen and phosphorus, and major ions. Box 13.3 is a case example based on extensive work by Lesack & Marsh (2010) on the Mackenzie Delta in the western Canadian Arctic that illustrates that the linkages between changes in climatic, hydrological and related water quality regimes have important implications for the structure, function and ecological diversity of Arctic deltaic systems.

It is apparent that such significant alterations in the cryosphere will have profound implications for the entrainment and transport of sediment through the watershed and related consequences on instream physical, chemical and biological processes, affecting bacterio-plankton, primary and secondary production and carbon cycling and associated structural and functional diversity of aquatic biota (Wrona *et al.* 2005, Vincent 2010).

### 13.3.2.2. General patterns of fish community diversity

Within northern environments, fish diversity tends to be greater in lakes than large rivers (Roy 1989). For example, in Nunavut and the Northwest Territories of Canada, a total of 45 established fish species have been reported to occur, with 40, 34 and 13 species, respectively, classified as lacustrine, fluvial or anadromous (Richardson *et al.* 2001). Similar trends are reported for northern Quebec, where large rivers are generally poor permanent fish habitat, and the numbers and diversity of fish increases in adjacent lentic habitats (Roy 1989). Lotic and lentic comparisons of fish abundance and biomass favor production in lentic habitats, with both lotic abundance and biomass being only 24-36% of that measured in lentic habitats (Roy 1989). The difference between habitat types owes much to the abiotic harshness, seasonal variability in light and nutrient availability, and low productivity of lotic habitats (Power & Power 1995). Furthermore, glacial events have dominated throughout much of the Arctic, and existing physical and biological conditions are a direct consequence of Pleistocene glacial events, with many systems having had less than 6,000 years to mature. As a consequence, resident organisms are recent colonizers selected from a set whose dispersal mechanisms and physiology have allowed arrival and survival. Thus, latitudinal gradients in fish community diversity are evident in larger, north-flowing rivers (e.g. Fig. 13.3). In the high Arctic, seasonally harsh conditions and accessibility limited to species capable of colonizing via coastal routes (Power *et al.* 1973) have limited diversity within the rivers to Arctic char or no species at all.

Lotic environments are among the most difficult habitats for Arctic fish to survive (Power 1997). Small streams and rivers may freeze to the bottom. Groundwater-fed streams and rivers provide only limited over-wintering habitat in isolated pools. River hydrographs typically include periods of run-off flows with discharges outside the range of those that provide good habitat for fish because of the associated increases in velocity. In summer, discharge can be unstable and dependent on limited summer precipitation (Power 1997). In winter and during spring break-up, ice dynamics can cause rapid changes in discharge, periods of substrate scouring and substrate ice formation that pose acute hazards to resident fish (Scrimgeour *et al.* 1994, Prowse & Culp 2003). The accumulation of these physical stressors on lotic environments has exerted strong selective pressure on flu-

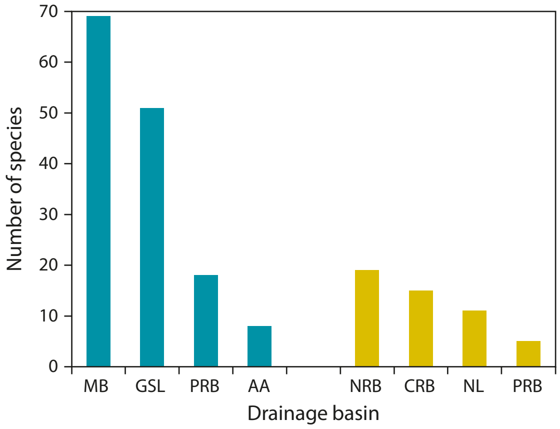


**Figure 13.3.** Number of species reported for drainage basins in western and eastern Canada arranged on a south to north gradient. Along the western gradient, blue bars: MB = Mackenzie River basin, GSL = Great Slave Lake and its tributaries, PRB = Peel River basin, and AA = Arctic archipelago. Along the eastern gradient, yellow bars: NRB is the Nottaway River basin, CRB is the Caniapiscau River basin, NL is northern Labrador and PRB is the Payne River basin. Data sources include: Lindsey & MacPhail (1986), Roy (1989), Power (1997) and Power *et al.* (2008).

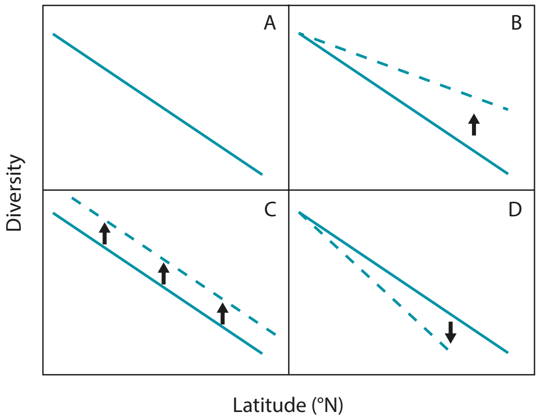


**Figure 13.4.** Theoretical changes in species diversity along river latitudinal gradients. Panel A depicts the current situation, as demonstrated in Figure 13.3. Panel B denotes the effect of physiological release whereby warming climates permit an increasing number of species to move north. Disproportionate impacts are expected in the north because of existing low diversity. Panel C depicts the impact of anthropogenic-facilitated invasions resulting from species transplants. Panel D depicts localized species extinctions caused by increased competition along the latitudinal gradient, with the largest impacts expected in the North.

vial fish stocks, selecting for species that can endure long periods of darkness, restricted space and low temperatures and have the ability to exist on accumulated energy reserves because of long periods of time with restricted feeding opportunities, and the ability to deal with sudden, often catastrophic, changes in their environment (Power 1997). As a result, many of the stocks that exist in Arctic rivers exist as small isolated units that favour the development of within-species genetic diversity.

Many of the large mainland Arctic rivers contain headwaters in temperate or sub-Arctic regions and are not strictly Arctic (Power & Power 1995). The connectivity to Arctic aquatic environments provided by these rivers will critically influence the evolution of fish diversity within the Arctic portions of the river basin. As further elaborated in Section 13.4 below, changes in climate that alter river thermal regimes will facilitate northward movement of eurythermal species currently confined to headwater regions and compress the distribution of resident stenothermic species to more northerly regions (Fig. 13.4).

Within northern river systems, estuaries are particularly notable for their fish diversity. The estuarine section can be large. In low Arctic Ungava Bay in northern Labrador, where tides can reach 17 m (Arbic *et al.* 2007), areas of marine influence can extend many kilometers upriver (i.e. Koksoak 50 km, Payne 80 km) with the result that both marine and freshwater species tolerant of brackish water conditions will co-occur (Roy 1989). Freshwater fish, however, will reside in brackish water only for purposes of summer feeding, leaving the area in late summer and early autumn as water temperatures fall. The phenomenon of stressful environments having low species richness yet high ß-diversity (turnover) has similarly been remarked on elsewhere (e.g. Price 2002) and provides another dimension to consideration of lotic biodiversity in northern rivers.

Rivers in northern regions tend to have a complexity of habitats adjacent to the main river, including side channels and side-sloughs, where turbidity and invertebrate drift favour juvenile rearing and over-winter survival (Milner *et al.* 2009). The complexity and availability of different habitat types has meant that northern fish often change habitat use with age. Variation in the ways in which fish can utilize available habitat has given rise to differences in life-history types within species, itself a form of diversity. As a result, in rivers, it is important to note differences in life-history types with the following being of prime importance for determining diversity within rivers:

- Adfluvial: fish that rear and remain in lacustrine environments for most of their life cycle, but spawn in rivers or streams. Adfluvial fish will contribute to significant site-specific seasonal variations in diversity but do not alter basin-related diversity measurements.
- Fluvial: fish that spawn, rear and remain in river or stream environments for most of their life cycle. Fluvial fish will be the prime drivers of local diversity within a river and may contribute to diversity complexity as a result of the spatial structuring of populations, especially in larger, north-flowing rivers. Fluvial fish may also vary with respect to movement tactics, with some remaining within the same reach throughout the life-cycle and others venturing along the course of the river as far as barriers to migration will permit.
- Anadromous: fish that spawn in freshwater environments and migrate along rivers to marine environments for a portion of their life cycle. Anadromous fish will contribute to significant site-specific seasonal variation in diversity but do not alter basin-related diversity measurements.

The need to adapt to varying adverse conditions in northern rivers manifests itself in a diversity of life-history tactics within populations. As an example, consider the Atlantic salmon *Salmo* spp. population of the Koksoak River system that include variant forms of landlocked, anadromous and estuarine life-history types that may spawn yearly, delay spawning until the year after returning from sea or spawn twice before returning to sea (Power 1969). Atlantic salmon are not unique, as many species exist in two or more life-history types. For example, Arctic lamprey *Lethenteron camtschaticum* and rainbow smelt *Osmerus mordax* exhibit all three life-history types. In contrast, lake chub *Couesius plumbeus* and Arctic grayling *Thymallus arcticus* exhibit adfluvial and fluvial life-history types, and inconnu *Stenodus leucichthys* and round whitefish *Prosopium cylindraceum* exhibit adfluvial and anadromous life-history types (Richardson *et al.* 2001, Stewart *et al.* 2007). More recent work, however, has demonstrated increasing complexity in life-history variation within species. For example, anadromy has been demonstrated in populations of lake trout from lakes in the west Kitikmeot region (~68° N and 107° W) of Nunavut, Canada (Swanson *et al.* 2010).

Differences in among-species abilities to exploit available food resources and optimize energy acquisition through adaptive behavior patterns (e.g. variations in life-history tactics) appear to have enabled some species to survive more easily than others in northern environments. For example, along latitudinal gradients of fish assemblages in northern Quebec rivers, perch and pike become scarce first, followed subsequently by lake whitefish and salmon *Salmo salar* (Roy 1989).

Changes in trends in fish biodiversity are already evident in many northern river basins as a result of increasing human activities (see further in Christiansen & Reist, Chapter 6).

#### 13.3.2.3. Biodiversity and productivity patterns of primary producers and invertebrates

Biodiversity and productivity of primary producers and consumers in Arctic rivers and streams vary with the size and physical characteristics of the system, including the primary water source (Prowse *et al.* 2006b, Culp *et*

## Box 13.4. Latitudinal changes in importance of carbon source on the structure of lotic Arctic benthic food webs

Across the latitudinal gradient of the Arctic, there is a shift in terrestrial vegetation from a bioclimate dominated by vascular plants up to 80 cm tall in the low Arctic to a primarily barren bioclimate dominated by moss or lichens < 2 cm tall in the high Arctic desert (Walker *et al.* 2005). The importance of allochthonous[1] material in lotic food webs might be expected to decrease with increasing latitude as a result of this decline in terrestrial vegetation. However, because the short growing season and low nutrient levels in high Arctic streams and rivers may not be sufficient to support high instream primary production (Prowse *et al.* 2006b, Wrona *et al.* 2006a), allochthonous inputs may remain important at any latitude.

In order to determine whether lotic food webs differ among low and high Arctic systems, stable isotope analysis was used to evaluate benthic food webs across a latitudinal gradient in the eastern Canadian Arctic (Lento *et al.* 2012). Benthic macroinvertebrates, periphyton, and terrestrial material were collected from a series of streams and rivers in four regions in northern Canada: the Koroc River basin and Torngat Mountains National Park in northern Labrador and Quebec (58° N), Iqaluit on Baffin Island (63° N), Sirmilik National Park on Baffin Island (72° N), and Quttinirpaaq National Park on Ellesmere Island (81° N). Stable carbon and nitrogen isotope analyses indicated an apparent shift in macroinvertebrate food source with an increase in latitude. However, rather than the expected decrease in allochthonous influence, the carbon signature of macroinvertebrates shifted to more closely resemble that of terrestrial material. At the lowest latitude (northern Labrador and Quebec), macroinvertebrate carbon and nitrogen signatures indicated that both allochthonous and autochthonous food sources were utilized. Isotopic signatures of mayflies Ephemeroptera generally indicated that terrestrial material was the primary food source, whereas isotopic signatures of dipteran flies suggested that periphyton was the dominant food source. With an increase in latitude, macroinvertebrate diversity declined until dipteran flies were the dominant taxa. Concurrently, the carbon signatures of the dominant dipteran families shifted to more closely resemble that of terrestrial material. The average carbon signature of craneflies Tipulidae displayed a clear declining trend from 63° N to 81° N, with a significantly lower carbon signature at 81° N, and the average carbon signature of midges Chironomidae was also significantly decreased at 81° N. Although periphyton carbon signatures were depleted in some samples, the average carbon signature remained significantly higher than that of terrestrial material, indicating a shift in dipteran diet from primarily autochthonous material to primarily allochthonous material (Lento *et al.* 2012).

This illustrates the important role of terrestrially derived carbon in high Arctic lotic food webs despite the lack of riparian vegetation. Moreover, periphyton biomass was found to be extremely low at the high Arctic sites, with average chlorophyll *a* values < 0.01 µg per cm$^2$. The low levels of periphyton biomass and the shift in dipteran food source indicate that periphyton may not be an important primary food source for macroinvertebrates in high Arctic lotic systems (Lento *et al.* 2012).

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[1] Allochthonous, from the Greek 'allos' (other) and 'khthōn' (ground), refers to something originating from somewhere other than where it is found while autochthonous, from the Greek 'autochthon' (native to the soil), refers to something originating from where it is found (Merriam-Webster Dictionary). In limnology, an allochthonous carbon source would be dissolved carbon originating from vegetation on the surrounding landscape while an autochthonous carbon source would be from plant matter grown within the water body.

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*al.* 2012). For example, glacially fed systems typically have low biodiversity and productivity as a result of harsh physical conditions and low nutrient input from the source water, whereas large rivers with temperate headwaters and smaller systems that drain lakes may have higher biodiversity and productivity due to higher nutrient inputs and a less variable physical environment (Prowse *et al.* 2006b, Wrona *et al.* 2006a). There is also a generally observed decline in richness and productivity with increasing latitude (Milner *et al.* 2005, Brittain *et al.* 2009) that reflects the latitudinal gradient in climatological extremes. However, studies of stream diatom species dispersed at a global scale suggest that the species diversity of unicellular benthic algae might be driven mainly by resources rather than climate or their biogeography (Passy 2010). Benthic primary production in Arctic lotic systems is limited due to variable light and temperature conditions, low nutrient levels and periodic scouring by high flows (Prowse *et al.* 2006b, Brittain *et al.* 2009). The short growing season that results from the long period of ice cover and cold temperatures at high latitudes also contributes to limiting algal production. Taxonomic richness of consumers is affected in part by the low temperatures at high latitudes, as temperature extremes may exceed the thermal tolerance levels of many taxa, reducing richness relative to more temperate areas (Milner *et al.* 2005). Those organisms that can tolerate the thermal extremes of high latitude systems display adaptations such as reduced growth rates in order to survive through the winter. Overwintering offers additional challenges where streams freeze to the substrate, and extreme ice breakup events can increase mortalities of invertebrates and fish, reducing biomass of consumers (Milner *et al.* 2005). Other constraints of the environment, including low food availability, habitat instability and high variation in flow, may exceed the tolerance level of many macroinvertebrate and fish species, contributing to the low richness in consumers (Brittain *et al.* 2009). As a result, riverine benthic macroinvertebrate species richness declines with latitude, such that assemblages at the highest latitudes are generally dominated by dipteran flies (Milner *et al.* 2005). Moreover, with increasing proximity to glaciers and associated adverse physical conditions, benthic macroinvertebrate assemblages are primarily composed of highly tolerant genera of midges (Brittain & Milner 2001). Studies of stream diatom species dispersed at a global scale suggest that unicellular benthic algae might be driven mainly by resources rather than climate or biogeography (Passy 2010).

Recent studies by Lento *et al.* (2012) in the eastern Canadian Arctic illustrate how levels of allochthonous terrestrial carbon change with increasing latitude and the resulting implications for lotic benthic invertebrate biodiversity, food web structure and productivity (Box 13.4).

Although difficult to generalize, large north-flowing rivers are generally devoid of aquatic macrophytes (except in backwaters, lagoons or deltas) at high latitudes due to higher current velocities, unsuitable substrata (e.g. shifting sand or gravel) and turbid water that limits light penetration. In contrast, smaller rivers and streams may be dominated by mosses and benthic algae (Hobbie 1984b, Milner & Petts 1994); higher aquatic plants are usually absent because they cannot stay attached in the strong current and coarse substrate (Fredskild 1981).

## 13.3.3. Wetland ecosystems

Wetlands, i.e. vegetated regions that are inundated with water on a permanent, seasonal or intermittent basis, are prominent freshwater ecosystems in the Arctic (Avis *et al.* 2011, Wheeler *et al.* 1999). They constitute a wide range of biophysical, geochemical and ecological conditions and can be broadly classified as, for example, peatlands, mires, fens or simply areas in the landscape saturated with water (Tarnocai & Zoltai 1988, Charman 2002, Woo & Young 2006). Mires are also known as bogs, fens, muskeg, moors and swamps. Fens are mires that are influenced by water outside of its own catchment limits, bogs are mires that receive their water solely from rain and/or snow falling on its surface, while marshes are fens containing large herbaceous vegetation, often with mineral substrate (Tarnocai & Zoltai 1988, Charman 2002).

More than 50% of global wetlands occur in the Arctic and sub-Arctic regions, and their occurrence is largely related to the presence of continuous and discontinuous permafrost (Tarnocai & Zoltai 1988, Smith *et al.* 2005). For example in Canada, peatlands (i.e. bogs, fens and marshes) are estimated to cover about 13% of the land surface, estimated to be 1.136 million km$^2$ (Tarnocai *et al.* 2005). They are defined as those areas with more than 40 cm of peat and include both peatlands and mires (*sensu* usage in some parts of Europe and Russia), and about 37% by surface area of the peatlands are perennially frozen (Warner & Rubec 1997). The Hudson Bay Lowlands, the northernmost ecozone in the province of Ontario, is an expansive peatland complex covering about 3.5% of the Canadian land surface and is among the largest peatland complexes in the world (Riley 2003, Abraham & Keddy 2005).

A wide range of wetlands/mires occur in northern areas of North America and Eurasia, many being characterized by the complex patterning of their surfaces formed by the arrangement of hollows, pools and hummocks and associated vegetation (Charman 2002). Wetlands in most of boreal Scandinavia are dominated by bogs of various types, while in sub-Arctic northern regions 'aapa' fen/mire complexes are predominant, characteristically typified by very low gradients and elongated, narrow ridges with hollows and pools running parallel with each other (Charman 2002). Similar 'ribbed' fens are found in the boreal region of Canada (Zoltai 1988). Palsa mires, which have permafrost mounds within the peat, are common throughout sub-Arctic northern Finland and Canada (Zoltai 1988). In the Arctic, extensive networks of polygon mires, which are typified by their characteristic polygonal patterning on the surface indicative of deep ice wedges and near-surface freeze-thaw processes, can occur (Tarnocai & Zoltai 1988, Vardy *et al.* 2005, Woo & Young 2006).

In general, the Arctic and, in particular, wetlands play an important role in the global carbon cycle by sequestering and storing carbon, and releasing carbon dioxide ($CO_2$) and methane ($CH_4$) through the decomposition of organic matter and related respiration pathways (ACIA 2005, IPCC 2007). Current studies estimate that the northern boreal forests and Arctic regions have been a sink for atmospheric $CO_2$ of between 0 and 0.8 Pg C per year in recent decades, which is up to 25% of the global net landscape/oceanic flux since the 1990s (McGuire *et al.* 2009). Moreover, wetlands in these regions are a significant source of $CH_4$ to the atmosphere, estimated to be between 32 and 112 Tg $CH_4$ per year (McGuire *et al.* 2009). CAFF (2010) has identified the distribution and abundance of Arctic peatlands as an important indicator of high latitude freshwater biodiversity.

### 13.3.3.1. Status and trends in biodiversity

Arctic wetlands provide unique and critical habitats to many aquatic and semi-aquatic plant and animal species. For many migratory species such as waterbirds and mammals, Arctic wetlands provide important breeding and feeding habitats. Waterbird species such as geese, ducks and shorebirds that breed in the Arctic are found on all the major international flyways, linking the Arctic to countries throughout both the Northern and Southern Hemispheres (see Fig. 4.2 in Ganter & Gaston, Chapter 4).

Arctic wetlands also provide a wide range of key ecological services such as the maintenance of permafrost, water regulation and filtration, store enormous amounts of greenhouse gasses, and are critical for global biodiversity and are also a source of livelihoods for local indigenous peoples. Ecological services provided by wetlands include subsistence hunting of waterfowl such as geese and ducks, trapping and/or hunting of aquatic and semi-aquatic mammals such as muskrat *Ondatra zibethicus*, American beaver *Castor canadensis*, moose *Alces americanus* and Eurasian elk *Alces alces*, as well as the harvesting of plants for food and traditional medicinal use (see Huntington, Chapter 18). In the high Arctic desert, although limited in occurrence, wetlands are an important but often limited productive aquatic habitat in an otherwise arid environment (Woo & Young 2006).

As already highlighted, the Arctic region is under increasing environmental and anthropogenic threats related to increasing temperatures and altered precipitation regimes arising from climate change, increasing melting of permafrost, and increasing land disturbance related to resource development such as mining and oil and gas exploration. Arctic wetlands are highly vulnerable to these disturbances given their complex character. As human-induced climate change has been shown to cause severe warming at high latitudes (ACIA 2005, IPCC 2007, AMAP 2011b), there is increasing concern that the role of Arctic ecosystems might consequently shift from a store (or sink) to a source of greenhouse gases ($CO_2$ and $CH_4$). Smol & Douglas (2007b) have shown that some wetland complexes have dried up to the point where they could become carbon sources.

Although Arctic wetland complexes are extremely abundant, very limited regional and long-term monitoring data exists on the biodiversity of Arctic wetland flora and fauna. In general, the species diversity of Arctic wetlands is low, often containing very specialized species (Wrona *et al.* 2005). An exception occurs with charismatic species such as migratory waterfowl, which are tracked and whose distribution and abundance status is regularly assessed in response to legislated or regulatory requirements specified in national and international agreements. The significant gap in systematic monitoring and assessment of freshwater biodiversity in Arctic wetland complexes highlights an ongoing impediment and challenge in the development of a suitable scientific base to adequately inform conservation and protection strategies and actions for these globally important freshwater ecosystems.

Trends in wetland persistence and extent at a global scale are difficult to predict and depend on local hydrologic regimes, climate, geologic setting and land use. The hydrology of wetlands and thermokarst lakes is closely linked to increases in wetland extent linked to permafrost thawing, whereas decreases are likely due to drainage (Smith *et al.* 2005, Marsh *et al.* 2009) (see Box 13.2). Unsurprisingly, many of the trends in wetland extent have been linked to climate change, but no apparent consensus emerges from the literature. While some have found increased wet conditions as a result of permafrost thaw (Vitt *et al.* 1994, 2000), others have found that increased evapotranspiration has led to the complete desiccation of ponds/wetlands (Smol & Douglas 2007b).

## 13.4. IMPACTS OF CLIMATE CHANGE AND INTERACTIONS WITH OTHER ENVIRONMENTAL STRESSORS

As discussed earlier, climate variability and change is the most prominent environmental and anthropogenic driver affecting Arctic freshwater ecosystems (Heino *et al.* 2009, AMAP 2011b). However, geographical patterns and future trends of freshwater biodiversity in high latitudes are less well understood than ecosystem- and population-level changes in relation to climate change (Rouse *et al.* 1997, Reist *et al.* 2006a, 2006b, Wrona *et al.* 2006a). Climate variability and change represents a complex interplay of related stressors, which include alterations in temperature regimes, increased frequency, intensity and/or duration of droughts, floods and extreme flow events, and altered responses of cryospheric components such as snow, ice and permafrost (Hodkinson *et al.* 1999, ACIA 2005, IPCC 2007, AMAP 2011b, Prowse *et al.* 2012a, 2012b). In turn, several 1st and 2nd order impacts on the physical, chemical and biological characteristics of aquatic ecosystems are projected, including for example:

- disruption or alteration of life-history phenology (timing of reproduction),
- shifts in the onset and duration of the growing season
- species invasions,
- species range extensions or contractions and changes in regional distribution and abundance patterns,
- shifts in relative abundances of co-occurring life-history types (e.g. migratory versus resident char) and ecological types (e.g. limnetic forms of fish versus benthic forms), likely to be a direct consequence of climate changes affecting aquatic ecosystems,
- distances between refugia (e.g. water oases),
- changes in ecosystem primary, secondary and bacterioplankton production,
- changes in the occurrence and/or shifts in the intensity and frequency of structuring/geomorphological processes (e.g. extreme flow events, floods, fires),
- changes in biogeochemical cycles related to fluctuations in catchment hydrology (alterations in precipitation/evaporation patterns, permafrost thaw and deepening of the active layer), and
- changes or declines in water availability and/or hydrological connectivity that can lead to loss of critical habitat (Hodkinson *et al.* 1999, Hellmuth & Kabat 2003, Prowse *et al.* 2006, Reist *et al.* 2006a, 2006b, Wrona *et al.* 2006a, Heino *et al.* 2009, Woodward *et al.* 2010, Prowse *et al.* 2012c).

### 13.4.1. Biogeographic shifts in the distributions of organisms

There has been increasing interest in understanding how historical and present-day changes in climatic regimes have and are affecting the structure, function and biodiversity of Arctic freshwater systems. The Arctic cryospheric and freshwater environments are complex and interactive, making the effects of climate variability and change and associated alteration of water and habitat availability on ecosystem structure and function difficult to predict (Hodkinson & Wookey 1998, Hodkinson *et al.* 1999, Wrona *et al.* 2006a, Prowse *et al.* 2011c). Lake and pond sediments that contain important archives of past changes in the fossil remains and associated geochemical constituents that are deposited chronologically can be used to reconstruct environmental change (Smol & Douglas 2007a, 2007b). Using these biological and geochemical indicators, it is possible to infer how communities and ecosystems have changed in structure and function (i.e. productivity), and to identify plausible causal mechanisms for the observed magnitudes and rates of change (e.g. climate change, landscape disturbance such as fire, etc.). A meta-analysis by Smol *et al.* (2005) of sediment cores from 45 circumpolar lakes provided evidence of significant shifts in diatom and invertebrate community structure starting from the mid- to late 19th century. They concluded that climate warming appeared to be the only likely explanation for the apparent dramatic changes, with regions that warmed the most in the Arctic showing the greatest magnitudes in responses, some being as high as almost 100% in assemblage shifts (Fig. 13.5). Interestingly, Smol *et al.* (2005) also concluded that compositional shifts within the lakes were not related to new colonizations, but rather the observed increases in community diversity, productivity and food web complexity were more likely related to enhanced numerical expansions of species populations that were already present (but in low abundance) in response to a warming climate. Other circumpolar studies by Michelutti *et al.* (2003, 2005, 2006), Perren *et al.* (2003), Birks *et al.* (2004), Solovieva *et al.* (2005), Antoniades *et al.* (2007, 2009) and Smol & Douglas (2007b) provide further evidence of unprecedented algal species assembly changes and associated production increases in high-latitude lakes and ponds since ~1850, indicating that important ecological thresholds have been crossed in response to marked changes in climate-related variables. These variables include, for example, decreased ice cover, increased thermal stratification and changes in water chemistry (Smol & Douglas 2007a, 2007b).

Among freshwater organisms, fish have received most attention in the context of climate change (cf. Rahel & Olden 2008). Chu *et al.* (2005) modeled the distributions across Canada of various fish species in relation to climatic conditions and found that the ranges of most species were largely determined by present-day regional climatic conditions. Thus, they predicted that there will be considerable range shifts by fish in response to changing climatic conditions, although the nature of these responses is likely to differ between species. In general, cold-water species were predicted to be extirpated from the southern parts of their present-day ranges, while cool- and warm-water species were assumed to be able to expand northwards (Chu *et al.* 2005; see also Mohseni *et al.* 2003 and Christiansen & Reist, Chapter 6). Expanding ranges of cool- and warm-water fish species have also been suggested in Finland, while cold-water species may show range restrictions along with shifts northwards (Lehtonen 1996, Hayden *et al.* 2013). Indeed, the distributions of warm-water fish species have been predicted to shift 500 km northwards with the climate warming trend expected in the near future (Eaton & Scheller 1996). These predictions also suggest that freshwater ecosystems in northern regions will gain additional fish species, which may profoundly change the structure and functioning of these systems. For example, smallmouth bass *Micropterus dolomieu* has been predicted to expand its northern distribution across Canada in the face of climate change (Sharma *et al.* 2007). Being an efficient predator, smallmouth bass may have serious consequences for northern fish communities and freshwater ecosystems in the future (Jackson & Mandrak 2002).

Although species diversity in Arctic freshwater ecosystems is low compared with more temperate ecozones, this appears to be offset to some degree within certain taxonomic groups such as the Arctic char and whitefish. These taxa exhibit extreme phenotypic and genotypic variability both within and between freshwater systems, which is manifested as a variety of life-history types, ecological types and morphological variants (Reist *et al.* 2006a, 2006b, Bernatchez *et al.* 2010, Siwertsson *et al.* 2010). Similar levels of diversity exist within other key components of Arctic freshwater systems such as invertebrates. The role of such intra-specific biodiversity is unclear, however. It appears to function in a manner similar to that typically assigned to species-level diversity elsewhere. That is, intra-specific diversity in Arctic ecosystems provides complexity and hence both stability (i.e. resilience to change) and adaptability to such ecosystems. Such biodiversity is generally poorly known and understood, but will greatly influence how the effects of a changing and more variable climate and alterations in ultraviolet radiation regimes are manifested at biotic levels in Arctic aquatic ecosystems, and how highly diverse Arctic ecosystem components are likely to respond.

Studies of the present-day distribution patterns of other freshwater taxa in northern regions have assumed a strong role for climate in shaping broad-scale species distributions. For example, in boreal northern Europe, the composition of regional freshwater biota is rather closely related to climatic variables, although there are some notable exceptions in the responses of taxonomic groups to climatic conditions (Heino 2001). While macrophytes, beetles and fish show clearer responses to regional climatic conditions with decreasing species richness towards Arctic regions and higher altitudes, stoneflies Plecoptera show an opposite pattern of species richness. Being mainly inhabitants of cold- and cool-water stream environments, these deviating responses of stoneflies are not completely unexpected (Heino 2009). Although taxonomic groups other than stoneflies include some cold-water species with ranges inclined towards high latitudes, they do not change the general pattern for the taxonomic groups as a whole. For example, although there are some species with northern distributions, most macrophyte species generally have ranges concentrated

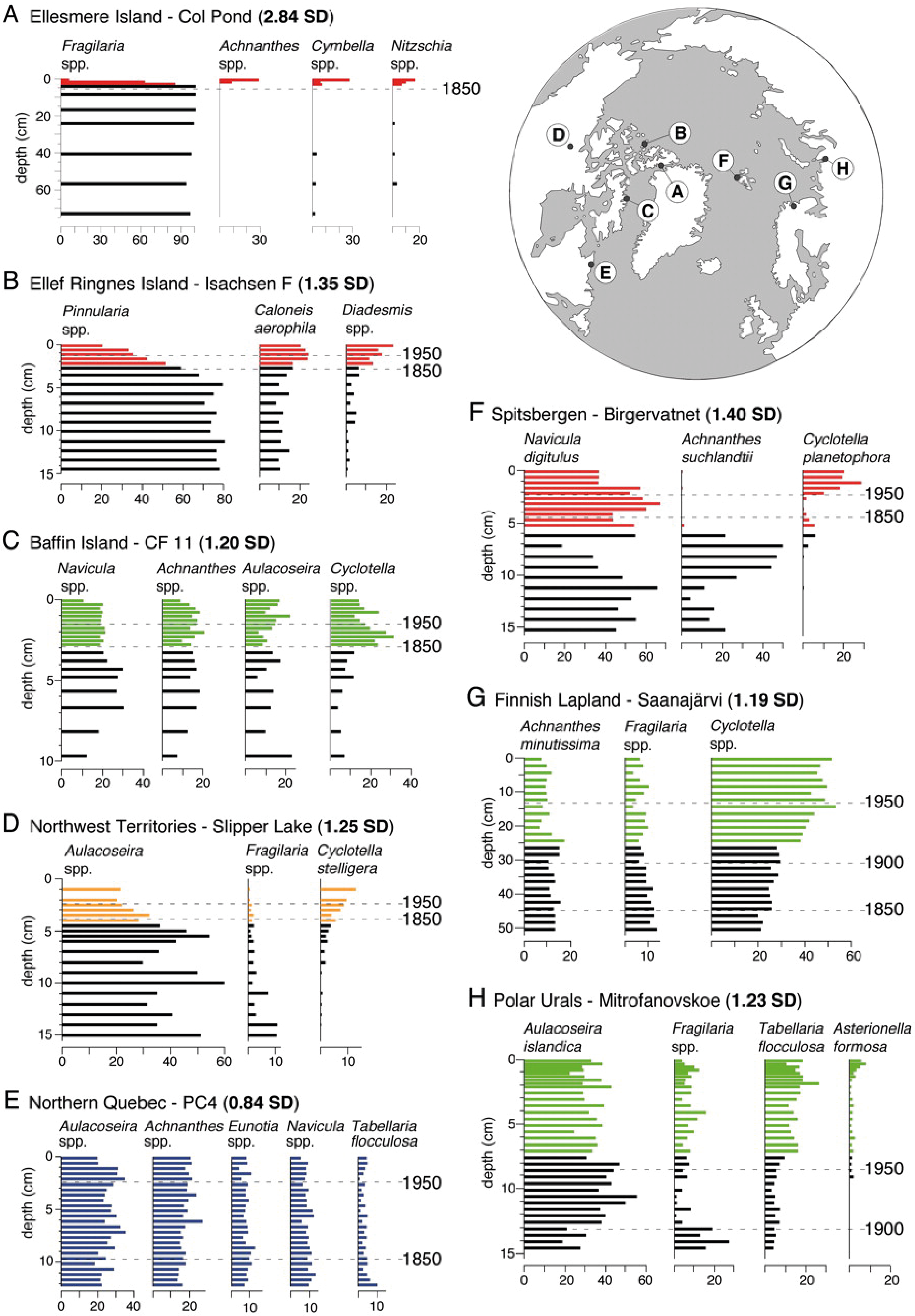
A Ellesmere Island - Col Pond (**2.84 SD**)
*Fragilaria* spp.
*Achnanthes* spp.
*Cymbella* spp.
*Nitzschia* spp.
depth (cm)
0
20
40
60
1850
0
30
60
90
30
30
20
B Ellef Ringnes Island - Isachsen F (**1.35 SD**)
*Pinnularia* spp.
*Caloneis aerophila*
*Diadesmis* spp.
1950
1850
depth (cm)
0
5
10
15
0
20
40
60
80
20
20
C Baffin Island - CF 11 (**1.20 SD**)
*Navicula* spp.
*Achnanthes* spp.
*Aulacoseira* spp.
*Cyclotella* spp.
1950
1850
depth (cm)
0
5
10
0
20
40
20
20
20
40
D Northwest Territories - Slipper Lake (**1.25 SD**)
*Aulacoseira* spp.
*Fragilaria* spp.
*Cyclotella stelligera*
1950
1850
depth (cm)
0
5
10
15
0
20
40
60
10
10
E Northern Quebec - PC4 (**0.84 SD**)
*Aulacoseira* spp.
*Achnanthes* spp.
*Eunotia* spp.
*Navicula* spp.
*Tabellaria flocculosa*
1950
1850
depth (cm)
0
5
10
0
20
40
20
10
10
10
A
B
C
D
E
F
G
H
F Spitsbergen - Birgervatnet (**1.40 SD**)
*Navicula digitulus*
*Achnanthes suchlandtii*
*Cyclotella planetophora*
1950
1850
depth (cm)
0
5
10
15
0
20
40
60
20
40
20
G Finnish Lapland - Saanajärvi (**1.19 SD**)
*Achnanthes minutissima*
*Fragilaria* spp.
*Cyclotella* spp.
1950
1900
1850
depth (cm)
0
10
20
30
40
50
0
20
10
20
40
60
H Polar Urals - Mitrofanovskoe (**1.23 SD**)
*Aulacoseira islandica*
*Fragilaria* spp.
*Tabellaria flocculosa*
*Asterionella formosa*
1950
1900
depth (cm)
0
5
10
15
0
20
40
60
20
20
20

**Figure 13.5.** Representative diatom profiles from the circumpolar Arctic showing the character and timing of recent assemblage shifts. Site locations (A-H) are shown on the map. Chronologies are based primarily on constant rate of supply modeling of excess sediment $^{210}$Pb activities. Beta-diversity values (in SD units) are shown in bold next to each site's name. Colored intervals demarcate major assemblage changes and are coded: blue = 0-1.0 SD, green = 1.0-1.24 SD, orange = 1.24-1.5 SD, red = > 1.5 SD. All data are expressed as relative frequency percentages of individual or collated diatom taxa based on counts of > 400 valves per sample. Siliceous algal remains, specifically the valves of diatoms (Bacillariophyceae) and the stomatocysts and scales of chrysophytes (golden brown algae Chrysophyceae and Synurophyceae), as well as chitinous invertebrate remains (Chironomidae, Diptera and Cladocera, Crustacea), are the primary paleoindicators in lake sediments that provide reliable records of changes in water quality, habitat and catchment processes. From Smol *et al.* (2005).

in the southern parts of boreal regions, reflecting an indirect response to climate conditions (Heino & Toivonen 2008). While maximum summer temperature itself may not necessarily determine the success of macrophyte species, the increase in the length of the growing season and ice-free period may have more profound effects on the geographic distributions of macrophytes in boreal regions (Alahuhta *et al.* 2011; cf. Hellmann *et al.* 2008). An important suggestion from these large-scale analyses is that different taxonomic groups may not show similar responses to climate change, which is again likely related to the proportions of cold-, cool- and warm-water species in a given taxonomic group.

Moreover, similarly as in stoneflies, species richness increases northwards in certain bird groups that are dependent on freshwater shorelines and wetlands. This pattern is caused mainly by the amount and heterogeneity of wetlands which increase northwards (Järvinen & Väisänen 1978). Due to climate warming, shallow ponds of northern wetlands are predicted to dry out considerably (Wrona *et al.* 2006a), and in fact this was documented in a long-term study on a series of ponds and wetlands on Ellesmere Island (Smol & Douglas 2007b). Also, ponds located on palsa mires in the sub-Arctic sporadic permafrost zone are predicted to dry out as permanently frozen peat hummocks melt, causing ultimately habitat homogenization. These processes are likely to cause habitat degradation for shorebirds and waterfowl breeding on these heterogeneous habitats (Luoto *et al.* 2004). This progress is of conservation concern, because northern regions are globally highly significant for shorebirds and waterfowl, especially so for populations of geese and sandpipers (Zöckler & Lysenko 2000; see also Ganter & Gaston, Chapter 4). However, in the wetlands and wet peatlands located in the extensive permafrost areas, permafrost degradation may have other types of significant, but largely unknown, ecological consequences. For example, in certain regions of the Canadian Arctic, extensive permafrost thaw is considered to lead to wetter, not drier, conditions (Luoto *et al.* 2004 and the references therein).

There is also additional information on the distributions of freshwater organisms based on surveys of streams and lakes across extensive geographical gradients. Surveys of streams in northern regions have suggested that biotic assemblages show at least some variability associated with latitude and co-varying temperature conditions. Support for this reasoning comes primarily from studies of macroinvertebrates in northernmost North America (Vinson & Hawkins 2003, ACIA 2005) and northernmost Europe (Sandin & Johnson 2000, Heino *et al.* 2002). Indeed, in addition to a suite of environmental factors at various other scales, regional climatic factors are also often important in determining the structure of stream assemblages (Sandin & Johnson 2004, Heino 2009, Heino *et al.* 2010).

There is also evidence that climate change may modify geographical patterns of lake communities, and its associated temperature increase is expected to have strong direct effects on both planktonic and benthic biomass in Arctic lakes and will probably change species composition (Jansson *et al.* 2010). Patalas (1990) observed that in the temperate zone, the maximum species richness of zooplankton peaked in regions where mean ice-free temperatures were approximately 15 °C, while species richness declined with both increases and decreases in temperature across a geographical gradient between 45° N and 55° N. This observation was explained by the overlap in the distributions of southern warm-water and northern cold-water species that were able to occupy the same regions and lakes. It is thus possible that regions with the highest regional and local diversity of zooplankton will move poleward in association with climate-induced shifts in the distributions of species (Schindler 1997). If these predictions are more generally applicable to northern regions, then at least the southern parts of Arctic regions may receive several new cool- and warm-water species, while cold-water species may or may not be negatively affected by changes in temperature. As water temperature isotherms shift northwards, zooplankton species are likely to extend their geographical ranges northwards, but their southern boundaries may also move northwards because of the expansion of other, warm-adapted zooplankton that will have a competitive advantage. As a consequence of new dispersals, the total number of zooplankton species is expected to change (Patalas 1990).

Direct and indirect effects of climate through increase in the length of the growing season may also be responsible for the present-day relationships between temperature and diatom distributions across lakes in northern regions (Weckström & Korhola 2001). It is not surprising, therefore, that diatoms are also predicted to respond strongly to projected climate change (Sorvari *et al.* 2002). Similarly to diatoms, surveys of lakes along large geographical gradients have shown that temperature is one of the most important factors accounting for variability in the assemblage structure of macroinvertebrates, both in Eurasia and North America (Walker *et al.* 1991, Nyman *et al.* 2005, Smol *et al.* 2005, Barley *et al.* 2006;

see also Hodkinson, Chapter 7). Hence, factors affecting aquatic insect diversity in the Arctic are those that with great probability will also change as climate changes; for example, temperature and accumulation of organic matter. It has been projected that climate warming could alter aquatic insect composition by shifting the locations of thermal optima northward by about 160 km per 1 °C increase in surface temperature (ACIA 2005).

Recent studies have also indicated that climate change along with various other anthropogenic drivers/stressors often pose multiplicative and interactive impacts on freshwater ecosystems (Schindler 1997, Wrona *et al.* 2006a, 2006b, Prowse *et al.* 2011c, see also Riddle & Muir 2008 and Ormerod *et al.* 2010). The following Sections 13.4.2 to 13.4.7 examine the potential effects of such interactions on freshwater biodiversity. The main focus here is on anthropogenic effects, such as acidification, eutrophication, land-use change, ozone depletion and UV effects, invasions of alien species and contaminants, but we acknowledge that many other anthropogenic and natural changes in ecosystem conditions may affect biodiversity (see Heino *et al.* 2009 for a wider discussion).

### 13.4.2. Climate change and acidification

Climate change will probably have complex interactions with acidification. Climate warming may accelerate the acidification of streams and negatively affect the recovery process of acidified lakes (Schindler 1997), although divergent observations of increasing alkalinity of lakes have also been made (Schindler *et al.* 1996). It is, therefore, difficult to predict the consequences of climate warming for the acidity of freshwater ecosystems, given that regional differences in atmospheric deposition of acidifying substances and acid runoff from the catchments may affect the degree of acidification or increased alkalinity of fresh waters (Schindler 1997). Increasing acidity generally leads to an impoverishment of freshwater biodiversity (Giller & Malmqvist 1998), whereas decreasing acidity typically has the opposite effect. Due to these opposing effects, the influences of climate change through acidity on biodiversity are similarly difficult to predict. One likely scenario is that freshwater ecosystems in a region liable to acidification are likely to show additional negative effects on biodiversity, whereas in regions that are naturally under no threat of acidification, biodiversity may show the reverse (Heino *et al.* 2009). However, even within a region, climate warming may have different effects on temporal changes in the biodiversity of streams with different levels of acidity (Durance & Ormerod 2007).

### 13.4.3. Climate change and eutrophication

Climate change may lead to either decreased or increased levels of nutrients entering freshwater ecosystems. Climate warming may lead to a decline in the phosphorus concentration of lake water arising from enhanced primary pelagic productivity (Schindler *et al.* 1990, Schindler 1997, 2009), which is likely to result in changes in biodiversity. Opposite effects of increased nutrient levels, for example through increased biomineralization due to warmer conditions as well as greater runoff from increased precipitation, may also be expected, and if increases are sufficient enough, they might result in changes in biodiversity as well. However, it is important to keep in mind that the effects of the increased levels of nutrients on biodiversity depend on the natural state of an ecosystem (Heino 2009, Heino *et al.* 2009). Because most Arctic freshwater ecosystems are naturally oligotrophic, even small increases in nutrient levels may result in increased species richness through cascading trophic effects which may subsequently impact native species and assemblages.

Climate warming may melt upper layers of permafrost, resulting in increased levels of phosphorus entering freshwater ecosystems in Arctic regions (Hobbie *et al.* 1999). Such nutrient increases are often seen in a higher production of diatoms. Increases in productivity and biomass at lower trophic levels are likely to have substantial effects throughout the food web. For example, fish predators are generally limited by very low levels of productivity typical of Arctic freshwater ecosystems, and increased algal productivity might allow these systems to support top trophic levels (Flanagan *et al.* 2003). If fish are absent, then the lake ecosystem may remain in a state where increased algal production is controlled by grazing zooplankton (Wrona *et al.* 2006a).

If nutrients are available abundantly, mosses may become dominant primary producers in streams and use most of the available nutrients (Hobbie *et al.* 1999). Changes in the abundances of such key organisms that provide structural habitat for other organisms may also have various effects (Stream Bryophyte Group 1999). Increased moss cover could result in increased abundance and diversity of benthic macroinvertebrates as well as algal taxa such as diatoms (Douglas & Smol 2010). Thus, changes in the community structure of Arctic streams may result from either direct effects of warming and eutrophication or indirect pathways (Heino *et al.* 2009). Either way, warmer and more nutrient-rich waters are likely to support novel communities in Arctic streams. These changes may however, displace or disrupt native species and assemblages through increased competition or range shifts in response to altered environmental conditions. The degree to which bottom-up and top-down forces control biodiversity, such as species richness and assemblage composition, awaits further studies in Arctic freshwater ecosystems.

Factors other than nutrients such as light and temperature are also known to affect productivity in high latitude lakes (Flanagan *et al.* 2003). For example blue-green cyanobacteria commonly associated with blooms in temperate lakes were not found to increase proportionally with nutrient additions in Arctic systems as they would in temperate systems (Vincent & Quesada 2012). This is likely because bloom-forming cyanobacteria tend to have high temperature optima for maximum growth. Consequently, as temperatures increase, high latitude lakes may become susceptible to nuisance blooms like their temperate counterparts (Vincent & Quesada 2012).

### 13.4.4. Climate change and land cover alterations

Climate change may affect freshwater ecosystems *via* alterations in the land cover of catchments and characteristics of riparian zones (Schlinder 2009, Schlinder & Lee 2010). These changes may be both natural consequences of shifts in terrestrial vegetation and anthropogenic alterations of land cover (Allan 2004). Climate change has been suggested to strongly modify terrestrial vegetation. Shifts in vegetation zones have been predicted following climate change in the future (Burns *et al.* 2003). At high-latitude treelines, the intrusion of forest vegetation to sparse sub-Arctic mountain birch woodlands and Arctic tundra (Krankina *et al.* 1997, Chapin *et al.* 2005) is expected to take place in due course, and where this happens, it can also alter community structure and ecosystem functioning in headwater streams and lake littoral zones. It may well be that headwater streams and lake littoral zones previously driven by autochthonous algal productivity may be changed to largely allochthonous systems fuelled by coarse detritus from newly-developed riparian trees and shrubs. These changes should, in turn, affect biodiversity, e.g. as changes in the taxonomic composition and functional structure of macroinvertebrate communities. Interactions between climate change and changes in land use may also affect ecosystems indirectly and unpredictably by altering ecosystem linkages. For example, dramatic increases in geese populations attributed to climate change and changes in land use were found to have a significant fertilizing (eutrophication) effect through increased droppings entering the lakes and ponds in Svalbard (Van Geest *et al.* 2007).

### 13.4.5. Climate change and species invasions

Climate change is projected to be an important driver affecting invasions of human induced alien species by (1) increasing the invasibility of ecosystems, (2) altering environmental conditions (i.e. increasing physiological stress) on native species and (3) enhancing the ability of alien species to invade new habitats/ecosystems (e.g. increased interconnectivity of Arctic lakes and ponds *via* permafrost thaw, increased span of road and shipping networks into remote areas) (Thuiller *et al.* 2007, Heino *et al.* 2009, AMAP 2011b; see also Lassuy & Lewis, Chapter 16). Climate warming is likely to be especially pertinent in northern regions by increasing the probability of the introduction of human-introduced species and through the expansion of species ranges from south to north. The northern range limits of such species are typically determined by minimum winter temperatures or growing degree days. Many northern freshwater ecosystems may, therefore, become suitable for the establishment of viable populations of various alien species, often with dramatic influences on native species, biotic communities and ecosystem processes (Wrona *et al.* 2006a, Rahel & Olden 2008). The negative impacts of alien species are undesirable especially if they (1) lead to general reductions in biodiversity, (2) are directed at keystone species, or (3) change trophic relationships in a recipient ecosystem (Heino *et al.* 2009). The invasion process and impacts of aquatic alien species have already been considered extensively in other contexts (Rahel 2002, Korsu *et al.* 2008), as well as in association with anticipated climate change (Lodge 1993, Hellmann *et al.* 2008, Rahel & Olden 2008).

While the number of alien species is likely to increase in northern freshwater ecosystems following climate change through increased spreading and establishment success of alien species, it may be difficult to predict with high certainty which particular alien species will ultimately spread into the high-latitude freshwater ecosystems. Most proactive attention should be targeted at alien species which (1) have strong dispersal capability or (2) may effectively pass geographical barriers through many dispersal vectors, (3) have a wide environmental tolerance (i.e. indicated by a wide ecological niche in the native range), (4) are able to compete successfully with native species and become dominant, and (5) can effectively spread to new localities from their stepping-stone sites (Hellmann *et al.* 2008). In general, freshwater species are less capable of tracking the spatial shifts in their climatic optima than terrestrial species (Rahel & Olden 2008), but there are exceptions to this pattern (Heikkinen *et al.* 2009). For example, species such as the highly invasive warm-water Canadian waterweed *Elodea canadensis*, ruffe *Gymnocephalus cernuus* and the common carp *Cyprinus carpio* may show an enhanced northern range expansion as a consequence of climate warming, thereby potentially becoming problematic invasives in Arctic freshwater ecosystems (Madsen & Brix 1997, Baidou & Goldsborough 2006, Heikkinen *et al.* 2009). Section 13.5.1 below further discusses the potential for enhanced invasion of freshwater parasite species in relation to Arctic climate warming.

### 13.4.6. Climate change and alterations in ultraviolet radiation regimes

Concurrent changes in the climate and ultraviolet radiation regimes in the Arctic are projected to have far-reaching impacts on the structure and function of terrestrial and freshwater ecosystems (Weatherhead *et al.* 2005, Wrona *et al.* 2005, 2006b). While Arctic stratospheric ozone levels display high natural seasonal and interannual variability arising from complex atmospheric dynamics, over the past several decades levels have been observed to be substantially lower in late winter and early spring (Weatherhead *et al.* 2005). At the species level, most studies on the effects of ultraviolet radiation (UVR) on Arctic and high mountain freshwater organisms show negative responses in survival and productivity, including bacteria and phytoplankton (Carrillo *et al.* 2002), zooplankton (reviewed by Rautio & Tartarotti 2010) and fish (Battini *et al.* 2000). Some studies further suggest that UVR is one of the major determinants of phytoplankton and zooplankton communities in oligo-

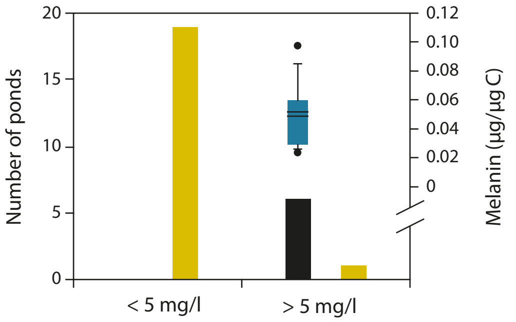

**Figure 13.6.** Occurrence and pigmentation of waterfleas *Daphnia* sp. in ponds with different dissolved organic carbon (DOC) concentrations. Yellow bars indicate the number of ponds where waterfleas are absent and the black bar the number of ponds with waterfleas. DOC of 5 mg per liter defines the transition from oligohumic to mesohumic waters. The blue box plot shows the concentration of melanin pigment (related to carbon biomass) in waterfleas. Data from Rautio & Korhola (2002).

trophic Arctic and alpine lakes (Cabrera *et al.* 1997, Williamson *et al.* 2001, Rautio & Korhola 2002) with, for example, UV-sensitive species such as waterfleas *Daphnia* sp. lacking from lakes where underwater UV-irradiance is high (Fig. 13.6) and cyanobacteria-dominated benthic communities packed with UV-screening pigments being most successful in UVR-exposed sites (Wrona *et al.* 2006b, Bonilla *et al.* 2009). At the community level however, there are contrasting reports about the vulnerability of aquatic systems to UVR. While some studies have shown strong negative community effects (Rautio & Korhola 2002, Marinone *et al.* 2006), many other studies have shown few or no UVR effects on the plankton community, i.e. on biomass, growth or species composition (Laurion *et al.* 1998, Hylander & Hansson 2010). Such variability in results arises from seasonally and ontogenetically changing plasticity of many species to UVR (Stutzman 1999) and from various biotic interactions that may be more important in shaping communities than UVR (Vinebrooke & Leavitt 1999). Consequently, it is a challenge to assess UVR impacts to aquatic communities accurately; however, UVR-tolerance ranking seems to apply to all pelagic communities.

Among phytoplankton, small phytoplankton cells are especially sensitive to UVR because they have a high illuminated surface to volume ratio, little self-shading and limited UV-screening pigmentation (Karentz *et al.* 1991), although picocyanobacteria may be an exception to this size-dependent sensitivity (Laurion & Vincent 1998). In many oligotrophic lakes, including many Arctic lakes, small phytoplankton are responsible for most of the pelagic primary productivity. In zooplankton and fish, the most UV-sensitive are the eggs and young. For example, Leech & Williamson (2000) showed that adults had up to 34% higher ability to tolerate exposure in relation to lethal dose to UVR than did nauplii. Because the eggs and young are most abundant early in the growing season, they are exposed to high and sudden changes in UVR exposure, resulting from the ice-out in June and from ozone destruction linked to higher UVR intensities in late spring. Scenarios of earlier ice-out, already occurring in many parts of the Arctic (Magnuson *et al.* 2000), predict that in the future, the first developmental stages will be exposed to even higher doses of UVR and its associated risks. Modeling analyses indicate that ice loss can result in much greater increases in underwater biological UVR exposure than moderate stratospheric ozone depletion (Vincent *et al.* 2007). Amongst the most UVR sensitive organisms are also those that are already influenced by one or several other stressors, such as acidification, eutrophication or low oxygen concentration. Low temperature in Arctic lakes is also often considered as a stressor that influences species UVR-tolerance. It has been suggested that UVR is a more important stressor at colder temperatures because enzymatic processes like UVR repair mechanisms and detoxification of reactive oxygen species is slower (Hessen 1996). Experimental evidence, however, is contradictory (Borgeraas & Hessen 2000), and it could be that acclimation of organisms to a certain temperature range is a key factor that determines how organisms will react to the combination of different UVR-temperature interactions.

Much of the variability in plankton responses to UVR is also related to the extent the species is able to use protection strategies against UVR (see Perin & Lean 2004 and Hansson & Hylander 2009 for reviews). The suite of protective mechanisms available for an aquatic community depends on the environmental characteristics of the lake and the species-specific affinities. Physically, moving away from damaging fluxes of UVR by undergoing vertical migration is a very efficient way to minimize UVR exposure, but the shallow ponds that are the most abundant type of water body in the Arctic are not often deep enough to provide such depth refugia. One important UVR defense strategy in zooplankton is the synthesis or accumulation of photo-protective compounds acting as sunscreens or as antioxidants. The known photoprotective compounds include dark melanin pigment, transparent mycosporine-like amino acids, and colorful carotenoids and scytonemin. Most species are not able to synthesize or accumulate all these photo-protectants but rather are specialized in using one of them as a protector against UVR. Pelagic cladocerans such as water fleas (e.g. *Daphnia* such as *Scapholeberis* spp.) often synthesize melanin in high-latitude clear lakes while copepods use carotenoids and mycosporin-like amino acids as shields against UVR. Pigments, however, make zooplankton more visible to fish and increase the risk of being eaten; in high UVR sites zooplankton need to adjust the level of pigmentation to best minimize these two threats (Wrona *et al.* 2006b, Vincent *et al.* 2007).

Previous exposure to UVR also determines the sensitivity of an organism to UVR. Species that routinely experience high levels of UVR in their natural environment are more tolerant to UVR than those that routinely experience low levels of UVR (Stutzman 1999, Zellmer *et al.* 2004). Whether organisms activate their shields with repeated exposure to UVR or whether different species and populations are genetically different in their protection strategies is not known. Nevertheless, because of the different lines of defense and the resultant and changing variability in the sensitivity to UVR, only results from one lake and from one time can be compared when accurately ranking species-specific UV-tolerances. More studies are needed at the community level to better understand the drivers that determine the multiple interactions in community responses to UVR, and to better predict how aquatic ecosystems respond to increases in UVR from climate change (Wrona *et al.* 2006b). Given the presence of UVR on the Earth since the beginning of life and often in greater intensities than during the anthropogenic stratospheric ozone depletion (Leavitt *et al.* 1997), it is evident that organisms have ways of coping with UVR. However, changes in species composition, abundance and food web structure are likely to occur with changing UVR, especially in oligotrophic high-latitude freshwater systems that are under strong abiotic regulation.

### 13.4.7. Climate change and contaminants

Climate change has been identified as a potentially important co-driver of altering contaminant distribution, fate and bioavailability and ultimately the chronic and acute effects on the biodiversity and function of Arctic freshwater ecosystems (AMAP 1997, 2003, 2011a, Macdonald *et al.* 2005, Wrona *et al.* 2006b, Carrie *et al.* 2010, Veillette *et al.* 2012). Although there is limited direct evidence of the interactions between climate warming and increased contaminant bioaccumulation in Arctic freshwater food webs (e.g. mercury; Stern *et al.* 2009), climate-induced changes in temperature regimes, related changes in water geochemistry from permafrost thaw, and changes in the hydrological cycle are all projected to collectively affect aquatic food webs by altering the fate, distribution and uptake of contaminants (AMAP 2003, 2011a). Veillette *et al.* (2012) postulated that climate change may result in increased retention of contaminants in the food web as a result of changes in ice cover and the hydrodynamic regime. Correspondingly, key ecological factors that will affect contaminant bioaccumulation in freshwater food webs include food availability, individual growth rates, changes in the distribution of species, productivity relationships and/or the complexity and lengths of the food webs (AMAP 2003, 2011a, Macdonald *et al.* 2005, Wrona *et al.* 2006b). In turn, the lethal and sub-lethal effects of contaminants on freshwater biota will influence patterns of biological and ecological structural and functional diversity.

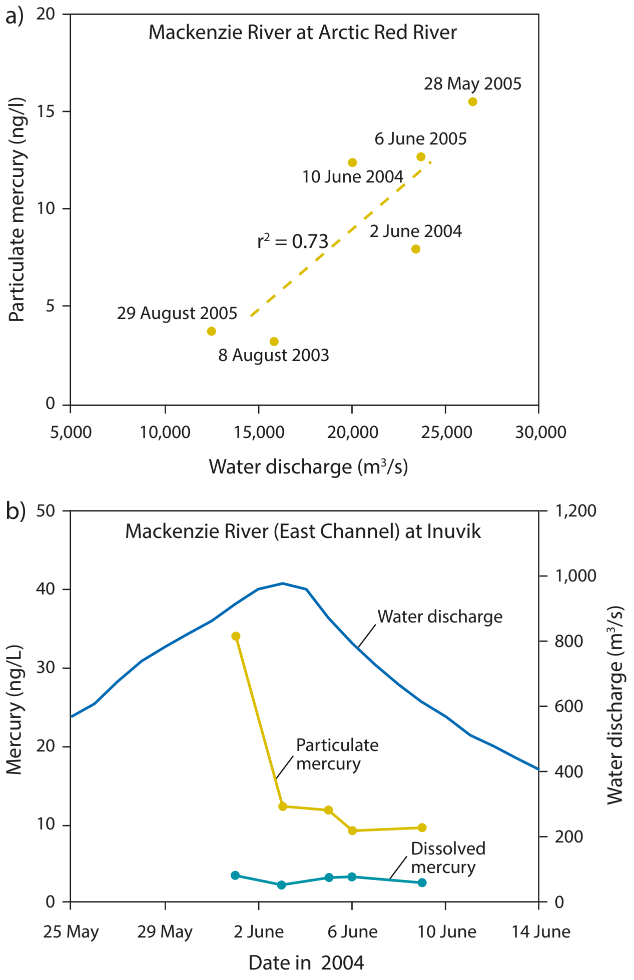

**Figure 13.7.** Relationship between (a) particulate mercury concentration and water discharge for the Mackenzie River at Arctic Red River, and (b) changes in particulate and dissolved mercury concentrations and water discharge for the Mackenzie River during the spring freshet 2004. (Source: Leitch *et al.* 2007 from Stern *et al.* 2012).

There are a growing number of studies and assessments examining the possible linkages between climate variability and change on the fate of mercury (Hg). Specific topics include thawing permafrost and related enhanced microbial mobilization (Grigal 2002, Klaminder *et al.* 2008, Xu *et al.* 2009), the effects of a changing cryosphere and hydrology on its transport and distribution in Arctic freshwater catchments (AMAP 2003, 2011a, Prowse *et al.* 2006b, Leitch *et al.* 2007), as well as the implications on aquatic ecosystems in relation to current and historic patterns of bioaccumulation in planktonic and fish communities (Muir *et al.* 2005, 2009, Outridge *et al.* 2007, Stern *et al.* 2009, 2012, Gantner *et al.* 2010a, 2010b). Leitch *et al.* (2007) have demonstrated linkages between particulate mercury concentrations and water discharge regimes in the Mackenzie River, Canada, with water discharge having an amplifying and disproportionate effect on Hg flux (Fig. 13.7). This illustrates the importance of understanding the interrelationships between atmospheric, climatological and hydrological processes in predicting potential availability and exposure of contaminants to aquatic biota in a rapidly changing climate.

Another example of the inter-relationships between climate, nutrient (productivity) and contaminant fluxes and their effects on freshwater ecosystem structure and function is provided by Arctic anadromous fish (Box 13.5).

There is a clear need for further research to elucidate the effects of anadromous fishes on nutrient and contami-

## Box 13.5. Arctic anadromous fishes as vectors of nutrients and contaminants

Extensive research conducted on the west coast of North America has revealed that semelparous[2] anadromous fishes, such as Pacific salmon *Oncorhynchus* spp., deliver significant amounts of marine-derived nutrients (MDN) and organic matter to freshwater ecosystems (e.g. Naiman *et al.* 2002). After hatching and rearing to species-specific smolt sizes in freshwater, semelparous anadromous fishes migrate to sea. They gain most of their mass at sea before returning to freshwater to spawn. Death occurs immediately after spawning, and marine-derived nutrients are transferred to freshwater spawning habitats *via* eggs and carcasses of post-spawning adults (e.g. Naiman *et al.* 2002, Stockner 2003). This has a profound effect on freshwater ecosystems including increased primary productivity (e.g. Naiman et *al.* 2002) and increased growth and biomass of stream invertebrates (e.g. Minakawa *et al.* 2002). The production and diversity of riparian plant communities (e.g. Helfield & Naiman 2001) are significantly affected by the deposition of MDN. Effects have been noted in salmon-bearing systems ranging from northern Alaska to southern British Columbia.

In addition to nutrients, semelparous anadromous fishes transport contaminants from marine to freshwater ecosystems. In Alaska, anadromous sockeye salmon *Oncorhynchus nerka* can be a more important source of organochlorine contaminants to lakes than atmospheric deposition, and it has been shown that freshwater fishes such as Arctic grayling *Thymallus arcticus* can have higher concentrations of PCBs and DDT in salmon nursery lakes than in non-nursery lakes (Ewald *et al.* 1998). It has also been shown that PCB concentrations in sediments of salmon nursery lakes can be predicted by the density of returning fish (Krümmel *et al.* 2003). Contaminant transport *via* anadromous fishes (i.e. biotransport) is of particular concern, because these contaminants are often readily bioavailable for accumulation and magnification through aquatic food chains (Ewald *et al.* 1998).

Many anadromous fishes in the Arctic are iteroparous (see footnote) rather than semelparous. Effects of iteroparous anadromous fishes on freshwater nutrient and contaminant concentrations have not been well-studied. Iteroparous anadromous fishes, such as Arctic char *Salvelinus alpinus*, Dolly Varden char *Salvelinus malma* and broad whitefish *Coregonus nasus*, can spawn multiple times during their lifetime; thus, MDN are not delivered to freshwater ecosystems *via* post-spawning *en masse* carcass deposition. Marine-derived nutrients may still be released into freshwater, however, through egg deposition, excretion of metabolic products and limited post-spawning or winter mortality. Effects of this nutrient deposition may be most ecologically relevant in oligotrophic Arctic systems, where it is more likely that MDN represent a significant portion of overall nutrient budgets (Nislow 2004).

Recently, Swanson & Kidd (2009) conducted a semi-quantitative assessment of nutrient transport achieved by anadromous Arctic char in a coastal lake situated in the Arctic territory of Nunavut, Canada. These authors found that masses of nutrients (nitrogen, phosphorus, carbon) transported by char likely had a negligible effect on lake water chemistry. In follow-up studies, food webs and mercury concentrations were compared between a series of lakes that did and did not contain anadromous Arctic char. There was no stable isotope evidence for char-mediated transport of MDN or organic matter (Swanson *et al.* 2010). Other ecological effects were noted, however. Freshwater lake trout were in better condition, had higher lipid content, and had lower mercury concentrations in lakes where anadromous Arctic char were present (Swanson & Kidd 2010, Swanson *et al.* 2010). The reasons for this were not entirely clear, but it is possible that through functioning as a high-quality alternate prey source, Arctic char increase the growth efficiency of sympatric lake trout. Interestingly, Arctic char and lake trout only exist in sympatry when the Arctic char population is anadromous. With very rare exceptions, landlocked Arctic char and lake trout cannot coexist (Johnson 1980). This is likely due to the relatively low carrying capacity of Arctic freshwater systems, and it suggests that even if anadromous Arctic char do not have a direct effect on water chemistry or primary productivity, they may impart an indirect marine subsidy to lakes that leads to increased fish biomass.

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[2] Semelparity is a reproductive strategy involving a single (usually large) reproductive event in the lifetime of the organism. In contrast, iteroparity occurs in organisms that possess the potential of multiple reproductive events in their lifetime.

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nant concentrations in Arctic freshwater ecosystems. This is particularly true for iteroparous (see footnote in Box 13.5) anadromous fishes. Iteroparous anadromous fishes have complex and variable life histories, low fidelity to their natal systems (e.g. Gyselman 1994), and large interannual variations in population numbers (e.g. Johnson 1989). All of these factors complicate mass-balance calculations. Furthermore, we have yet to consider the effects of multiple sympatric anadromous species (e.g. sympatric anadromous Arctic char and lake trout) on the ecology of freshwater lakes.

## 13.5. ALTERATIONS IN ECOLOGICAL INTERACTIONS AND IMPLICATIONS FOR BIODIVERSITY

In addition to the effects arising from large-scale physical and chemical environmental and anthropogenic drivers such as climate change, landscape disturbance and enhanced pollution, the outcomes from ecological interactions such as competition, predation and parasitism can also have significant implications for the structural and functional diversity of freshwater systems. The relative associations of existing interactions may be further modified in response to anthropogenic stressors, thus altering ecosystem biodiversity. This will be in addition to the alterations resulting from colonization of invasive species, which were dealt with above. Below we provide examples of functional interactions that are being modified by environmental and/or anthropogenic drivers, highlighting the complexities associated with understanding causal mechanisms and predicting changes in structural and functional biodiversity in Arctic freshwater systems.

### 13.5.1. The importance of host-parasite relationships

Studies of biodiversity typically do not consider parasites, in part because they may be cryptically hidden within their hosts, and in part because many do not consider them important components of biodiversity (Marcogliese 2004, 2005). In addition to information herein, the ecological importance and biogeographic significance of parasites are further reviewed in Hoberg & Kutz (Chapter 15).

Most of the literature describing the parasite fauna of freshwater fishes in Arctic and sub-Arctic waters pertains to salmonids and coregonids, but also sticklebacks *Gasterosteus* spp. Approximately 300 parasite species have been found in these waters in northern Europe and Siberia (Rumyantsev 1984). They include protozoans, myxozoans, monogeneans, trematodes, cestodes, nematodes, acanthocephalans, leeches, crustaceans and molluscs. Monogeneans, myxozoans, trematodes and protozoans are the most diverse taxa in these waters. Using Arctic char as an example, 107 parasite species have been found world-wide, with 66 being found in North America, 69 in the former USSR and 18 in Norway (Dick 1984). In the Palearctic, Arctic freshwater parasites number about half those of the boreal plains, and in northern Europe they comprise approximately 24% of parasite species (Rumyantsev 1984). Parasites that use copepods or amphipods as intermediate hosts are most common from these three areas (Dick 1984), while the acanthocephalans and protozoans are under-represented in Norway and North America (Kennedy 1977, Dick 1984). Twenty-three species are considered circumpolar (Curtis 1995). The most widespread parasites are generalists that infect a wide variety of fish species (Carney & Dick 2000), and Arctic and sub-Arctic parasites occur in high abundance (Rumyantsev 1984). They tend to be associated with the distribution of relict crustaceans, which often function as intermediate hosts. Most parasites in northern lakes have complex life cycles and rely on trophic interactions for transmission (Curtis 1995, Amundsen *et al.* 2009). In lakes on high Arctic islands, the most important intermediate hosts are copepods, and thus cestodes are common, as are parasites with direct life cycles, such as monogeneans (Curtis 1995). Despite the isolation of these high-latitude islands, parasite diversity on Svalbard and Jan Mayen is equal to that on the sub-Arctic mainland of Norway (Kennedy 1977). Parasites of Arctic fishes comprise a distinct fauna, with some variation in the distribution of certain species among regions (Kennedy 1977, Dick 1984, Rumyantsev 1984, Curtis 1995). Indeed, for certain fishes such as the whitefishes, their parasite fauna is more diverse in the North than in southern waters (Rumyantsev 1973). Species richness in salmonid and coregonid hosts ranges from four to 18 parasite species in sub-Arctic and Arctic ecosystems (Miller & Kennedy 1948, Pennell *et al.* 1973, Kennedy 1977, Dick 1984, Bouillon & Dempson 1989, Albert & Curtis 1991, Hartvigsen & Kennedy 1993, Curtis 1995, Due & Curtis 1995, Knudsen *et al.* 2003, Kristmundsson & Richter 2009). In addition, there is a great deal of sharing of parasites among fish species within subfamilies, particularly the chars and coregonids (Curtis 1988, 1995). Some parasites, but not all, are shared between the salmonids (Knudsen *et al.* 2008, Kristmundsson & Richter 2009).

The most diverse parasite communities also include marine parasites, which are obtained during the seawater phase in anadromous populations. Indeed, parasites may be used effectively to discriminate anadromous fishes from non-migrants (Kennedy 1977, Dick 1984, Bouillon & Dempson 1989). Species richness in other hosts such as trout-perch *Percopsis omiscomaycus* tends to be lower than in salmonids and coregonids (Nelson *et al.* 2010). However, there are comparatively few studies on this fish, which is smaller than and not as long-lived as salmonids and coregonids. Similarly, parasite richness in threespine stickleback *Gasterosteus aculeatus* ranges from one to 11 in Arctic and sub-Arctic waters, but is usually under seven (Poulin *et al.* 2011).

To date, most changes in the parasitofauna of Arctic and sub-Arctic fishes have been linked to fishing practices and eutrophication. Managed reductions in densities of top predators such as Arctic char to improve fisheries results in increased fish growth and improved condition, but also leads to higher abundances of parasites, some of which are pathogenic (Albert & Curtis 1991, Curtis 1995, Knudsen *et al.* 2002). The opossum shrimp *Mysis relicta* has been introduced in sub-Arctic lakes of sub-Arctic northern Sweden to improve coregonid and salmonid fisheries (Curtis 1988). Their introduction has promoted the transmission of certain larval cestodes to planktivorous whitefish, while at the same time reducing transmission to benthivorous whitefish as a result of shifts in the corresponding pelagic and benthic food web structure (Curtis 1988). Eutrophication of northern waters in Russia has led to the reduction or disappearance of parasite species in the Arctic freshwater complex (Rumyantsev 1997). During initial stages of eutrophication, some of these parasites may increase in abundance (e.g. parasites transmitted to fishes by relict crustaceans and zooplankton, and trematodes of fish that mature in birds). However, further eutrophication generally results in a reduction in diversity of parasites of the Arctic freshwater complex, associated with an overall reduction in faunal diversity (Rumyantsev 1997).

The Arctic and sub-Arctic regions are among the most vulnerable to climate warming (ACIA 2005a, Fischlin *et al.* 2007, Parry *et al.* 2007, AMAP 2011a). Reduction in ice cover will affect lakes and rivers by increasing productivity (Prowse *et al.* 2006b, Prowse *et al.* 2011c, AMAP 2011a). Host species distributions will be altered, with many warm-water fishes expanding their current range into northern habitats (Reist *et al.* 2006a, 2006b, Wrona *et al.* 2006a, Parry *et al.* 2007), bringing with them their parasites (Marcogliese 2001, 2008). Fish introductions will also cause niche shifts and changes in the parasite fauna of the chars away from benthically-transmitted parasites towards those transmitted by zooplankton (Dubois *et al.* 1996, Bergeron *et al.* 1997, Knudsen *et al.* 2010). Climate change not only will affect water temperatures, but will also impact water levels and flow rates, eutrophication, stratification, ice cover, acidification, ultraviolet light penetration and weather extremes, all of which can affect parasite transmission and disease (Marcogliese 2001). More specifically, reduced ice cover and longer growing seasons will lead to faster growth rates, earlier maturation, more parasite generations per year and a prolonged transmission window, possibly resulting in increased pathology, virulence and outbreaks of disease (Marcogliese 2001, 2008). Since contaminant levels are also expected to increase in the Arctic and sub-Arctic (Macdonald *et al.* 2005, Wrona *et al.* 2006b, Parry *et al.* 2007), the cumulative effects of pollution and parasitism may lead to enhanced pathogenicity and disease in animals (Marcogliese 2008, Marcogliese & Pietrock 2011).

The ecological and environmental changes associated with climate change will cause reductions in the populations of cold-water fishes, especially the salmonids (Reist *et al.* 2006a, 2006b, Wrona *et al.* 2006a, Parry *et al.* 2007). As salmonid habitat is lost and populations become reduced or extirpated (Wrona *et al.* 2006a), their host-specific parasites will also be at risk (Marcogliese 2001). This may be more problematic than it first appears, because parasites have been shown to be important components of food webs in terms of linkages and structure, including in northern ecosystems (Lafferty *et al.* 2006, Kuris *et al.* 2008, Amundsen *et al.* 2009), and may contribute to food web stability and resilience (Lafferty *et al.* 2008, Poulin 2010). Indeed, healthy ecosystems should have rich and diverse parasite communities (Marcogliese 2005, Hudson *et al.* 2006). Better and more comprehensive baseline parasite biodiversity data are required to enable more accurate predictions and fully comprehend changes as they occur in the Arctic and sub-Arctic (Hoberg *et al.* 2003; see also Hoberg & Kutz, Chapter 15). Box 13.6 provides a case study of the potential combined effects of two anthropogenic

## Box 13.6. *Gyrodactylus salaris* – a disastrous pathogen in northern Europe

*Gyrodactylus salaris* is a small (0.5-1 mm) viviparous monogenean freshwater parasite that lives mainly in Atlantic salmon *Salmo salar* parr in rivers in Fennoscandia. Noteworthy is that Baltic salmon are resistant to this parasite but Atlantic salmon have no similar resistance (Bakke *et al.* 2002).

The parasite thus causes damage only to Atlantic salmon, in spite of the fact it can also be found on some other salmonid fishes, e.g. Arctic char *Salvelinus alpinus* and rainbow trout *Oncorhynchus mykiss* (Bakke *et al.* 2002, Olstad *et al.* 2007, Robertsen *et al.* 2007, 2008). *G. salaris* has had a detrimental influence to Atlantic salmon parr mainly in Norwegian rivers (Heggberget & Johnsen 1982, Johnsen & Jensen 1991, 1992). This parasite has also been discovered in the river Keret on the sub-Arctic White Sea coast where the density of salmon was reduced dramatically after the appearance of *G. salaris*, and the parr density was very low during the period 1992-1998 compared with the years 1990 and 1991 (Johnsen *et al.* 1999).

The native distribution area of *G. salaris* includes the Karelian part of Russia, the Baltic coast and waterbodies of Finland and Sweden (Meinilä *et al.* 2004). Dispersion to northern coastal waters and rivers took place when infected salmon parr were transferred from fish farms from the Baltic Sea basin to Norway. Migrations of infected fish have also spread the parasite to new rivers and brackish water fjords (Johnsen 2006).

The parasite was spread from the Baltic basin during the 1970s when salmon farming grew rapidly in Norway and Norwegian parr production was not able to satisfy the demand. *G. salaris* was discovered for the first time in Norway in the river Lakselva in 1975 (Heggberget & Johnsen 1982). Since then, the parasite has been found in a number of rivers. The colonization of rivers after parasite introduction has taken place in 1-3 years. For example, in the large river Vefsna, the parasite was found in the lower parts in 1978 but by 1980 had spread throughout the entire watercourse (Johnsen & Jensen 1988). Today *G. salaris* has been found in 45 Norwegian rivers.

*G. salaris* usually occurs on the fins of infected Atlantic salmon but also in other parts of the body (Mo 1992). Parasites are found less commonly on the gills. In Norway, the salmon harvest from infected rivers is on average 87% less than in non-infected rivers. The total yearly loss to the river fishery caused by *G. salaris* is estimated to about 45 tonnes. The enhanced geographic distribution and observed infection rates of this fish parasite since the 1970s illustrates the potential implications of accelerated species invasions under a rapidly changing Arctic.

stressors (aquaculture first, with parasite transfer to local native fish populations, followed by projected climate-change-induced range expansion of the parasite) affecting ecosystem services and associated economic loss of fisheries harvesting. While the example is based primarily on boreal fish studies, it provides important insights into potential future effects of climate warming on Arctic fish populations and the corresponding negative ecological and economic effects of their associated parasites.

### 13.5.2. Modifications of ecological interactions through anthropogenic and/or ecological drivers

As discussed previously, significant challenges exist in determining causal environmental factors, their magnitudes and range of effects in influencing the observed geographic patterns of community structure and related diversity of Arctic freshwater species. No single environmental and/or anthropogenic driver operates in isolation (Fig. 13.1), hence understanding their cumulative effects on biological and functional diversity requires a systematic approach of synoptic, regional monitoring coupled with focused process-based, hypothesis-driven supportive research. To date, such efforts have been limited in scope in Arctic freshwater systems.

A taxonomic complex that has been extensively studied in the Arctic is pelagic zooplankton communities, where numerous work has focused on assessing the relative importance of physical, chemical, biological and ecological factors involved in influencing the distribution and abundance of zooplankton communities (e.g. Hamilton 1958, Hutchinson 1967, Kettle & O'Brian 1978, O'Brien *et al.* 1979, 1990, 1997, 2004, Hobbie 1980, Stross *et al.* 1980, Dillon *et al.* 1984, Pienitz *et al.* 1995, Jansson *et al.* 2000, Rautio *et al.* 2008, 2011).

A comprehensive study by O'Brien *et al.* (2004) on 104 Arctic lakes in the Toolik Lake region of Alaska highlights the complexities and challenges involved in defining the causal relationships related to describing zooplankton community distribution and diversity in relation to changes in physical, chemical and biological drivers. In their study, they assessed the relationship between the presence and diversity of zooplankton and lake morphometry (i.e. lake size, lake depth), water chemistry and the presence of fish and the structure of the associated fish communities. They found a significant relationship between lake depth and zooplankton species richness, with higher richness in larger and deeper lakes. In addition, smaller body-sized species were more numerically dominant in deep lakes, while larger species were more prevalent in shallow lakes. Species richness was found to be unaffected by chlorophyll *a* concentration (a measure of algal biomass) or lake water chemistry (ionic strength). As expected, when fish were present, few large zooplankton species co-occurred. In contrast, however, the relationship between the presence and density of smaller-sized zooplankton species and the presence of fish species was complex. Two zooplankton species (the waterflea *Daphnia pribilofensis* and the copepod *Cyclops scutifer*) were present and abundant in almost all of the 104 lakes, whereas very large body-sized species (*Daphnia middendorfiana*) were much less dense and occurred only in lakes without fish. The presence/absence of remaining zooplankton species that were of intermediate body-size had a complex distribution across the landscape. The effect of fish communities on the presence/absence of zooplankton was less than expected, since no particular fish community type was found to have a significant effect on any particular zooplankton species, with the exception of the unexpected result of the copepod *Heterocope septentrionalis* being less likely to occur in the presence of an Arctic char and sculpin community, though neither fish is very planktivorous.

In addition, while fish presence in Arctic lakes can exert a top-down control on zooplankton communities resulting in dominance of smaller and transparent taxa, food availability is also a factor (Christoffersen *et al.* 2008, Rautio *et al.* 2008). Some species (e.g. large species such as fairy shrimps *Artemiopsis* spp.) are absent in fish-bearing waters. Standing crop abundances and diversity appear to be stable in the presence of 'typical' fish diversity in unexploited Arctic lakes. Most Arctic lakes have short, simple food webs dominated typically by Arctic char, lake trout, lake whitefish or ciscoes *Coregonus* spp. (Power *et al.* 2008). Frequency distributions of fish size and age in unexploited populations tend to be wide overall (i.e. larger, older individuals are present in reasonable abundances) albeit with grouping around length modes limited by resources (i.e. prey) (Power *et al.* 2008). Adults within these fish populations tend to control juvenile survival and recruitment (Johnson 1976) imposing top-down stability. This in turn maintains the fish population in a 'climax' condition (Johnson 2002). Presumably, this stability is transferred to prey populations (i.e. other fish species, zooplankton). Exploitation re-equilibrates these climax fish populations by truncating the upper tail of age and size distributions thus reducing mean age and size within the species. Altered size selection of prey may ensue, potentially releasing size-controlled predation on smaller fishes and subsequently affecting the zooplankton upon which they rely (i.e. relative abundance of juveniles of that species increases thus exerting greater predation upon their food resources).

This scenario is not well researched, however. It is likely self-correcting in that as food becomes limiting, the growth, survival and abundance of juvenile fish is reduced, which relaxes predation upon zooplankton. In situations of relatively stable harvest of the fish population, it is likely that a similar stability is established in target populations albeit at a different level from that of an unexploited climax system. Due to the complex life histories of Arctic fishes (Power *et al.* 2008), it should be noted that the scenarios explored above apply primarily to lakes where non-migratory fish populations reside. Marine migrations by sea-run fishes are the focus of most human harvesting; moreover, significant alterations of predator-prey relationships result from anadromy (see also Christiansen & Reist, Chapter 6). Implications of top-down shifts triggered by the exploitation of fisheries may alter fish biodiversity as well as the underlying biodiversity among lower trophic levels. Assuming human exploitation of top predatory fishes increases under a climate-warming scenario, a projected consequence may also be a destabilization of the entire system as described above. Appropriate in-depth analyses and testing are required to verify these scenarios and projected outcomes.

These examples highlight the need for integrated monitoring and research studies that focus on elucidating the complex relationships between environmental drivers and observed patterns of structural and functional diversity, particularly in the context of cumulative effects. It also further emphasizes the need to ensure that this gap is addressed across relevant and often large spatial scales.

## 13.6. CONSERVATION AND PROTECTION OF FRESHWATER BIODIVERSITY IN A RAPIDLY CHANGING ARCTIC

Rivers, streams, lakes, ponds and wetlands are prominent and integral features of the Arctic landscape. They display a complex range of physical and geochemical features and provide a diverse range of habitats for the biological communities they contain. Substantial changes have been observed over the past century in the hydrology and physical and chemical properties of Arctic freshwater systems in response to climate variability and change and other environmental and anthropogenic drivers (Wrona *et al.* 2006a, White *et al.* 2007, Heino *et al.* 2009, Moss *et al.* 2009), and there is increasing evidence that over the last several decades the rates of change are increasing (White *et al.* 2007, AMAP 2011b, Callaghan *et al.* 2011). As illustrated in this chapter, understanding and predicting the ultimate effects of a rapidly changing Arctic on freshwater ecosystems and their related biodiversity (structural and functional) is complex and will be region and system dependent. With warming temperatures and permafrost thaw, the active layer will thicken and thermokarst formation will be enhanced, resulting in hydrological and geochemical alterations. In regions of continuous permafrost, lakes, ponds and wetland complexes may be expected to increase, while in other areas of the Arctic they may shrink and disappear (Prowse *et al.* 2006a, White *et al.* 2007, Smol & Douglas 2007b, AMAP 2011b). Stream and river discharge patterns will change, as will the connectivity of drainage networks, but not in ways predictable from simply knowing alterations in evapotranspiration or precipitation regimes because of potential changes in landscape storage (White *et al.* 2007).

Climate change and other environmental and anthropogenic drivers (i.e. eutrophication, acidification, overexploitation of fish stocks, invasions of parasites or non-native species) are likely to have profound effects on the structure, function and resulting biodiversity of freshwater ecosystems. Consequently, a major scientific and ecosystem management challenge will be to understand and predict how biological communities within freshwater ecosystems will adapt to such changes. Biological/ecological adaptations can take several forms ranging from short-term responses (i.e. phenotypic and/or behavioral changes) to longer-term evolutionary changes (i.e. selection of new genotypes that are better suited to new environmental conditions). Because of the rapidity of environmental change being observed in the Arctic (AMAP 2011b), it is more likely that the dominant observed adaptation response by organisms will be phenotypic adaptation rather than genotypic adaptation (Callaghan *et al.* 2005, Usher *et al.* 2005). Various species will respond differently to changing environmental conditions according to their genetic make-up and related phenotypic plasticity, with populations at their most environmentally extreme physiological and/or ecological boundaries being the first to be affected in terms of being either ameliorated or expanding their distributions (Callaghan *et al.* 2005).

In addition to natural ecological adaptation responses by freshwater biota, planned ecosystem management approaches through human intervention could also be used to conserve and protect freshwater biodiversity. Planned adaptation will likely play an increasing role in biodiversity conservation and protection in a rapidly changing Arctic (see Hannah *et al.* 2002, Pöyry & Toivonen 2005, Heino *et al.* 2009, Schindler & Lee 2010, and references therein). Possible actions could include, for example:

- generation of protected-areas networks that account for known and projected changes in environmental and anthropogenic drivers,
- protection of large and heterogeneous areas, including whole catchments (e.g. Schindler & Lee 2010),
- identification and maintenance of dispersal corridors for freshwater taxa,
- restoration and management of close-to-natural ecosystems and viable populations,
- management of the matrix of aquatic ecosystems and their associated habitats among different protected areas in an integrated and holistic manner, and,
- where appropriate, re-introduction of key species to areas from which they have disappeared.

Another important consideration is that the conservation and protection actions taken must be adaptive and responsive, particularly in a rapidly changing Arctic. For example, additive and non-additive responses to multiple drivers and stressors could amplify or mitigate the effects of a key driver such as climate variability and change, making interactions between them difficult to tease apart. Enhanced efforts are needed to develop a better mechanistic understanding of how freshwater ecosystem structure and function and resulting biodiversity are linked and affected by changes in environmental and anthropogenic drivers. Such an understanding will only be achieved through the development and application of appropriate integrated models, process-based studies, experiments and coordinated local, regional and circumpolar monitoring across ecosystem types, multiple spatial and temporal scales and levels of biological/ecological organization (individual, population, community and ecosystem). Other promising approaches involve using linking traits to species diversity and community structure as a possible approach to explain and predict current and future species distributions along environmental gradients (e.g. Litchman *et al.* 2010).

## 13.7. CONCLUSIONS AND RECOMMENDATIONS

Arctic freshwater ecosystems are undergoing rapid environmental change in response to the influence of both environmental and anthropogenic drivers. Primary drivers affecting the distribution, abundance, quality and hence diversity of freshwater lentic and lotic ecosystems and associated habitats include climate variability and change, landscape-level changes to the cryospheric components (i.e. permafrost degradation, alterations in snow and ice regimes), and changes to ultraviolet radiation (UVR). Key secondary environmental and anthropogenic drivers that are gaining circumpolar importance in affecting Arctic freshwater ecosystem quantity and quality include increasing acidification and pollution from deposition of industrial and other human activities (wastewater, release of stored contaminants, long-range transport and biomagnification of pollutants), landscape disturbance from human development (dams, diversions, mining, oil and gas activity, population increase) and exploitation of freshwater systems (fisheries, water withdrawals).

Changes in the magnitudes, duration and interactions among environmental and anthropogenic drivers will have profound effects on the distribution and abundance of Arctic freshwater ecosystem types, the quantity and quality of their habitats, and associated structural and functional biodiversity. In response to the observed and projected types and magnitudes of changes in environmental and anthropogenic drivers affecting the Arctic ecozone, freshwater ecosystem diversity (i.e. the range and types of freshwater systems), related changes to associated freshwater habitats, and corresponding faunal biodiversity will be affected at local, regional and circumpolar scales. Given the levels of ecological complexity and associated uncertainty with linking changes in physico-chemical factors to biological interactions, quantifying and monitoring changes in beta and gamma diversity in relation to changes in key drivers will be fundamental to the conservation and management of Arctic freshwater ecosystems and their biota.

Similarly, the biodiversity within freshwater ecosystems is being rapidly altered by natural and anthropogenic drivers, thus a parallel understanding of functional diversity (food web structure and complexity, productivity, carbon and nutrient dynamics) is required to develop and implement appropriate conservation and management measures to ensure continued ecosystem services. Together, these observations also contribute understanding of factors promoting services provided by freshwater ecosystems.

Currently, knowledge of Arctic freshwater ecosystems and related biodiversity and stability is very limited due to a paucity of long-term monitoring sites resulting in large spatial and temporal time-series gaps particularly in remote areas. In the face of a rapidly changing Arctic, developing appropriate knowledge of reference states will be critical to assessing the variability and significance of change.

Significant gaps also remain in our understanding of how biodiversity contributes to, and how changes affect, freshwater ecosystem functions. The future conservation and protection of Arctic freshwater ecosystems and their associated biodiversity requires appropriate long-term monitoring across relevant spatial and temporal scales. An important step to improving efforts in this area has been the approval for implementation of the circumpolar freshwater biodiversity monitoring plan developed by the Arctic Council Conservation of Flora and Fauna (CAFF) working group and its Circumpolar Biodiversity Monitoring Program (CBMP). The Arctic Freshwater Biodiversity Monitoring Plan (Culp *et al.* 2012) details the rationale and framework for improvements related to the monitoring of freshwaters of the circumpolar Arctic, including ponds, lakes, their tributaries and associated wetlands, as well as rivers, their tributaries and associated wetlands. The plan also provides Arctic countries with a structure and a set of guidelines for initiating and developing monitoring activities that employ common approaches and indicators.

Process-based studies are required to better understand the abiotic and biotic controls on ecosystem properties and to obtain a predictive understanding of how ecological communities are structured in response to changing anthropogenic and environmental drivers. Given the complex interactions between the abiotic and biotic drivers affecting rapid change in the Arctic, trans-disciplinary approaches will be instrumental in identifying and understanding key processes (Hodkinson *et al.* 1999).

Most analyses of status and trends of biodiversity and its change have been linked to the monitoring and assessment of species richness. Standard species-based approaches may misrepresent true structural and functional diversity and thus ecosystem stability and resilience in the face of change. Future assessments of biodiversity and its changes must also include consideration of ecosystem and functional attributes using both empirical and experimental approaches. There is also an identified need to develop integrated biological/hydro-ecological models (in particular regarding changes in cryospheric components) to predict freshwater biodiversity responses to a changing climate (Hodkinson *et al.* 1999, Prowse & Brown 2010b, 2010c, AMAP 2011b).

- The establishment of a long-term, circumpolar network of integrated freshwater research observatories and monitoring sites is required to achieve the above goals. The focus should be inclusive of biodiversity in ecosystems, biota and key physical and chemical drivers, as well as anthropogenic influences, across appropriate spatial scales.

Rapid Arctic change is outpacing present capacity for Arctic freshwater conservation and management. Moreover, spatial displacement of key habitats, rapid shifts in the nature of processes and colonization by southern biota all indicate that static approaches are insufficient to understand and manage these complex systems.

Given the large spatial scale of potential changes in Arctic freshwater ecosystems (e.g. losses, shifts amongst types, productivity changes), systematic wide scale observations are required.

- Accordingly, management actions for conservation and protection of Arctic freshwater ecosystems must be adaptive in nature and the development of novel approaches is required.

Development of appropriate wide-scale and focal-point approaches to monitoring is required. These could include, for example, genomics-based diversity assessment, space-based remote sensing, networks of automated sensors systems operating at varying spatial and temporal scales, and inter-disciplinary transfer of key approaches. In addition, community-based monitoring can be an effective method to provide continuous data from remote inhabited areas. Such work could range from simple observation and documentation to the collection of samples including tissue samples taken from harvested species by subsistence hunters and fishers.

Freshwater ecosystems serve as trans-ecosystem integrators (e.g. linking terrestrial, freshwater and oceanic environments) of multiple environmental and anthropogenic drivers and stressors. In particular lakes act as sentinels and integrators of biological, geochemical and ecological events occurring in catchments and in lacustrine environments (Schlinder 2009). Ecological transition zones within and between ecosystems concentrate key processes, drivers and diversity, thus are focal areas of rapid ecosystem change and thus represent ‘hotspots’ ideal for early warning.

- Consideration should be made of using basin or ‘catchment-based’ integrative approaches (e.g. Schinder 2009, Schindler & Lee 2010) for the development of appropriate monitoring and research programs that could link individual, population, community and ecosystem responses to changes in environmental and anthropogenic drivers. In addition, such an integrated approach will allow for the assessment of the current state of ecosystem health and cumulative impacts associated with biodiversity change.

There is a growing recognition and concern regarding the lack of understanding of the potential loss or gain of species and the consequent implications for associated ecosystem function (e.g. Hooper *et al.* 2005, Vaughn 2010). Given the functional importance of biota living in aquatic environments and the difficulties associated with cataloging their diversity and distribution, innovative approaches and studies must be taken along a range of spatial, temporal and organizational (e.g. system-based and species-based) scales to better understand the connections (e.g. the necessity of obtaining an improved mechanistic understanding of the individual effects and interactions among environmental stressors/drivers on all trophic levels and related ecosystem structure and function; see Bordersen *et al.* 2011). In addition, in a rapidly changing Arctic, there is a need to be aware of and to develop ways to detect and understand possible ecological ‘surprises’, which are unexpected findings or outcomes that are well outside what is expected to happen or not happen (Lindenmayer *et al.* 2010).

- Research involving a range of comparative short- and long-term field-based empirical studies, field experiments (including experimental manipulations) and laboratory experiments should be conducted to investigate and better understand the linkages and effects of biodiversity on ecosystem function and, consequently, on the ecological goods and services that Arctic freshwater ecosystems provide.

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Perennial as well as seasonal sea ice make up an important habitat for Arctic marine ecosystems, where polynyas and leads make room for diverse species assemblages of birds and marine mammals. Walruses in a lead in the summer sea ice in Baffin Bay. Photo: Cherry Alexander, B&C Alexander.

*Chapter 14*

# Marine Ecosystems

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## Contents

> » **All Eskimos (Siberian Yupik) emphasize their connection with the sea – boys have dreams of becoming hunters. The sea gives birth to our whole life …**
>
> Tatyana Achirgina in Novikova (2008).

# SUMMARY

Arctic marine ecosystems host a vast array of over 2,000 species of algae, tens of thousands of microbes and over 5,000 animal species, including unique apex species such as the polar bear *Ursus maritimus* and narwhal *Monodon monoceros*, commercially valuable fish species, large populations of migratory birds and marine mammals, and some of the largest colonies of seabirds on the planet. Current estimates also suggest that many species are yet to be discovered.

The marine Arctic is characterized by a wide range of and large variability in environmental conditions. The Arctic Ocean has the most extensive shelves of all oceans, covering about 50% of its total area. It comprises diverse ecosystems such as unique millennia-old ice shelves, multi-year sea ice, cold seeps and hot vents, and their associated communities.

The Arctic is undergoing major and rapid environmental changes including accelerated warming, decrease in sea ice cover, increase in river runoff and precipitation, and permafrost and glacier melt. These changes together with new opportunities for economic development create multiple stressors and pressures on Arctic marine ecosystems.

Throughout the Arctic, ecosystem changes are already being observed. Changes in the distribution and abundance of key species, range extensions and cascading effects on species interactions are taking place, influencing Arctic marine food web architecture. Unique habitats such as ice shelves and multi-year ice are rapidly shrinking.

With continued warming and sea ice decline, measures should be put in place to monitor areas of particular biological significance and uniqueness in support of preservation and protection measures. Moreover, the complexity and regional character of Arctic ecosystem responses to environmental changes calls for the establishment of long-term marine ecosystem observatories across the Arctic, in support of sustainable management and conservation actions.

## 14.1. INTRODUCTION

Arctic marine ecosystems are important constituents of global biodiversity. Arctic marine ecosystems are habitats to a vast array of over 5,000 animal species and over 2,000 species of algae and tens of thousands of microbes (see Josefson & Mokievsky, Chapter 8, Daniëls *et al.*, Chapter 9 and Lovejoy, Chapter 11). The marine Arctic also provides habitat for large populations of marine mammals and birds (see Reid *et al.*, Chapter 3 and Ganter & Gaston, Chapter 4), some of which form colonies that are among the largest seabird colonies on the planet. The unique characteristics of Arctic marine ecosystems also contribute directly to global diversity. For example, Arctic sea ice ecosystems support biodiversity at various scales ranging from unique microbial communities to apex predator species such as the polar bear *Ursus maritimus* and walrus *Odobaenus rosmarus* whose ecology is closely associated with the sea ice environment.

Indirectly, the Arctic Ocean plays a key role in shaping the global biodiversity of marine and terrestrial ecosystems as it plays an essential role in the Earth climate system. The Arctic Ocean also influences marine ecosystems of the Atlantic Ocean directly, as waters and sea ice exiting the Arctic Ocean affect the physical, chemical and biological characteristics of the North Atlantic. Conversely, the Arctic Ocean receives waters from the Pacific and Atlantic Oceans, and therefore Arctic marine ecosystems are influenced by global changes that influence biodiversity in these oceans.

The Arctic is subject to rapid environmental changes. The current increase in global temperature is most rapid in the Arctic, with a predicted summer temperature increase of up to 5 °C over this century (IPCC 2007), and surface water temperature anomalies as high as 5 °C recorded in 2007 (Steele *et al.* 2008). Arctic sea ice, a key defining characteristic of the Arctic Ocean, is declining faster than forecasted by model simulations (Fig. 1.5 in Meltofte *et al.*, Chapter 1), with the potential for a summer ice-free Arctic within the next few decades (Stroeve *et al.* 2007, Wang & Overland 2009). The effects of these and other environmental changes (e.g. changes in freshwater input, shoreline erosion) on Arctic marine ecosystems are already documented (e.g. Wassmann *et al.* 2010, Weslawski *et al.* 2011). These changes, together with increased economic interest and development in the Arctic, put pressure on the biodiversity of Arctic marine ecosystems and on the species that inhabit them.

## 14.2. GENERAL CHARACTERISTICS OF THE MARINE ARCTIC

The Arctic Ocean is the smallest of the world's oceans (total area c. 10 million km$^2$) and consists of a deep central basin, the Arctic Basin, surrounded by continental shelves (Fig. 14.1). The Arctic Basin is further divided by the Lomonosov Ridge (maximum sill depth: 1,870 m; Jakobsson *et al.* 2008) into the Eurasian and Amerasian Basins. Maximum depths (c. 5,260 m) are found near the Gakkel Ridge, an extension of the North Atlantic Mid-Ocean Ridge system that divides the Eurasian Basin along a line from northern Greenland to the East Siberian shelf (Jakobsson *et al.* 2004). The Arctic Ocean has the most extensive shelves of any ocean, covering about 50% of its total area. The circumpolar marine Arctic comprises the Barents Sea, Kara Sea, Laptev Sea, East Siberian Sea, Chukchi Sea, Beaufort Sea, Canadian Arctic Archipelago and Greenland Sea. The Barents, Kara, Laptev, East Siberian and Chukchi shelves are shallow and broad (400-800 km) while the shelves from Alaska to Greenland are narrow (< 200 km).

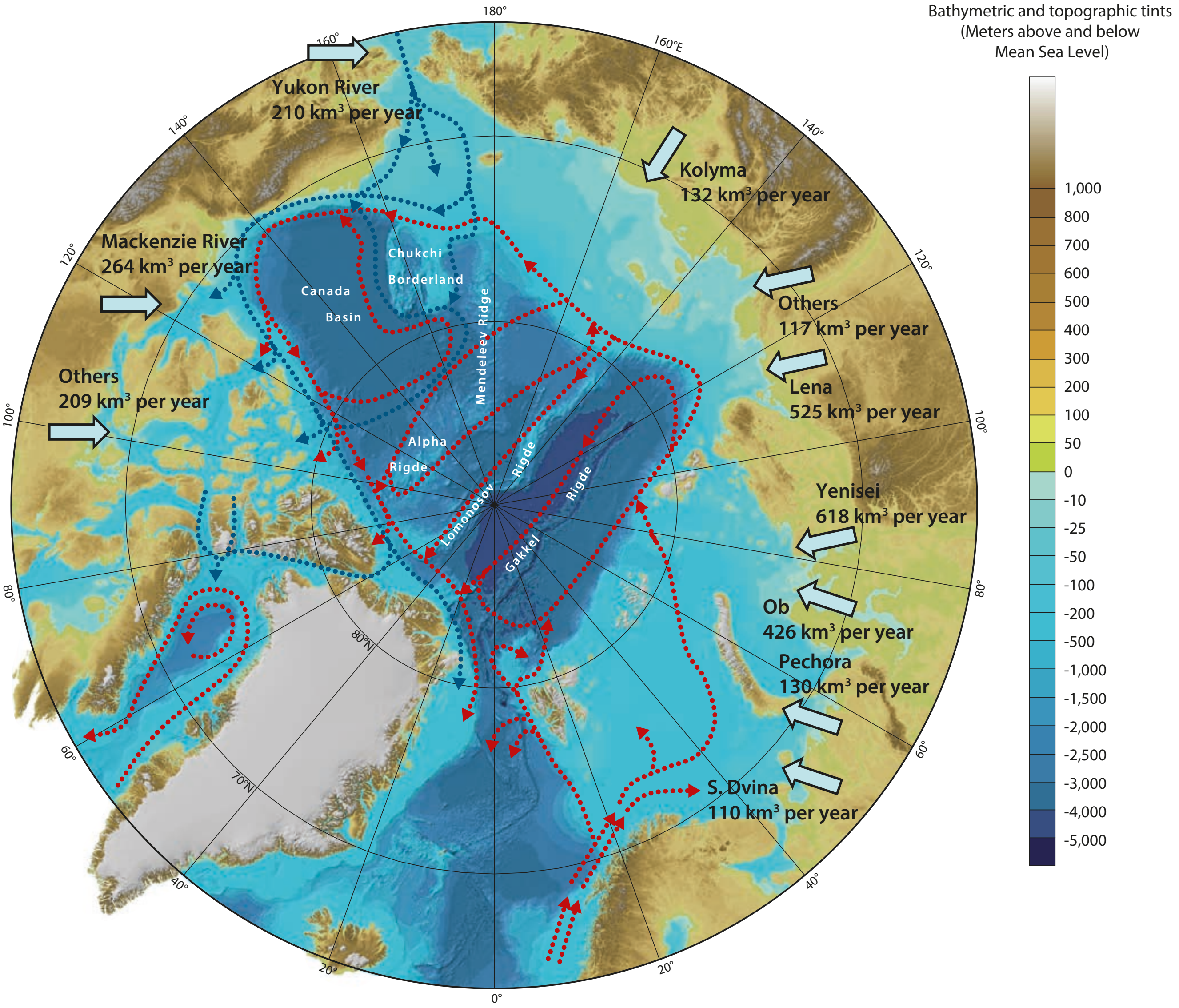


**Figure 14.1.** Bathymetric map of the Arctic Ocean showing general circulation and the importance of riverine inflow. (Adapted from Carmack 2000 and Jakobsson *et al.* 2004, 2008).

Several classifications exist for the marine Arctic, including eco-regions (Spalding *et al.* 2007) and Large Marine Ecosystems (LMEs) which are described as large regions (200,000 km$^2$) with distinct bathymetry, hydrography, productivity and trophically-dependent populations (Sherman *et al.* 1993). Seventeen (of 64) LMEs have been defined in the Arctic (Sherman & Hempel 2008), some of which corresponding to traditional Arctic seas/shelves while others represent sectors of Arctic or sub-Arctic seas (e.g. eastern and western Bering Sea). Numerous smaller domains within these large ecosystems have unique physical and biological characteristics making them 'hotspots' for marine productivity and biodiversity supporting large populations of marine birds and mammals. One example is the Pribilof Islands in the Bering Sea, which are renowned as an important breeding area for pinnipeds and seabirds. Despite historical depletion of northern fur seals *Callorhinus ursinus*, the Pribilof Islands domain supports the highest biomass of pinnipeds and marine birds of any island or island group of comparable size in the North Pacific (Hunt *et al.* 2008). As another example, the North Water polynya region in Baffin Bay supports the largest single-species aggregation of marine birds anywhere on earth, namely the vast colony of little auks *Alle alle* at Crimson Cliffs at Thule, N Greenland (see also Ganter & Gaston, Chapter 4).

The very nature of the marine environment makes it difficult to establish ecosystem boundaries, as water masses are modified and displaced seasonally and shift at interannual to interdecadal or longer time scales, causing repositioning of fronts and associated ecological features. In this context, we do not define ecosystem boundaries or delineate Arctic marine ecosystems as part of this chapter. We will refer to Arctic and sub-Arctic Seas/shelf regions and, as required, direct more attention to ecosystem features of ecological significance such as polynyas and marginal ice zones (MIZs). In order to provide a pan-Arctic perspective, we first offer a brief overview of characteristic features of the circumpolar Arctic seas.

Some of the key physical forcings and structuring elements for the biodiversity of Arctic marine ecosystems are then described, followed by an overview of current and emerging dominant stressors and observations to date with respect to impacts on ecosystem biodiversity.

The Kara and Laptev Seas are profoundly influenced by large amounts of freshwater runoff from Siberian rivers. The Kara Sea receives more than one third of the freshwater runoff (mainly from the Ob and Yenisei Rivers) delivered to the Arctic Ocean, contributing to the low salinity surface layer of the Arctic Ocean (see Fig. 14.3). The Kara Sea is typically cold (< 0 °C) throughout the year and ice-covered for most of the year. It exhibits strong temporal and spatial variations in salinity due to fluctuations in river runoff, as well as ice formation and melt (Kulakov *et al.* 2006, Pivovarov *et al.* 2006). Interannual variability in sea ice cover is associated with wind forcing (Divine *et al.* 2005). Differences in species richness, abundance, biomass and zonation patterns of phytoplankton, zooplankton and benthic communities are related to the salinity gradient associated with the Ob and Yenisei outflows and differ between the two river systems (Deubel *et al.* 2003, Hirche *et al.* 2006).

The Laptev Sea is strongly influenced by the Lena River. The main hydrographic features include a surface mixed layer of c. 5-10 m in summer (Pivovarov *et al.* 2006), variable circulation patterns that are mainly forced by winds, and an overall slow cyclonic surface layer motion in summer (Pavlov 2001). The Laptev shelf exports more ice to the Arctic Ocean than any other shelf, feeding the transpolar drift with sediment-laden ice (Rigor & Colony 1997, Eicken *et al.* 2000). As in the Kara Sea, distribution patterns of planktonic and benthic communities are linked to salinity gradients associated with the river outflow, in addition to water depth, ice cover and sediment characteristics (Abramova & Tuschling 2005, Steffens *et al.* 2006).

The East Siberian Sea is the largest, broadest and shallowest of the Siberian shelves. The East Siberian Sea comprises two regions that are hydrographically distinct. To the west, surface waters are influenced by direct river input from the Lena River and relatively fresh water from the Laptev; to the east, surface waters are influenced by Pacific inflows and surface waters from the Arctic Basin (Pivovarov *et al.* 2006). The frontal zone between the two regions can vary interannually by as much as 10 degrees of longitude (Semiletov *et al.* 2005). The East Siberian Sea represents a distributional barrier for a wide variety of biota (e.g. Mironov & Dilman 2010), but is also the most poorly described of the Russian shelves.

The Barents and Chukchi Seas are inflow shelves (*sensu* Carmack *et al.* 2006) and are profoundly influenced by the interaction between Arctic and sub-Arctic (Atlantic and Pacific, respectively) waters, as well as by processes associated with the presence of the Marginal Ice Zone (MIZ) (Darby *et al.* 2006). The Barents Sea covers c. 1.4 million km$^2$ extending eastwards from the Norwegian Sea to Novaya Zemlya and northwards from the coasts of Norway and Russia into the Arctic Ocean and is the deepest of the Arctic shelf seas (average depth 230 m). The complex hydrography and circulation patterns in the Barents Sea strongly influence its biological production. Warm saline Atlantic waters are carried by the Norwegian Atlantic Current into the Barents Sea. Inshore of the Atlantic waters is the relatively fresh Norwegian Coastal Current, whereas in the northern part of the Barents Sea, cold low salinity Arctic waters flow in a northeast-southwest direction, separated from Atlantic waters by the Polar Front (Fig. 14.2; Drinkwa-

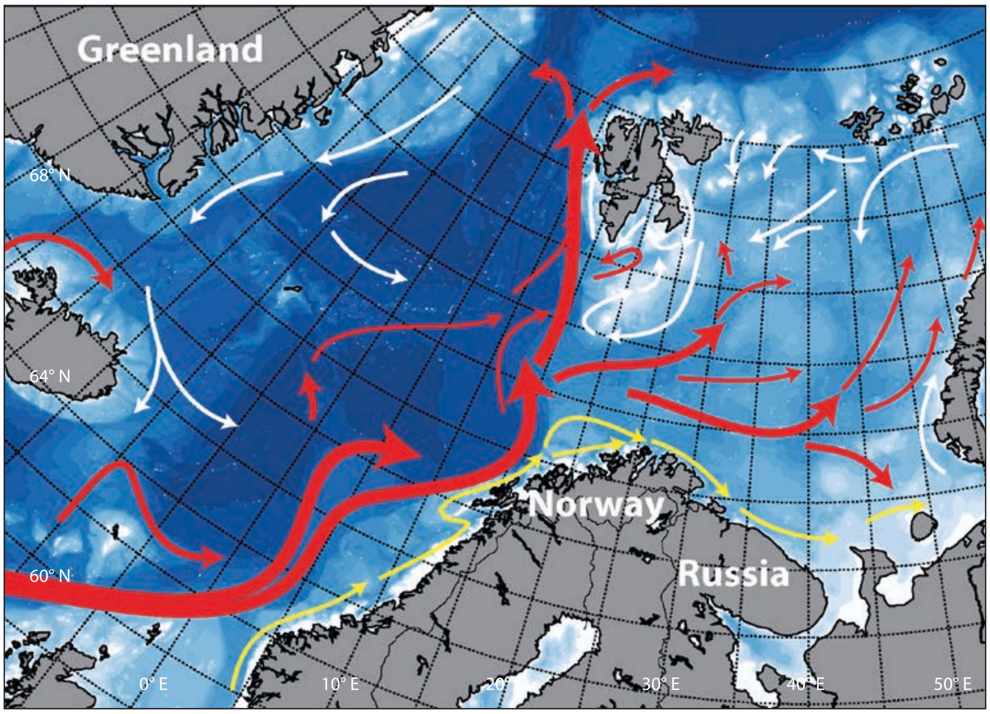


**Figure 14.2.** Surface circulation of the Norwegian and Barents Seas. The red arrows represent the warm, saline Atlantic waters; the white the cold, fresher Arctic waters and the yellow the low salinity coastal waters. (Source: Drinkwater 2011; see also Fig. 8.9 in Josefson & Mokievsky, Chapter 8).

ter 2011, also see Loeng & Drinkwater 2007). In the permanently ice-free, Atlantic-water-influenced southwestern Barents Sea (i.e. where surface temperatures > 0 °C), the onset of thermal stratification in spring initiates the development of the phytoplankton bloom. In contrast, the northern Barents Sea, which is influenced by Arctic waters, has a highly variable seasonal ice cover (both in duration and extent), and the phytoplankton bloom is typically associated with the retreat of the MIZ (e.g. Sakshaug 2004). Production is significantly higher and shows less interannual variability in the Atlantic compared with the Arctic sector of the Barents Sea (e.g. Sakshaug *et al.* 2009, Reigstad *et al.* 2011). In the former, annual primary production ranges between 110 and 130 g C per $m^2$ per year, whereas it is estimated to be around 55-65 g C per $m^2$ per year in the latter (Reigstad *et al.* 2011). The Barents Sea supports highly productive fisheries, one of the largest seabird concentrations in the world (Anker-Nilssen *et al.* 2000; see also Ganter & Gaston, Chapter 4) and is host to 27 migratory or resident marine mammal species (ICES, 2009, Reid *et al.*, Chapter 3). Recent efforts in characterizing seabed nature and habitat also contribute invaluable knowledge on benthic habitat and diversity (e.g. Dolan *et al.* 2009; see also Josefson & Mokievsky, Chapter 8). The Barents Sea is one of better understood marine ecosystems of the Arctic (e.g. Wassmann 2011).

The Chukchi Sea receives a high inflow of Pacific waters, entering through Bering Strait. This inflow of relatively fresh, cold and nutrient-rich waters constitutes a key structuring element of marine ecosystems in this broad (c. 400 km) and shallow (average depth of approximately 50 m) sea. There is high interannual variability in the seasonal ice cover in the Chukchi, and highly productive polynyas are found along the coast. Fuelled by the nutrient-rich inflow of Bering shelf/Anadyr water, the production in hotspots of the southern Chukchi Sea ranks amongst the highest in the world's oceans (e.g. Grebmeier *et al.* 2006a).

The Beaufort Sea receives water from the Alaskan Coastal Current to the west, while to the east, the Canadian Beaufort Sea is strongly influenced by freshwater, as well as dissolved and particulate material input from the Mackenzie River. Waters of Pacific origin entering through Bering Strait form halocline waters on the Beaufort shelf. Landfast sea ice, pack ice and the presence of a flaw lead polynya are typical of winter conditions in the Beaufort Sea. In summer, wind-driven upwelling enhances productivity in zones of hydrodynamic singularities at the shelf break (Williams & Carmack 2008). Compared with the highly productive and strongly Pacific-influenced Chukchi Sea shelf, biomass and numbers of Pacific-origin species sharply decrease towards the east (Dunton *et al.* 2005).

The Bering Sea comprises the continental shelves of Alaska and Kamchatka, also defined as separate LMEs (Sherman *et al.* 1993), and the deep central basin between them. The eastern Bering Sea Ecosystem LME is over 500 km wide in some areas, whereas the western Bering Sea Ecosystem LME has a relatively narrow shelf. Ocean circulation in the Bering Sea is well described by Stabeno *et al.* (1999). The general cyclonic circulation entails the Kamchatka Current flowing southward and forming the western boundary current, and the Bering Slope Current flowing northward and forming the eastern boundary current. Circulation in the Bering Sea is strongly influenced by the Alaskan Stream entering the Bering Sea through Aleutian passes. The inflow into the Bering Sea is balanced by outflow through Kamchatka Strait, so that circulation in the Bering Sea Basin can be described as a continuation of the North Pacific sub-Arctic gyre. Transport into the Bering Sea can vary by a factor of two or more, at time scales of weeks to years. Sea ice extends over the shelves in winter. In summer, sea ice retreats into the Chukchi and Beaufort Seas. Large-scale variability is strongly influenced by atmospheric patterns which, combined with sea ice conditions, influence primary productivity and fish and benthic assemblages (Hunt *et al.* 2011). The southeastern Bering Sea supports high numbers of demersal and pelagic fish and shellfish, and productive commercial fisheries. As an example, Alaska pollock *Gadus chalcogrammus* stocks alone yield 0.8-1.5 million metric tons a year, and are the most commercially valuable in total numbers, followed by salmon *Oncorhynchus* spp. Sockeye salmon *O. nerka* production fluctuates widely, yielding on average about 20 million fish annually (see Section 14.4.2).

The Canadian Arctic Archipelago is a complex array of islands and channels, stretching from Banks Island in the west to Baffin and Ellesmere Islands in the east. The Canadian Arctic Archipelago is a transit region for waters from the Arctic Ocean flowing into the Labrador Sea and the North Atlantic (McLaughlin *et al.* 2006 and references therein). These waters, mainly of Pacific origin, are modified by physical (e.g. mixing, freezing and sea ice melt) and biochemical processes during their transit. The Canadian Arctic Archipelago is covered by ice year-round in places, with a mix of locally-produced first-year ice and multi-year pack ice from the Arctic Ocean. A number of small polynyas are also present, many of which occur together with tidally-enhanced mixing in the narrow channels of the archipelago (Hannah *et al.* 2009). Major seabird colonies and summering areas for migrant whales are concentrated in Lancaster Sound, Barrow Strait and adjacent waters. Little is known of most of the Canadian Arctic Archipelago outside of the Northwest Passage (from Banks Island to Baffin Bay).

The Greenland shelves are intrinsically linked to the network of fjords and glaciers along the Greenland coastline. The E Greenland shelf is influenced by the southward flow of polar waters carrying pack ice from the Arctic Ocean, the East Greenland Current. The W Greenland shelf is influenced by a northbound branch of the West Greenland Current penetrating as far as Smith Sound (Melling *et al.* 2001). These ocean currents strongly influence oceanographic conditions and productivity of the Greenland shelves, as do glacier retreat and melt impact (Heide-Jørgensen *et al.* 2007). The W Greenland shelf is a productive shelf with important fisheries, especially for northern shrimp *Pandalus borealis* and Greenland halibut (or turbot) *Reinhardtius hippoglossoides*. These fisheries are essential for the economy of Greenland (Buch *et al.* 2004).

## 14.3. KEY FORCINGS AND STRUCTURING ELEMENTS OF ARCTIC MARINE ECOSYSTEM BIODIVERSITY

Seasonal extremes in photoperiod, river runoff and ice conditions all constitute key forcings to Arctic marine ecosystem functioning and biodiversity. In addition, the structure, functioning and biodiversity of Arctic marine ecosystems is fundamentally linked to the main hydrographic features of the Arctic Ocean, namely the connection to the Pacific and Atlantic Ocean, strong stratification and critical influence of the large continental shelves and riverine input.

### 14.3.1. Water masses

The Arctic Ocean is connected to the Pacific and Atlantic Oceans with which it exchanges water and associated physical, chemical and biological properties. Relatively warm and saline (c. 34.8‰) Atlantic waters enter the Arctic Ocean through Fram Strait and influence the biodiversity of species and ecosystems as they circulate cyclonically, following the bathymetry of the Arctic Ocean (see Carmack & Wassmann 2006) (Fig. 14.1). Pacific waters enter the Arctic Ocean through the shallow (50 m) and narrow Bering Strait. Pacific waters are less saline and dense than Atlantic waters and, as a result, form a distinct layer on top of the Atlantic layer. Pacific waters (mainly in the Anadyr Current) are also nutrient-rich, with especially high silicic acid concentrations (up to 50 uM; Codispoti *et al.* 2005), a nutrient required by diatoms for the formation of their cell walls. Access to this nutrient-rich water fosters the development of productive diatom blooms in parts of the Arctic (e.g. Tremblay *et al.* 2011) supporting highly productive food webs.

The knowledge that currents and water mass distribution influence physical conditions and the distribution of marine organisms is reflected in traditional ecological knowledge.

> » *The currents are the marine animals' access to [food]. Inuit also need the currents, and we are always watching the currents for hunting. Seals come and go with the currents. There would be no whales if there were no currents.*
>
> (McDonald *et al.* 1997).

There is inherent biodiversity associated with the presence and circulation of Atlantic and Pacific water masses in the Arctic Ocean. In the Barents, Norwegian and Greenland Seas, species associated with warm Atlantic waters such as deep-water shrimp, Atlantic herring *Clupea harengus*, NE Atlantic cod *Gadus morhua* and capelin *Mallotus villosus* thrive and sustain productive commercial fisheries (NMFCA 2010). The warm Atlantic Waters carry plankton species and planktonic larvae of benthic species into the Kara and Laptev Seas and into the Canadian Basin within the intermediate Atlantic layer (e.g. Sirenko 2009). In the Chukchi Sea, the distribution and diversity of zooplankton species is strongly linked to water mass distribution, with different assemblages associated with nearshore, Pacific-origin, and oceanic waters (Hopcroft *et al.* 2010). Pacific benthic species are mainly found in the Chukchi, Beaufort and the northern part of the East Siberian Seas in areas influenced by Pacific waters entering the Arctic Ocean through Bering Strait (Dunton 1992, Sirenko 2009). The presence of silicious sponge communities reported north of the Queen Elizabeth Islands in the Canadian Arctic Archipelago (Van Wagoner *et al.* 1989) points to the past and present occurrence of Pacific-origin waters in this region.

Atlantic zooplankton species dominate the Arctic Ocean as contemporary Pacific zooplankton species advected into the Arctic can spawn on Pacific-influenced Arctic shelves (e.g. Chukchi Sea; Hopcroft *et al.* 2010), but do not successfully reproduce in the Arctic Ocean (e.g. Nelson *et al.* 2009). Therefore, while these pelagic Pacific species advected into the Arctic Ocean contribute to the functioning of Arctic marine food webs, they only contribute temporarily to the biodiversity of species. In the benthos, Pacific-origin species permanently contribute to Arctic biodiversity in regions close to the Pacific gateway. There is no apparent zoogeographic barrier between the Canadian and Eurasian basins for zooplankton (Kosobokova *et al.* 2011) or benthos (Bluhm *et al.* 2011) except for these sub-polar expatriates. Vertical changes in zooplankton species diversity have been linked to the vertical distribution of different water masses in the Eurasian and Canadian Basins with maximum zooplankton species diversity in the Atlantic layer (between 300 and 2,000 m) (Kosobokova & Hopcroft 2010). Overall, there appears to be a low degree of endemism on the Arctic shelves and a dominance of boreal-Arctic Atlantic species in the marine Arctic due to the constant inflow of waters from the boreal zoogeographic region (Sirenko 2009).

Adding to the stratification originating from the presence of Atlantic and Pacific waters, the large amount of freshwater from rivers and sea ice melt contributes to the formation of a low salinity surface layer, the polar mixed layer, characterizing the Arctic Ocean (Fig. 14.3). This strong stratification also plays an important role in shaping Arctic marine ecosystem biodiversity through its influence on the availability of light and nutrients for primary producers and its effects on the composition of plankton communities. This is because different functional groups and species of primary producers thrive under different conditions associated with stratified/

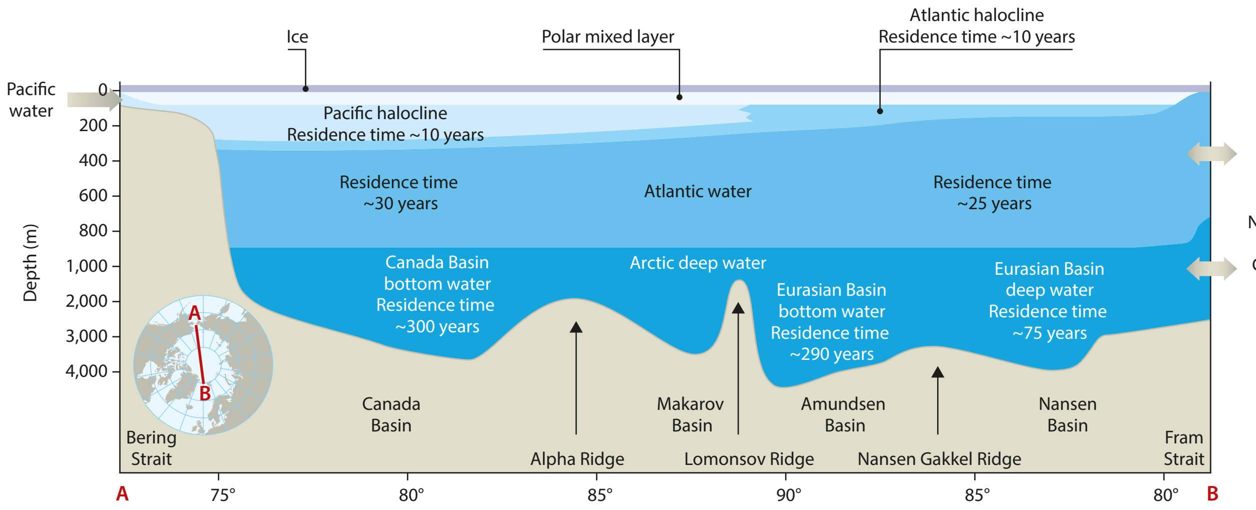


**Figure 14.3.** Schematics of different water masses in the Arctic Ocean, emphasizing vertical stratification (source: AMAP 1998).

well-mixed waters (Cullen *et al.* 2002). Diatoms, which have high nutritional requirements, thrive in environments where nutrients are periodically replenished through mixing and upwelling. In contrast, small cells have high surface/volume ratios and are better adapted to stratified environments where nutrients can quickly become depleted. These groups have different functionalities in marine food webs, as discussed below.

## 14.3.2. Seasonality

Arctic marine ecosystems are characterized by a short productive period in spring-summer. Therefore many key Arctic species have adapted to take advantage of the brief pulse in food availability after surviving the dark winter on stored energy reserves. These observations, together with the conspicuous presence of vast populations of marine birds and mammals, contributed to the early view that Arctic marine ecosystems have efficient trophic transfers and short, simple (low diversity) food webs (see Horner 1985). Opposing this simplistic view, we now know that Arctic marine ecosystems are intricate and multifaceted. Arctic marine food webs range up to six trophic levels and comprise diverse trophic pathways including complex microbial food webs and recycling pathways (e.g. Iken *et al.* 2005). Several thousand species of microbes and protists (including bacteria, archea and photo- and heterotrophic protists), hundreds of zooplankton taxa dominated by crustaceans (Kosobokova *et al.* 2011), and thousands of uni- and multicellular benthic taxa such as diatoms and seaweeds, foraminifera, sponges, turbellarians, cnidarians, polychaetes, mollusks and crustaceans contribute to the diversity of Arctic marine ecosystems (Gradinger *et al.* 2010, Bluhm *et al.* 2011, Piepenburg *et al.* 2011, Poulin *et al.* 2011). While there appear to be comparatively fewer species that channel the bulk of food to apex predators in polar than in lower latitude marine food webs, the complexity and diversity of the planktonic and benthic food webs that support these species are equivalent to those in temperate latitudes (Smetacek & Nicol 2005).

The ecological diversity of microbial assemblages that form the base of Arctic marine food webs (e.g. Lovejoy *et al.* 2011, Poulin *et al.* 2011) is essential in order to maintain diverse trophic pathways within Arctic marine ecosystems. As a general rule, high-latitude marine ecosystems that are structured around the high seasonality in solar radiation sustain a high production of large cells (> 5 µm) during a short period in spring/summer (e.g. Tremblay *et al.* 2006). These systems are considered to be high export systems that can sustain abundant pelagic and/or benthic populations of fishes and marine mammals. In contrast, ecosystems where small cells (< 5 µm) dominate are typically considered to fuel food webs where little material is exported from the system, therefore not providing for a dependable human harvest. A large part of the primary production on highly productive Arctic shelves (e.g. Bering Sea, Barents Sea and the western part of the Greenland Sea) falls within the first category and supports commercial harvest, while the central Arctic basins currently fall within the second category.

The episodic primary production in the Arctic influences the annual cycling of nutrients as surface nutrients drop near detection levels following the spring/summer phytoplankton bloom and remain low until autumn (Aguilera *et al.* 2002), unless there is resupply, e.g. via upwelling (Williams & Carmack 2008). Since nutrient supply is essential to sustain primary producers, such seasonality determines potential growth and biomass accumulation at lower trophic levels (Tremblay & Gagnon 2009). The phenology of polar seaweeds (kelps) is strongly tuned to the strong seasonal changes in underwater radiation and nutrient availability. Day length triggers the onset of reproduction and growth particularly in endemic species. Arctic kelps, such as Arctic suction-cup kelp *Laminaria solidungula,* are optimally adapted to seasonal changes in nutrient concentrations and utilize storage compounds synthesized during summer to fuel growth during winter (Wiencke *et al.* 2009).

### 14.3.3. Temperature

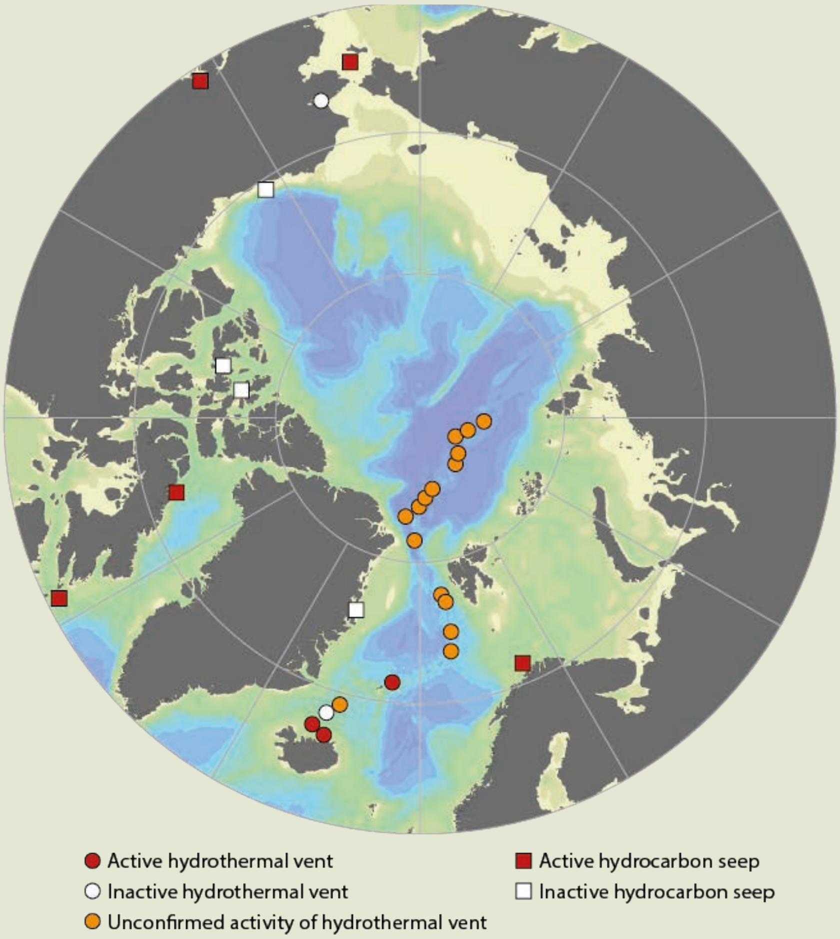
Notwithstanding its effect on water column stratification, temperature is a major structuring factor for biodiversity in the marine environment. Temperature impacts the life cycle of marine species, influencing their physiology and phenology (i.e. timing of events) and geographic distribution (e.g. Beaugrand *et al.* 2002a, Edwards & Richardson 2004, Angilletta 2009). For example, recruitment of key macroalgae and rocky bottom invertebrate species in high Arctic systems appears to be much slower than in temperate systems (Dunton *et al.* 1982, Konar 2007). Temperature also influences species interactions, i.e. competition and prey-predator interactions, with consequences for biodiversity and the functioning of ecosystems (e.g. Edwards & Richardson 2004). Homoiotherms such as marine birds are generally independent of direct temperature effects on their survival. However, water temperature affects their relationship with their prey, predators and competitors. An example of such is underwater pursuit divers (auks, loons, cormorants) for which warmer temperatures generally increase the swimming speed of their prey and competitors without commensurate increase in their own foraging ability, reducing their hunting efficiency. This effect may account for the high abundance and diversity of diving birds in the Arctic and may place a southern bound on their distributions (Cairns *et al.* 2008).

While the overall cold temperature in the Arctic may have offered selection for cold-adapted species, low temperatures *per se* are not related to low biodiversity at lower trophic levels in pelagic (Poulin *et al.* 2011) or in benthic communities (Kuklinski & Bader 2007). Although it does affect their metabolism, temperature is typically not the primary structuring factor of planktonic (Kosobokova & Hopcroft 2010) or benthic (Conlan *et al.* 2008, Bluhm *et al.* 2009) communities in the Arctic except nearshore, where temperature fluctuations are much higher than offshore (Weslawski *et al.* 2010). Overall, the generally low temperatures result in low metabolic rates for invertebrates, and the consequences include slower growth, longer life cycles and higher longevity than in lower latitude systems (e.g. Bluhm *et al.* 1998). The range of thermal tolerance of a species will also determine its capacity to respond and adapt to changes in temperature. In this context, stenotherms (narrow range of thermal tolerance) are likely to be

## Box 14.1. Hot vents and cold seeps (mud volcanoes)

Hydrothermal vents, also called hot vents, and cold seeps are widespread features of the world's oceans that support unique communities and contribute to the biodiversity of species and ecosystems. Hot vents have water temperatures up to 400 °C and are located on active (volcanic) spreading plate boundaries, while cold seeps correspond to areas of seepage consisting of 'warm' or 'lukewarm' porewater, gas and mud from the seafloor. The food webs at hot vent locations are based on bacterial rather than algal growth. The chemosynthetic production of bacteria at these sites is dependent primarily on hydrogen sulphide or methane.

Hot vents are documented in the Arctic, but our current knowledge is limited, suggesting that more remains to be discovered. Hot vents are found at continental plate boundaries such as the Gakkel and Mohn Ridges (Edmonds *et al.* 2003) (Box 14.1 Fig. 1). It is known that the fauna of Atlantic and Pacific hot vents can have distinct communities including large-sized bacteria, clams, tubeworms and unique life forms. Communities on the Gakkel Ridge are as yet



**Box 14.1 Figure 1.** Known locations of hydrothermal vents and hydrocarbon seeps in the Arctic. Map created using Ocean Data View, Schlitzer 2010. (sources: Beaulieu 2010, Campbell 2006)

more negatively impacted than eurytherms (wide range of tolerance), entailing possible shifts in species dominance and the structure and functionality of ecosystems. Of importance is the adaptation potential and range of thermal tolerance of species. Sessile species or species with narrow ranges of thermal tolerance may not be able to adapt to rapid physical and/or chemical changes in their environment, as opposed to planktonic or mobile organisms that may shift their distribution in relation to changes (e.g. Sirenko & Gagaev 2007, Mueter *et al.* 2009).

In the marine Arctic, temperature is considered to be relatively stable in central basins and in deep waters. However, seasonal and spatial gradients can be important on the shelves. In addition, extremes in temperature directly contribute to the biodiversity of Arctic marine ecosystems, with minima inside the brine channel system of Arctic sea ice in winter (down to –35 °C; see Section 14.3.5) and maxima within ‘warm features’ such as hydrothermal vents (up to 400 °C) and so-called cold seeps (see Box 14.1).

unexplored, and new species are expected to be found due to the isolated geographical nature of these vents (Edmonds *et al.* 2003). A recent study of the Jan Mayen vents on the Mohn Ridge found 180 species including a few new species, although the majority were common to surrounding waters (Schander *et al.* 2010). This site did not contain high biomasses of vent-endemic fauna, similar to the Kolbeinsey vents near Iceland. However, the communities at these two vent locations shared almost no fauna in common (Schander *et al.* 2010), highlighting differences in regional biodiversity.

Cold seeps are widely distributed in the Arctic, occurring on the Beaufort shelf, Barents Sea slope, Norwegian shelf and Arctic mid-ocean ridge (Box 14.1 Fig. 1). Many sites (e.g. the Haakon Mosby Mud Volcano, Barents Sea) represent hotspots of biodiversity in deep waters (Vanreusel *et al.* 2009), with the diversity of organisms varying widely between sub-habitats such as microbial mats or the outer rim area (Van Gaever *et al.* 2006). Fishes such as scalebelly eelpout *Lycodes squamiventer* and several species of skates are known to utilize the rich resources of deep-water cool seeps. Mud volcanoes in shallower water (e.g. Beaufort shelf) can also create habitat for distinct nearshore benthic communities (Conlan *et al.* 2008).

## 14.3.4. Continental shelves

Most of the biological production in the Arctic Ocean takes place on its large continental shelves. The Arctic shelves are highly dynamic environments where the presence, formation and melt of annual sea ice influence the biogeochemical cycling of organic carbon and other elements. In addition, coastal erosion, riverine runoff and movement of anadromous species between freshwaters and the coastal ocean all contribute to shaping the biodiversity of Arctic marine ecosystems.

The wide range of environmental conditions on Arctic shelves, e.g. gradients in salinity (from freshwater to marine environments), temperature, nutrient concentrations, suspended matter and sediment characteristics, is fundamental to their biological diversity. The littoral zone, the nearshore part of the shelf where wave action can move sediments, is a dynamic zone where land-ocean interactions dominate. Key processes affecting littoral zone dynamics are coastal erosion, input of sediments by rivers, and sediment accretion and redistribution by winds, waves and currents, tidal action and ice gouging and scouring. These processes influence the distribution and structure of benthic communities via their impact on sediment grain size and availability of rocky substrates. For example, macroalgae and sessile fauna such as sponges, hydroids and many ascidians depend on rocky substrates for attachment. The distribution of seaweeds is generally restricted to rocky habitats without ice coverage for at least 4-6 weeks during the polar summer (Lüning 1990). Accordingly, the actual northern Arctic boundary for seaweeds exceeds 80 °N, but excludes most of the Russian Arctic coastlines that are mainly composed of soft bottoms and hence do not provide adequate substratum for seaweeds.

The macroalgal flora in Svalbard and the White Sea (areas with abundant hard bottom) is generally composed of species also found in other regions of the North Atlantic, some boreal species at the limit of the northern distribution range (e.g. forest kelp *Laminaria hyperborea*; Müller *et al.* 2009), and very few species with a strong distributional center in the Arctic (e.g. Arctic suction-cup kelp and the red algae *Devaleraea ramentacea*). On the Alaskan Beaufort Sea shelf, macroalgae are restricted to small areas where hard substrata protected from ice scour are available (Wulff *et al.* 2009 and references therein). Ice scouring in nearshore areas can also regularly eradicate benthic communities, resulting in a mosaic of succession stages in those areas (Conlan & Kvitek 2005). This emphasizes the role of sea ice in structuring benthic ecosystems (see also next Section). On the shelves, the main sessile primary producers are seaweeds and, to a lesser extent, benthic diatoms. To date, a total of more than 200 seaweed species have been recorded for the Arctic (Wilce 1994, Archambault *et al.* 2010, Mathieson *et al.* 2010, Daniëls *et al.*, Chapter 9). In some areas, perennial seaweeds are abundant and serve as food and habitat to a diversity of invertebrate and fish species (Dunton *et al.* 1982, Mathieson *et al.* 2010). Therefore, changes in this

## Box 14.2. The role of polynyas for Arctic seabirds and mammals

Polynyas are recurrent areas of open water amidst ice-cover. They occur throughout the Arctic as flaw leads that form along the edge of fast ice areas (Box 14.2 Fig. 1), or as latent (driven by wind forcing) or sensible (driven by the upwelling of warmer water) heat polynyas (see Williams *et al.* 2007) and play an important role in the productivity and biodiversity of Arctic marine ecosystems.

Polynyas of all kinds may be sites of enhanced or early season productivity, making them important biological hotspots (e.g. Bursa 1963, Hirche *et al.* 1991, Stirling 1997). In summer, the region of the North Water Polynya in Baffin Bay supports some of the largest concentrations of seabirds anywhere in the Arctic (Stirling 1980, 1997), dominated by little auks *Alle alle* which breed in the tens of millions in N Greenland (Kampp *et al.* 2000). Little auks time their arrival to coincide with the availability of copepods *Calanus* spp., their primary prey in May-July. Thus, the timing and location of little auks in the region is determined by primary production and the consequent upward migration of copepods, rather than by the availability of open water itself (Karnovsky & Hunt 2002).

Large recurrent polynyas provide conditions for a diverse array of birds to remain for the winter, especially common eiders *Somateria mollissima*, and to a lesser extent long-tailed ducks *Clangula hyemalis* and king eiders *Somateria spectabilis* (Gilchrist & Robertson 2000), as well as ice-associated seals and whales (Kingsley *et al.* 1985, Heide-Jørgensen & Laidre 2004, Moore & Laidre 2006). The overwintering of ice-associated whales within mobile pack ice and impermanent polynyas occasionally causes entrapments (Nerini *et al.* 1984, Finley 2001) sometimes involving hundreds of whales (Harwood & Smith 2002). This is a well known phenomenon (named *sassat* in Inuit) re-occurring at certain sites in Arctic Canada and Greenland, where local hunters may take advantage of the opportunity to secure large amounts of narwhal or beluga meat (see Siegstad & Heide-Jørgensen 1994).

In regions of very high tidal currents, such as those produced in narrow inlets, small tidal polynyas remain open throughout the winter, providing refuges when shore-leads close temporarily. Such predictable areas serve to concentrate a wide variety of marine birds, and sometimes whales and seals. The resulting aggregations of potential prey attract ice-based predators (polar bears and Arctic foxes *Vulpes lagopus*) and raptors such as gyrfalcons *Falco rusticolus* and snowy owls *Bubo scandiaca* (Brown & Nettleship 1981, Kingsley *et al.* 1985, Stirling 1997, Therrien *et al.* 2011). Numerous small polynyas of this sort occur in the Belcher Islands (Sanikiluaq), where they are essential to the year-round existence of a large population of common eiders (Freeman 1970). The common eiders forage in shifting flaw leads while retreating to the permanent tidal polynyas over night (Gilchrist & Roberston 2000, Gilchrist *et al.* 2006). Similarly, the entire world population of spectacled eiders *Somateria fischeri* winters in leads and polynyas south of St. Lawrence Island in the eastern Bering Sea (Petersen *et al.* 1999), an area of strong benthic-pelagic coupling that supports a high density of bivalve prey for the eiders (Lovvorn *et al.* 2003, Grebmeier *et al.* 2006a). (See also Ganter & Gaston, Chapter 4.)

community are expected to influence various trophic levels in marine Arctic ecosystems.

The immense freshwater inflow into the Arctic Ocean not only produces a permanent halocline throughout the Arctic (Fig. 14.1 and 14.2), but also results in large horizontal salinity gradients in nearshore waters. These gradients are reflected in the zonation of biological communities, ranging from freshwater near river mouths to brackish water and full marine species assemblages. These varying conditions on Arctic shelves contribute to increasing the overall biodiversity of Arctic marine ecosystems (e.g. Deubel *et al.* 2003, Steffens *et al.* 2006).

Linking freshwater systems to the sea, Arctic shelves also host a diversity of anadromous fishes, i.e. fishes that use freshwater environments for spawning and early life history (and in the Arctic overwintering) and estuaries/coastal environments for feeding and rearing. Of the 39 species of anadromous fishes that are found in the Arctic and sub-Arctic (see Christiansen & Reist, Chapter 6), many are regarded as being of high importance for harvest by local communities (e.g. Arctic char *Salvelinus alpinus*, brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta* and whitefish *Coregonus* spp.). Anadromous fish species such as Arctic char are distributed throughout the circumpolar Arctic (see Fig. 6.3 in Christiansen & Reist, Chapter 6). Many sub-species exist, and their biodiversity is still poorly understood. Seaward migration in Arctic anadromous fishes, although facultative, appears to be advantageous as anadromous species take advantage of marine coastal production.

Arctic shelves also serve as feeding areas and migration corridors for resident or migrant whales in the Arctic. The three endemic species of Arctic cetaceans, the narwhal *Monodon monoceros*, beluga *Delphinapterus leucas* and bowhead whale *Balaena mysticetus*, exploit different habitats (Heide-Jørgensen 2009, O'Corry-Crowe 2009, Rugh & Shelden 2009). Narwhals primarily occupy the Atlantic sector of the Arctic, north of 60° N latitude. They overwinter in dense pack-ice habitats along the continental slope where they feed intensively from November to March, and spend the summer months in ice-free shallow bays and fjords. Belugas occupy estuaries, continental shelves/slopes, and deep basins in conditions

**Box 14.2 Figure 1.** Circumpolar map of known polynyas. Note that some polynyas no longer exist in the form known from their recent history. (Source: Barber & Masson 2007.)

ranging from dense annual pack ice to open water. Some belugas (e.g. along the Alaska coast, in the Canadian high Arctic and Hudson Bay) undertake long migrations between summer and wintering sites, while others remain in the same region year-round (e.g. Lydersen *et al.* 2001, Richard *et al.* 2001). Bowhead whales migrate from sub-Arctic seas in winter into the high Arctic in summer. Bowheads often feed in polynyas (see Box 14.2) or areas covered with loose sea ice in spring or in open water areas in late summer and autumn when sea ice has retreated offshore (Moore *et al.* 2010). A variety of other baleen whales such as the gray whale *Eschrichtius robustus* together with a few toothed whales (e.g. the killer whale *Orcinus orca*) also migrate into Arctic waters during summer, but the presence of sea ice represents a distributional barrier to these animals (Higdon *et al.* 2011). (See also Reid *et al.*, Chapter 3.)

## 14.3.5. Sea Ice

In the Arctic, sea ice is a major structuring element of marine ecosystems. The presence of sea ice impedes surface mixing, influences freshwater and heat fluxes, and in combination with snow cover decreases light availability for primary producers. Therefore, snow cover and sea ice melt/break-up appear to control the timing of the ice-associated (i.e. ice algae) and pelagic (i.e. phytoplankton) blooms by acting on the availability of light (e.g. Michel *et al.* 2006, Lavoie *et al.* 2009).

Sea ice is also an ecosystem in itself, therefore contributing directly to the biodiversity of the marine Arctic. The unique physical and chemical conditions in sea ice, and their wide range, create a variety of habitats for a diversity of microbial and meiofaunal communities. For example, sea ice salinity can range from nearly zero (freshwater) in multi-year ice to $>$ 200‰ in sea ice brine channels and pockets that range from less than 1 micro m to 1.2 mm in size (Krembs *et al.* 2000). Temperature and light conditions also vary widely, spatially and seasonally. The sea ice ecosystem harbors an abundance and diversity of microbes including viruses, archaea and bacteria of the groups Proteobacteria and Cytophaga-Flavobacterium-Bacteriodes (CFB) (Deming 2010, Lovejoy *et al.* 2011, Lovejoy, Chapter 11). Sea-ice bacterial communities comprise species of *Marinobacter*, *Shewanella* and *Pseudomonas*, with apparent potential to degrade hydrocarbons (Gerdes *et al.* 2005). Thousands of protist species are also found in sea ice (Różańska *et al.* 2009, Poulin *et al.* 2011), but there is still much debate with respect to the endemic character of some of these protist species. The colonial diatom, *Nitzschia frigida*, is considered a pivotal species of land-fast ice across the Arctic as it is the most frequent, most abundant and most consistently observed species in first-year sea ice (Różańska *et al.* 2009). Protist species living in sea ice are adapted to the extreme conditions in their environment. Productive cryo-tolerant microbial communities are found on ice shelves (see Box 14.3; Mueller *et al.* 2005) and ice algal species *Chlamydomonas* sp. can grow at –5 °C and at salinities ranging from 2.5 to 100‰ (Eddie *et al.* 2008). A diverse community of multi-cellular organisms also lives within the ice (often referred to as ice meiofauna), including over 20 species of crustaceas (mainly Harpacticoida), nematodes, Acoela, Rotifera and Cnidaria (Gradinger 2002, Bluhm *et al.* 2010). In addition, meroplanktonic larvae and juveniles stages of benthic Polychaeta and Gastropoda inhabit the ice for periods of a few weeks to months (Gradinger *et al.* 2010, Josefson & Mokievsky, Chapter 8). Grazing by sea ice meiofauna does not appear to limit the accumulation of ice algal biomass (Michel *et al.* 2002).

Recently, the key role of ice algae in Arctic pelagic and benthic food webs has been clearly demonstrated using biomarkers (McMahon *et al.* 2006, Søreide *et al.* 2006, 2008, Tamelander *et al.* 2008). For example, Søreide *et al.* (2010) showed that ice algae are essential for the development and survival of *Calanus glacialis*, a key zooplankton species consumed by fishes, seabirds, seals and bowhead whales across the Arctic. Sea-ice associated amphipods are also a main food resource for the polar cod *Boreogadus saida* and ice cod *Arctogadus glacialis* (Bradstreet & Cross 1982, Christiansen *et al.* 2012), which are the only ice-associated marine fish species in the Arctic. Polar cod occurs in variable-sized schools ranging from small groups to several million fishes across the Arctic (Andriashev 1964, Craig *et al.* 1984). Both fish species are important food items for higher trophic levels (Bluhm & Gradinger 2008), including ringed seals *Pusa hispida*, narwhals and belugas (e.g. Labansen *et al.* 2007). Arctic sea birds (fulmars, murres, guillemots, kittiwakes etc.) also feed on polar cod throughout the Arctic (e.g. Lønne & Gabrielsen 1992, Hobson 1993, Weslawski *et al.* 2007, Karnovsky *et al.* 2008).

Sea ice also serves as an essential structuring element for habitat used by seals, polar bears and cetaceans (Reid *et al.*, Chapter 3). All seven seal species found in the Arctic are closely associated with the ice ecosystem, and use the ice habitat either for birthing, feeding or as a resting platform (e.g. Laidre *et al.* 2008, Kovacs *et al.* 2011a). For example, ringed seals, which are the most abundant Arctic seals, use the sea ice for birth, rearing and molt. Ringed seals have a circumpolar Arctic distribution and constitute a major food item for polar bears (Thiemann *et al.* 2008) and humans. Polar bears are closely associated with the sea ice as they use it extensively for foraging and for transportation to/from terrestrial denning areas, often found along slopes near shorelines where snowdrifts accumulate sufficient snow (Stirling 2009).

Ice shelves also constitute unique Arctic ecosystems. They directly impact ecosystem biodiversity, as they create unique habitats for diverse microbial communities forming thick mats (Vincent *et al.* 2000, 2004). These

## Box 14.3. Extremophiles in the marine Arctic

The lowest temperature at which active life has been found on Earth is about –20 °C, with records of bacteria living in permafrost and sea ice (D'Amico *et al.* 2006). Cold-adapted organisms are called psychrophiles. Psychrophilic species can grow at temperatures < 0 °C, have an optimum growth temperature < 15 °C and cannot grow above 20 °C (Thomas & Dieckmann 2002). Psychrophilic organisms represent a diverse group of bacteria, archaea, yeasts, fungi and algae and play a key role in nutrient cycling and the transformation of organic matter.

Within Arctic sea ice, extremophile habitat consists of channels or pockets that contain liquid brine. These liquid habitats within the sea ice can persist at temperatures as low as –35 °C (Deming 2002). The liquid inclusions are reduced in size and connectivity as ice temperatures decrease, and the salinity of the brine can exceed 200‰, compared with values of about 32‰ in surface waters of the Arctic. Therefore, sea-ice extremophiles are adapted to survive not only cold temperatures but also high salinity, and can be faced with other challenges such as nutrient availability within these micro-habitats.

Extremophile adaptations are primarily associated with cellular proteins (e.g. enzymes of high specific activity; D'Amico *et al.* 2006), as they control the balance between cellular substrates and production, nutrient fluxes, removal of waste products and the assembly of cellular components including DNA. The production of polyunsaturated fatty acids as well as other changes in the composition of lipid membranes is also critical for maintaining membrane fluidity and proper functioning of the cells (Thomas & Dieckmann 2002). Outside the cell, cryoprotectant materials such as exopolymers have multiple roles that aid the survival of bacterial and algal extremophiles in the sea ice (Krembs & Deming 2008). There is still much to learn about the biodiversity of these extreme habitats and extremophiles as well as the mechanisms they use to survive within the sea ice and extremely cold environments.

cryotolerant microbial mats are hypothesized to have provided refugia for the survival, growth and evolution of a variety of organisms during periods of extensive ice cover such as the Proterozoic glaciations (Vincent *et al.* 2000). Calving ice shelves and icebergs also impact the biodiversity of ecosystems through which the ice travels (see Box 14.5, Section 14.5.2).

## 14.4. STRESSORS AND THREATS TO ARCTIC MARINE ECOSYSTEM BIODIVERSITY

The Arctic is undergoing major and rapid environmental changes including accelerated warming (Zhang 2005, Steele *et al.* 2008), decrease in sea ice cover extent (Stroeve *et al.* 2007, Comiso *et al.* 2008) and duration (Stroeve *et al.* 2006), increase in runoff and precipitation (Dyurgerov *et al.* 2010), and permafrost and glacier melt (IPCC 2007). The rapidly diminishing Arctic sea ice cover, in particular the decline in thick multi-year ice, has unlocked tremendous opportunities for economic development through the exploitation of natural resources that were previously unreachable, new transportation and shipping routes and increased tourism.

The main currently anticipated threats to biodiversity are both direct, such as the change in land use and oil spills, and indirect, such as the ability of key organisms to acclimate to new conditions of temperature, $CO_2$, and ice, freshwater and seawater dynamics. The immense changes in climatic forcing of the Arctic over relatively short evolutionary time scales suggest that its ecosystems are capable of reorganization, but the range and survival of individual species is less certain (Carmack & Wassmann 2006).

### 14.4.1. Climate-related changes

Fluctuations in climate are documented from geological records and ice cores. Sedimentary records from Arctic continental margins reveal centennial- to millenial-scale fluctuations in ice drift patterns, the position of the marginal ice zone and temperature and salinity in surface and subsurface water masses (Darby *et al.* 2006). Notably, over the past thousand years, alternate warming and cooling of the North Atlantic occurred during the Medieval Warm Period (9th to mid-15th century) followed by the Little Ice Age (mid-16th to early 20th century) (Darby *et al.* 2006). Evidence for impacts of past climate fluctuations on Arctic marine biota are numerous. For example, oral as well as written records from the last centuries and archaeological remains of Inuit hunting communities from the last 4-5 thousand years provide evidence for large distributional and numerical fluxes of sea mammals and sea birds in response to climatic fluctuations (Vibe 1967). Another example is the boreal blue mussel *Mytilus edulis* that was established as far north as Svalbard during early postglacial periods, after which the species disappeared until this decade (Berge *et al.* 2005). In the 1920s and 1930s, the North Atlantic experienced a dramatic increase in atmospheric and ocean temperatures resulting in marine ecosystem changes (reviewed by Drinkwater 2009) including a northward range expansion of boreal fish species (Perry *et al.* 2005), phytoplankton species (e.g. Smyth *et al.* 2004) and benthic invertebrates into the Barents Sea (Blacker 1957).

The rapid decrease (13% per decade) in the minimum (summer) Arctic sea ice extent over the past three decades (Comiso *et al.* 2008) and accelerated melt compared with model predictions (Barber *et al.* 2009, Wang & Overland 2009; see Fig. 1.5 in Meltofte *et al.*, Chapter 1) prompts concerns that the Arctic Ocean could be virtually ice free in summer by 2040 (Meier *et al.* 2011). Multi-year ice, so far considered a permanent feature of central Arctic basins and typically representing about half of the Arctic sea ice coverage, has declined rapidly over the last decade to make up less than 15% of summer sea ice extent in 2010 (National Snow and Ice Data Center 2010). The total multi-year ice volume in winter experienced a net loss of > 40% in the four years following 2005 (Kwok *et al.* 2009). Arctic climate patterns observed over the last decade are distinctly different from those in the past century, resulting in enhanced sea ice loss (Overland *et al.* 2008).

The rapid warming taking place in the Arctic, exemplified by the rise in seawater temperatures of up to 4 °C expected in the Atlantic sector of the Arctic Ocean (Müller *et al.* 2009), is expected to have direct and indirect impacts on the biodiversity of marine ecosystems. It has been proposed that critical temperature thresholds exist in marine ecosystems, leading to abrupt ecosystems shifts rather than gradual changes (Beaugrand *et al.* 2008). One such example is the shift from a boreal to a temperate ecosystem, associated with a surface temperature increase of just over 1 °C in the North Sea over the last 40 years (Beaugrand *et al.* 2008). Warming in the North Atlantic and adjacent seas has also been linked to large-scale biogeographic changes in the biodiversity of calanoid copepods over the period 1960-1999 (Beaugrand *et al.* 2009).

Temperature modulates the biodiversity of marine ecosystems through its combined effects on species phenology, interactions and geographic distribution. For example, temperature requirements for growth, reproduction and survival are the major factors responsible for determining geographical distribution boundaries of macroalgae. The eurythermal character of some Arctic species should benefit these species under increasing water temperatures. There are many species in the Arctic that also grow in cold-temperate regions. However, it seems that temperature tolerance for survival is, in contrast to temperature requirements for growth and reproduction, a very conservative trait (e.g. Hirche *et al.* 1997), which probably only changes over long evolutionary periods. Hence, the pace of species adaptation to the rapidly warming Arctic may well lag behind that needed for survival.

Warming combined with increased precipitation has caused an increase in freshwater discharge into the Arctic Ocean (Dyurgerov *et al.* 2010). Increased river outflow is expected to cause larger marine areas to be impacted by estuarine circulation patterns leading to a displacement of marine taxa, with potential loss of diversity (Bluhm & Gradinger 2008). Inputs of inorganic sediments and organic carbon to the Arctic Ocean by rivers and eroding coast lines may have changed as well, but analyses of available time series do not show identifiable long-term trends (Holmes *et al.* 2002).

In addition to direct impacts of changing sea ice conditions (i.e. sea ice structure, extent and distribution) on Arctic ecosystems, indirect impacts of the warming Arctic include increased erosion and changes in the timing of sea ice melt and freeze-up. The melt period was, on average, 13 days earlier in the 2000s compared with the 1980s (Stroeve *et al.* 2006, 2007). Freeze-up is also delayed, up to seven days per decade later for the Chukchi/Beaufort and Laptev/East Siberian Seas, making the open water period 20 days longer (Markus *et al.* 2009). Later freeze-up and earlier melt in coastal areas is extensively reported in traditional ecological knowledge. Peter Elachik, from Kotlik, Alaska, reports large changes in the time when safe travel can take place on the ice at the mouth of the Yukon River.

> » *So there's a lot of difference between 1945 and 2005. Big change.*
>
> (Peter Elachik, Kotlik; in Fienup-Riordan & Rearden 2010).

Warming, changes in stratification, diminished ice cover, delayed ice formation and advanced break-up, and a longer open water period have tremendous impact on individual species (e.g. polar bear; see Reid *et al.*, Chapter 3) and on the characteristics of ecosystem production and its channeling to higher trophic levels (e.g. Grebmeier 2012). For example, earlier ice melt might limit ice algal production and its contribution to Arctic primary productivity, but cause earlier and increased phytoplankton productivity (Arrigo & van Dijken 2011). Earlier ice melt might also favor a shift from a benthic to pelagic dominated food web on the shelves, as suggested for the Bering and Chukchi Seas (Grebmeier *et al.* 2006b, Bluhm & Gradinger 2008). Changes in the timing of the ice algal and phytoplankton bloom may have important consequences for trophic transfers in Arctic food webs (Michel *et al.* 2006, Leu *et al.* 2011). Long-term studies in W Greenland provide evidence for such effects (see Section 14.5.3). The duration of the open water period is also critical to the distribution of marine birds and mammals in ice-covered regions such as the Canadian Arctic Archipelago. Examples of observed changes and trends in relation to climate-associated changes are discussed in Section 14.5.2.

## 14.4.2. Exploitation of marine resources

The marine Arctic offers a wealth of natural resources, especially fossil fuels and fisheries whose exploitation, together with climate change, is resulting in increasing pressures on Arctic marine ecosystems.

### 14.4.2.1. Hydrocarbons

Extensive oil and gas activity has occurred in the Arctic, primarily land-based, with Russia extracting 80% of the oil and 99% of the gas to date (AMAP 2008). Furthermore, the Arctic still contains large petroleum hydrocarbon reserves and potentially holds one fifth of the world's yet undiscovered resources, according to the US Geological Survey (USGS 2008) (Fig. 14.4). While much of the currently known Arctic oil and gas reserves are in Russia (75% of oil and 90% of gas; AMAP 2008), more than half of the estimated undiscovered Arctic oil reserves are in Alaska (offshore and onshore), the Amerasian Basin (offshore north of the Beaufort Sea) and in W and E Greenland (offshore). More than 70% of the Arctic undiscovered natural gas is estimated to be located in the W Siberian Basin (Yamal Peninsula and offshore in the Kara Sea), the E Barents Basin and in Alaska (offshore and onshore) (AMSA 2009). Associated with future exploration and development, each of these regions would require vastly expanded Arctic marine operations, and several regions such as offshore Greenland would require fully developed Arctic marine transport systems to carry hydrocarbons to global markets. In this context, regions of high interest for economic development face cumulative environmental pressure from anthropogenic activities such as hydrocarbon exploitation locally, together with global changes associated with climatic and oceanographic trends.

Oil spills are considered to be the largest environmental threat from oil and gas activities in the Arctic marine environment, but habitat fragmentation and disturbances also constitute pressures to various ecosystem components (AMSA 2009). For example, noise associated with hydrocarbon activities can be deleterious to marine mammals. Increased noise can disrupt their behavior or prevent detection of other sounds that are important to the marine mammals (e.g. Richardson *et al.* 1995, Nowacek *et al.* 2007). The accidental release of oil into the Arctic marine environment threatens all trophic levels (e.g. Cross *et al.* 1987, Muir *et al.* 1999). Most obvious to the public are effects on birds and mammals, by compromising their feathers and fur, resulting in hypothermia and potential mortality. Metabolic effects are also documented for invertebrates, birds and mammals (e.g. Suchanek 1993, Muir *et al.* 1999). Arctic seabirds and marine mammals are particularly susceptible to oil spills because they congregate in large numbers to breed, nest and rear young at certain times and locations each year. Moreover, the logistical challenges of cleaning up an oil spill in the Arctic could lead to oil persistence in affected areas, consequently causing uptake of oil in marine and coastal food webs.

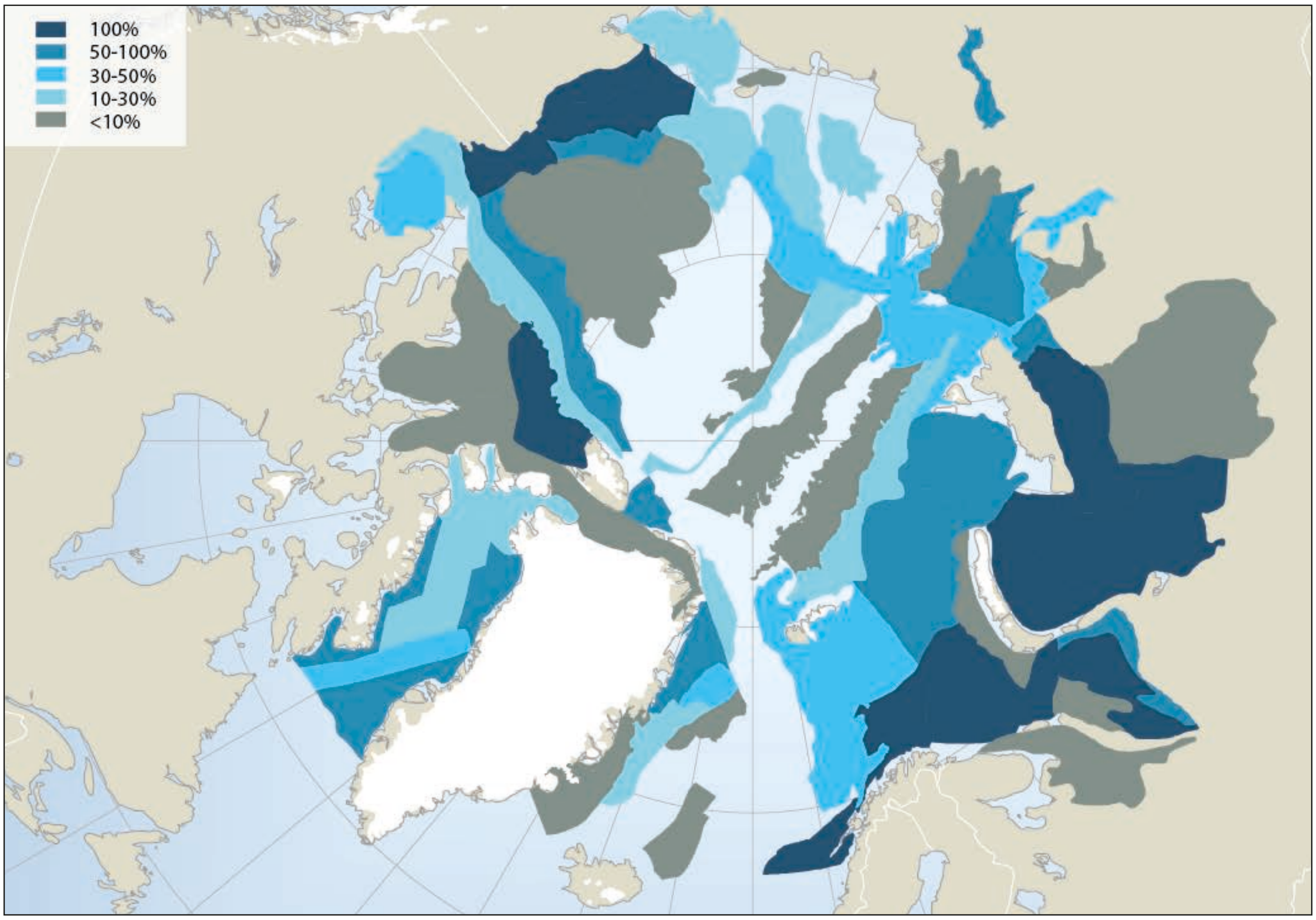


**Figure 14.4.** Circumpolar distribution and probability of potential petroleum reserves in the North (source: US Geological Survey 2011).

### 14.4.2.2. Vessel activity

Most information presented here is derived from the recent Arctic Marine Shipping Assessment (AMSA 2009). Current vessel activities in the Arctic can be categorized into four main groups: community re-supply, cargo ships, fishing activity and tourism. The majority of vessel activity, and consequently ship accidents, takes place along the coast (Fig. 14.5). Therefore continental shelves, which are areas of high biodiversity and production and large aggregations of Arctic marine fauna, are most susceptible to impacts from ship traffic.

The decrease in multi-year ice and longer open water season opens new shipping routes and opportunities for tourism, while offshore leases for oil and gas exploration (e.g. in the Beaufort, Chukchi and Barents Seas) are expected to stimulate coastal-offshore marine activity over the next decade(s). Increased marine traffic is now a reality in the Arctic. The Northwest Passage (Canadian Arctic Archipelago) has seen increased vessel transits over the past three decades, and especially in the past five years (Fig. 14.6a).

A potentially ice-free Arctic Ocean in summer in a few decades also opens opportunities for increasing scientific, exploration and tourism vessel activity in central Arctic basins.

Cargo traffic for community re-supply is expected to expand in the near future, mainly due to economic development and population increases in Arctic communities, but also due to the shortened seasonal use of ice-roads. Cruise ships to the Arctic have already significantly increased in numbers over the past few years. Over 2.5 million cruise ship passengers traveled to the Arctic in 2007, a number more than twice the estimate for 2004. In Greenland alone, the number of cruise ships has more than doubled from 2003 to 2008 (Fig. 14.6b). Similar increases can be expected in some other coastal regions of the circumpolar Arctic, where there is adequate access to major ports.

On a global scale, the total number of vessels navigating in the Arctic represents a small proportion of the world's fleet. However, impacts on Arctic marine ecosystems can still be significant due to their unique characteristics and to the limited infrastructure and variable emergency response preparedness in remote Arctic locations.

A significant threat from ships to the Arctic marine environment is considered to be the release of fuel and/or oil, which is routinely discharged into the marine environment through tank washings, deck runoff and bilge water discharges. The introduction of alien and possibly invasive species via ballast water discharge can also be a serious threat to marine ecosystem biodiversity (see Lassuy & Lewis, Chapter 16). Impacts of ballast water

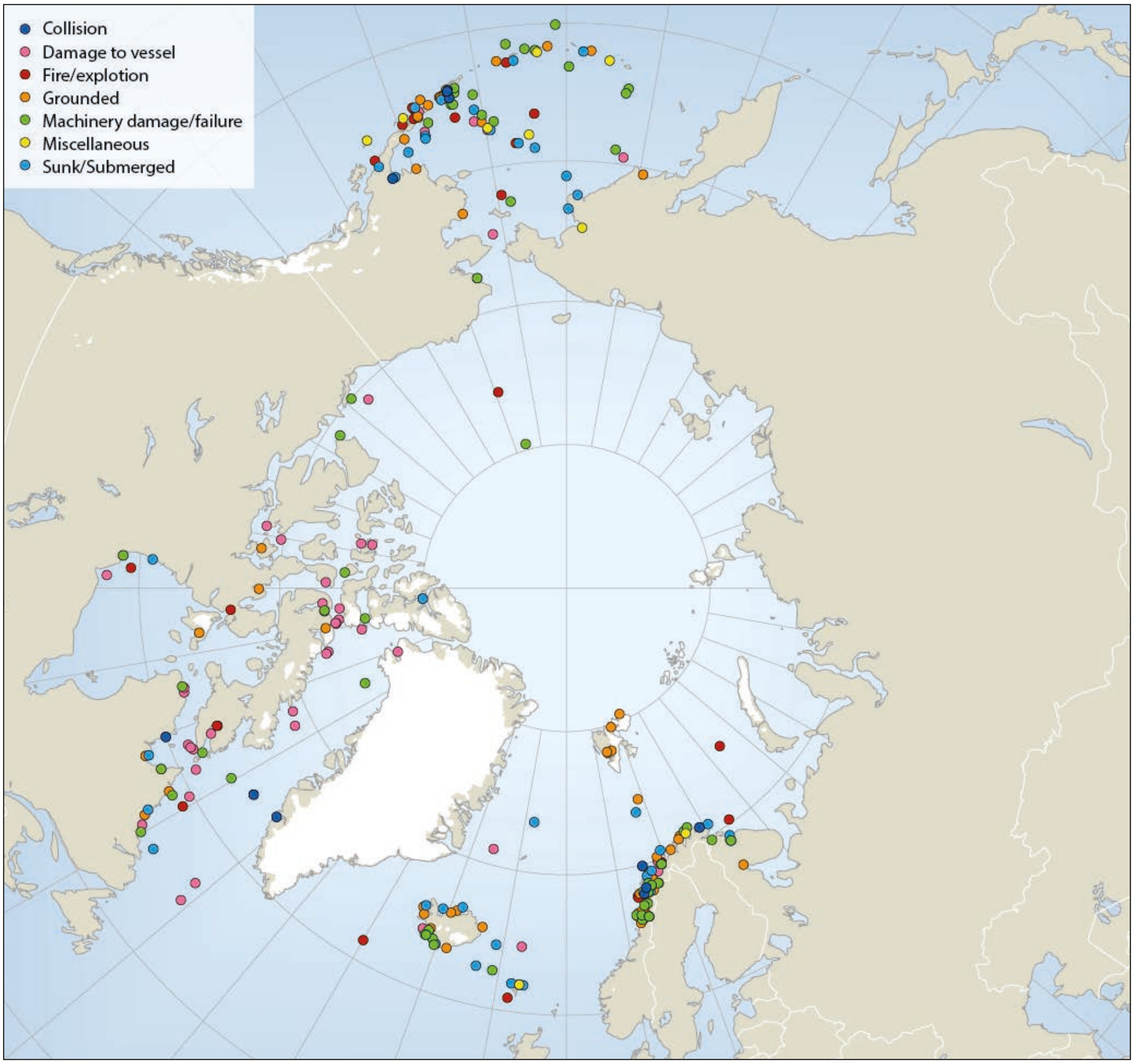


**Figure 14.5.** Locations of sub-Arctic and Arctic shipping accidents and incident causes, 1995-2004 (source: AMSA 2009).

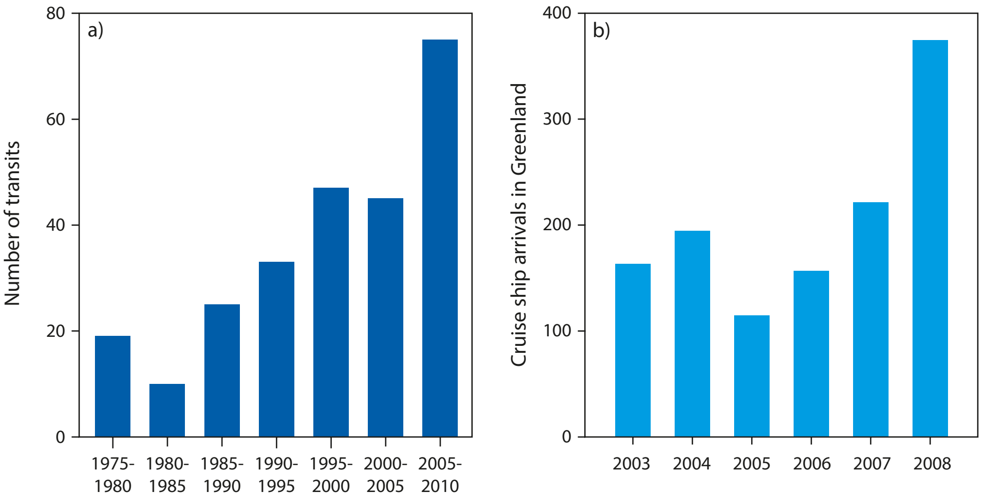


**Figure 14.6.** Number of ships a) transiting through the Northwest Passage (five year intervals, from 1975 to 2010), and b) landing in Greenland (cruise ships only, from 2003 to 2008. (Sources: AMSA 2009 updated with 2010 data and NORDREG 2009; se also Fig. 16.1 in Lassuy & Lewis, Chapter 16).

introductions have been reported to modify food webs and trophic interactions in other marine environments (Molnar *et al.* 2008). Other potential impacts include the release of grey water sewage, accidental strikes of marine fauna and the introduction of noise or other acoustics (e.g. sonar).

Of concern is that the presence of ships and their noise may disrupt habitat and migratory patterns of marine mammals (Tyack 2008). There is a broad geographical correspondence between the routes used by marine mammals (bowhead, beluga, narwhal, walrus) on their spring migration to summer feeding grounds in the Arctic and Arctic shipping routes, notably through the Bering Strait, Lancaster Sound and the Kara Gate. At present, most shipping movements take place after the mammals have migrated through these choke-points. With less sea ice there may be a longer season of navigation with the potential for more conflicts between migratory species and ships. Key sensitivities of Arctic marine ecosystems to vessel activities include the presence and role of sea ice and the importance of Arctic shelves as migration routes, feeding and nursery areas for anadromous fishes, marine birds and mammals.

### 14.4.2.3. Commercial harvest

Exploitation and harvest of living marine resources has historically contributed to shape, and continues to be a major stressor on, Arctic ecosystem biodiversity. The Steller's sea cow *Hydrodamalis gigas* became extinct (IUCN 2008) in 1768, less than 30 years after the only remaining Holocene population was discovered (in 1741) in the Bering Sea. Hunting records combined with life-history data indicate that overexploitation was the cause for this extinction (Turvey & Risley 2006). Commercial Arctic whaling from the 1700s onward has also severely depleted populations of almost all the baleen whale species (Reeves & Kenney 2003). For example, the large population of resident bowhead whales between Greenland and Svalbard was subject to intensive harvest during the period of commercial exploitation by European whaling vessels (1611-1911). At the end of this period, the initial resident population estimated at many tens of thousands appeared to be on the verge of extinction (Allen & Keay 2006, Wiig *et al.* 2007; see also Reid *et al.*, Chapter 3).

The historical harvest of marine birds is less clear because no logbook records of the sort available for marine mammals were kept by harvesters. The remaining populations of flightless or near-flightless seabirds in the sub-Arctic (spectacled cormorant *Phalacrocorax perspicillatus* and great auk *Pinguinus impennis*) were eliminated by over-harvest in the nineteenth century (Fuller 2001). Colonies of flying auks, particularly the thick-billed murre *Uria lomvia* were decimated on the west coast of Greenland between the 1930s and 2000s, mostly by harvesting of breeding birds at the colonies, and have not recovered (Kampp *et al.* 1994, F. Merkel pers. com.; see also Ganter & Gaston, Chapter 4 and Huntington, Chapter 18). Similarly, numbers of murres in Novaya Zemlya remain considerably depressed following harvesting of eggs in the 1940s (Bakken & Pokrovskaya 2000). Many local reductions probably took place as a result of incidental harvest during whaling and sealing expeditions, but these are unknown.

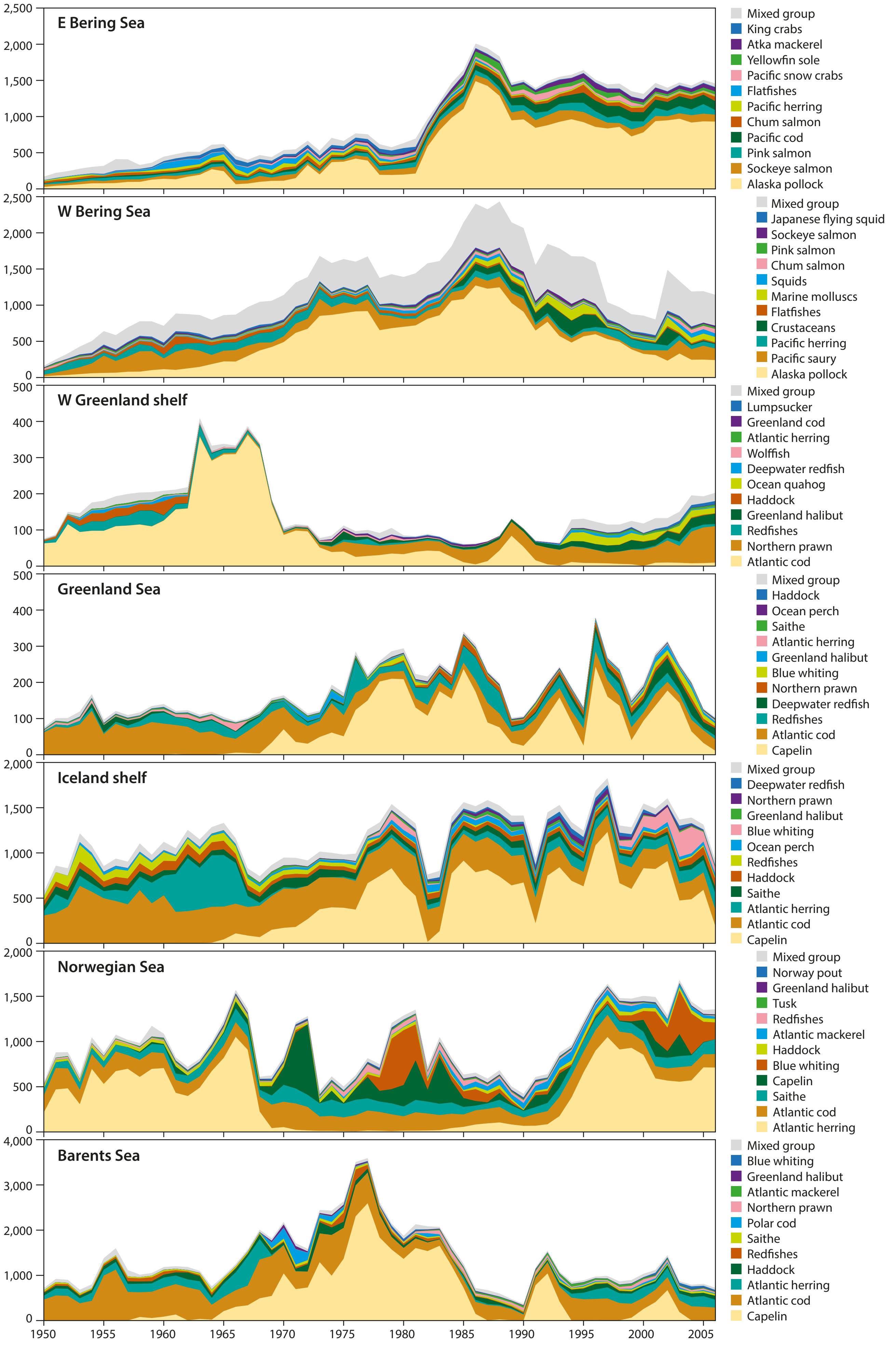
The impact of historical harvest of marine mammals and seabirds on the current architecture of Arctic marine ecosystems is unknown. However, it is certain that the removal of the large biomass of targeted species or functional groups contributed to shape the flow of energy and materials and trophic interactions within present-day Arctic marine food webs. This is discussed in Section 14.5.1.

Today, commercial fisheries are found in the productive Barents, Bering, Norwegian and Greenland Seas and around Iceland, supporting high catches of various fish and invertebrate species (e.g. capelin, pollock, halibut, Atlantic cod, shrimps and crabs). Time-series of commercial fish catches, from the 1950s onward, and indicators of the sustainability of fisheries and ecosystem structure (see Section 14.5.3) are well-documented for seven Arctic LMEs, i.e. the Barents, Norwegian, E and W Greenland, E and W Bering Seas together with the Iceland shelf (see Sherman & Hempel 2008). In the other Arctic LMEs, commercial fisheries and subsistence harvest are estimated based on sparse data and records (Sherman & Hempel 2008); therefore they are excluded from this chapter. A recent study estimated that catches in the Amerasian Arctic (FAO statistical area 18) from 1950 to 2006 were actually 75 times higher than what was reported to the FAO, although these catches were very low (Zeller *et al.* 2011).

Commercial Arctic and sub-Arctic fisheries harvest millions of tonnes of fishes annually, for an economic value reaching billions of US dollars. Commercial harvest ranged, in 2006, from approximately 100 thousand tonnes annually in the E and W Greenland LMEs to a maximum of approximately 1.3 million tonnes for the Iceland shelf and Norwegian Sea LMEs. For the W Bering and Barents Seas LMEs, commercial fisheries yielded respectively approximately 1.1 million and 720 thousand tonnes in 2006 (Fig. 14.7). Large fluctuations in commercial harvest, both in terms of numbers and species composition, have been observed over the past decades in these LMEs.

Of significance, total landings in W Greenland have decreased dramatically since the early 1970s and, as in other areas of the North Atlantic, have shifted from a strong dominance of Atlantic cod to deep-water shrimp (see Fig. 1.2 in Meltofte *et al.*, Chapter 1). In E Greenland and around Iceland, a similar shift is observed with capelin now being the most abundant species in landings (Fig. 14.7).

In the Barents Sea, total landings were highest (3.3 million tonnes) during the mid-1970s, coinciding with


E Bering Sea
2,500
2,000
1,500
1,000
500
0
Mixed group
King crabs
Atka mackerel
Yellowfin sole
Pacific snow crabs
Flatfishes
Pacific herring
Chum salmon
Pacific cod
Pink salmon
Sockeye salmon
Alaska pollock
W Bering Sea
2,500
2,000
1,500
1,000
500
0
Mixed group
Japanese flying squid
Sockeye salmon
Pink salmon
Chum salmon
Squids
Marine molluscs
Flatfishes
Crustaceans
Pacific herring
Pacific saury
Alaska pollock
W Greenland shelf
500
400
300
200
100
0
Mixed group
Lumpsucker
Greenland cod
Atlantic herring
Wolffish
Deepwater redfish
Ocean quahog
Haddock
Greenland halibut
Redfishes
Northern prawn
Atlantic cod
Greenland Sea
500
400
300
200
100
0
Mixed group
Haddock
Ocean perch
Saithe
Atlantic herring
Greenland halibut
Blue whiting
Northern prawn
Deepwater redfish
Redfishes
Atlantic cod
Capelin
Iceland shelf
2,000
1,500
1,000
500
0
Mixed group
Deepwater redfish
Northern prawn
Greenland halibut
Blue whiting
Ocean perch
Redfishes
Haddock
Saithe
Atlantic herring
Atlantic cod
Capelin
Norwegian Sea
2,000
1,500
1,000
500
0
Mixed group
Norway pout
Greenland halibut
Tusk
Redfishes
Atlantic mackerel
Haddock
Blue whiting
Capelin
Saithe
Atlantic cod
Atlantic herring
Barents Sea
4,000
3,000
2,000
1,000
0
Mixed group
Blue whiting
Greenland halibut
Atlantic mackerel
Northern prawn
Polar cod
Saithe
Redfishes
Haddock
Atlantic herring
Atlantic cod
Capelin
1950
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005

a high dominance of capelin. Large fluctuations in total landings and yield of major species have occurred over the past decades, likely due to fishing mortality and environmental changes (e.g. Mathishov *et al.* 2003; also see Section 14.5.5). The Norwegian Sea also saw large fluctuations in total fish landings and their composition, particularly for herring and capelin. Over the past two decades, total landings increased from less than half a million tonnes in 1990 to 1.5 million tonnes in 2004 (Fig. 14.7). The E and W Bering Sea LMEs have also seen large changes in fisheries catch over the past decades, with a large increase in pollock landings in the E Bering Sea since the 1980s and a decrease in the W Bering since the 1990s (Fig. 14.7).

Careful management of fishing stocks remains vital to Arctic biodiversity, as illustrated by the large fluctuations in landings and dramatic shifts in species composition in Arctic LMEs over the past decades. The paucity of baseline data and long-term monitoring in the Arctic compared with other marine ecosystems, combined with rapid climate-associated changes, also speaks to using a precautionary approach for fisheries and resources management. In US waters of the Arctic, for example, commercial fishing has recently been prohibited as per the Arctic Fisheries Management Plan until more information is available to support sustainable management of potentially harvestable species (NPFMC 2009). Sustainable yield is also central to commercial fishing in Arctic areas (e.g. Barents Sea) where fisheries resources constitute a major socio-economic driver.

Subsistence fisheries are important in the Arctic and can influence marine ecosystems. In Hudson Bay, subsistence fisheries targeting mainly Arctic char, but also polar cod and fourhorn sculpin *Myoxocephalus quadricornis*, reached almost 900 tonnes in 1962 to decline to approximately 300 tonnes by the early 2000s. This decline is attributed to the transition from sled dogs to snowmobiles as a means of transportation and the lesser need of local harvest as food for the dogs (Boot & Watts 2007). Such an example illustrates the effects of economic development and societal choices in directing the use of ecosystem services and in creating associated impacts (see also Huntington, Chapter 18).

Besides the direct impact of the catch, commercial harvest affects ecosystem biodiversity through impacts on habitats (particularly by botton trawling) and by-catch species as in other oceans (see also Josefson & Mokievsky, Chapter 8). For example, the reef-forming stony coral *Lophelia pertusa* forms massive reef complexes up to tens of kilometres long and 30 m high (e.g. Fosså *et al.* 2002, Freiwald *et al.* 2002), which provide habitat for a rich community of invertebrates (Mortensen & Fosså 2006). The coral *Lophelia pertusa* is widely distributed and particularly abundant on the Norwegian shelf and slope, where bottom trawling has impacted many reefs. Harvest measures are now in place in Norway to protect the coral reefs from further damage (Fosså *et al.* 2002, Fosså & Skjoldal 2009). In the Canadian Arctic Archipelago (Baffin Bay), restrictions have been placed on the Greenland halibut fishery to protect deep-sea coral habitats and over-wintering grounds of narwhal. The bottom trawls posed a treat to several cold-water coral species including the gorgonian species *Acanella arbuscula* and *Paragorgia arborea* (DFO 2007).

### 14.4.3. Ocean acidification

The oceans have absorbed about one third of the anthropogenic $CO_2$ released to the atmosphere (Sabine *et al.* 2004). This increase in $CO_2$ concentrations in the ocean contributes to ocean acidification. As the solubility of gases, including $CO_2$, is higher in cold than warm waters, the Arctic Ocean is especially prone to acidification (Bates & Mathis 2009). Ocean acidification reduces the concentration of carbonate ions ($CO_3^{2-}$) and directly impacts a large and diverse group of marine organisms that require carbonate ions to build their calcareous skeleton or shell, in the form of aragonite or calcite. This taxonomically-diverse group includes protists such as coccolithophores and foraminiferans, small planktonic animals such as pteropods, pelagic and benthic taxa such as mollusks including sea urchins, shellfish and corals, and fishes. Under typical conditions, the surface ocean is saturated with calcium carbonate ($CaCO_3$), and calcareous shells or exoskeletons are subject to dissolution only at depths below the lysocline, where $CaCO_3$ is undersaturated. Model simulations predict that surface waters of the Arctic Ocean will become undersaturated with aragonite within a decade (Steinacher *et al.* 2009), thereby reducing suitable habitat for calcifying species requiring aragonite.

Predicted changes in carbonate saturation have now been substantiated with observations. In 2008, surface waters of the Canada Basin were found to be undersaturated with respect to aragonite, as a direct consequence of extensive sea ice melt (Yamamoto-Kawai *et al.* 2009). Aragonite is an essential constituent for the shell of the pteropod *Limacina helicina* (see opening photo for chapter 8), an important plankton species found in the upper (top 50 m) Arctic Ocean. The same species is a prominent plankton species in the Ross Sea (Antarctica) and is considered an indicator of ecosystem health (Seibel & Dierssen 2003). There is experimental evidence that the calcification of pteropod shells is reduced in response to ocean acidification and conditions of aragonite undersaturation (Orr *et al.* 2005, Comeau *et al.* 2009). Large reductions in *L. helicina* calcification rates are predicted for the Arctic, based on empirical relationships combined with model predictions for aragonite saturation (Comeau

**Figure 14.7.** Total landings of commercial fish species (x 1,000 tonnes) in seven Arctic Large Marine Ecosystems (source: Sherman & Hempel 2008 and SeaAroundUs Project 2010).

*et al.* 2012). Increased $CO_2$ concentrations in the ocean also influence biodiversity via species-specific effects on macroalgal growth and photosynthesis (e.g. Mercado *et al.* 1999, Gordillo *et al.* 2001). Recent experimental work shows that $CO_2$ stimulates growth in some species such as the brown algae *Alaria esculenta* and *Saccorhiza dermatodea*, negatively affects others such as *Desmarestia aculeata*, and has no effect on the growth rates of yet others species such as the red algae *Ptilota* spp. and *Phycodris rubens* (F. Gordillo pers. com.). Therefore, changes in Arctic Ocean chemistry are expected to affect populations of calcifying species as well as other species affected by changes in the inorganic carbon cycle, thereby impacting biodiversity and trophic pathways within polar marine ecosystems.

### 14.4.4. Range extensions and invasive species

Species distribution range extensions and invasive species are considered to have a major impact on biodiversity at local and global scales, as they can disturb trophic interactions and pathways, causing tremendous changes in ecosystems (Wassmann *et al.* 2010, Weslawski *et al.* 2011, Lassuy & Lewis, Chapter 16). In the Arctic, the low degree of endemism also suggests that range extensions may, at least temporarily, increase species and genetic biodiversity by the introduction of new species. However, this is not a gain to global biodiversity.

Arctic marine ecosystems are influenced by advection from the Atlantic and Pacific Oceans (see Section 14.3.1). Inflow shelves (sensu Carmack *et al.* 2006), which are influenced by Atlantic (e.g. Barents Sea) and Pacific (e.g. Chukchi Sea) inflows, are susceptible to range extensions of sub-Arctic species via the transport of planktonic larvae or adult animals (see Section 14.5.4). However, interior shelves (e.g. Kara, Laptev, East Siberian Seas) are not directly subject to range extension through transport of sub-Arctic species. In these areas, range extensions are instead associated with increasing temperatures or the opening of migration/transportation corridors with decreasing sea ice cover (Weslawski *et al.* 2010).

Reduced ice cover extent and duration is expected to favour northward migrations of sub-Arctic species (see Section 14.5.4). However, this may not necessarily lead to increases in abundance of species that are also dependent on warm temperatures for survival and reproduction. For example, the northward range extension of bottom fish species typically observed in the southeastern Bering Sea is believed to be limited by cold bottom water temperatures together with the seasonal occurence of sea ice (Sigler *et al.* 2011).

Introductions can be intentional or unintentional, as for the red king crab *Paralithodes camtschaticus* and the snow crab *Chionoecetes opilio*, respectively, in the Barents Sea. The red king crab is a native species in the Bering Sea where it supports a high value commercial fishery (e.g. Kruse *et al.* 2000). In the 1960s the red king crab was intentionally introduced to the Barents Sea (Orlov & Karpevich 1965). The Barents Sea red king crab population increased rapidly in the 1990s and now supports a productive commercial fishery. The current distribution of red king crab is expanding eastwards in Russia and westwards along the Norwegian coast (see UNEP/GRID-Arendal 2010a) and is expected to spread northward. There has been much concern for the ecological impacts of this introduced species on the ecosystem of the Barents Sea (Jørgensen & Primicerio 2007). A comprehensive research program initiated in 2002 showed that the red king crab feeds on a wide range of benthic animals and that it may affect recruitment of some fish species through predation.

The snow crab is native to the North Pacific and the NW Atlantic and, in the Arctic, it is a native species in the Bering and Chukchi Seas and in W Greenland. The species is considered to have been introduced to other Arctic areas via ballast waters (Kuzmin 2000). The snow crab was first detected in the Barents Sea in 1996 (Kuzmin 2000), then in Norwegian waters in 2003 (Alsvåg *et al.* 2009). The abundance of snow crab has been increasing in the Barents Sea, where the species is now considered to have established a viable population (Alsvåg *et al.* 2009).

## 14.5. STATUS AND TRENDS IN ARCTIC MARINE ECOSYSTEM BIODIVERSITY

> » *The world can tell us everything we want to know. The only problem for the world is that it doesn't have a voice. But, the world's indicators are there. They are always talking to us.*
>
> (Quitsak Tarkiasuk, Ivujivik).

### 14.5.1. Historical and current status of Arctic marine ecosystem biodiversity

The Arctic Ocean is young in terms of geology and biogeography. The evolutionary origin of marine invertebrates, mammals and Arctic seaweeds reflects an ancient Pacific origin dating back to the opening of the Bering Strait 3.5 million years ago (Adey *et al.* 2008). Throughout most of the Tertiary, the Arctic Ocean region supported a temperate biota, and fully Arctic conditions developed only during the latest part of this period. This short history contributes to the presence of few endemic Arctic marine species on the shelves (Dunton 1992, Adey *et al.* 2008) and the possibly lower diversity compared with lower latitude marine ecosystems (Tab. 14.1). Regional differences in species diversity can also be related to time for diversification. For example, there are over 350 benthic species in coastal Norwegian waters (Weslawski 2004), and these waters can supply propagules for the Svalbard region. However, at present, only 80 intertidal benthic species have been identified for Svalbard indicating that an increase in littoral diversity

**Table 14.1.** Estimated number of taxa within Arctic seas (modified after Bluhm *et al.* 2011 and references therein).

| Group | Estimated number of taxa |
|---|---|
| Bacteria | 4,500-450,000 |
| Archaea | up to 5,000 |
| Protists | 2,800 |
| Macrophytes | 160 |
| Invertebrates | ~ 5,000 |
| Fishes | 243 |
| Birds | 82 |
| Mammals | 16 |

can be anticipated in the future since both areas have similar coastal geomorphology and water mass characteristics (Weslawski *et al.* 2010).

So far, the biodiversity of the marine Arctic is poorly documented, and current estimates suggest that many species are yet to be discovered (Ausubel *et al.* 2010, Bluhm *et al.* 2011), although the Census of Marine Life has added substantially to the inventory (e.g. Piepenburg *et al.* 2011). As an example, a recent survey of zooplankton composition in the Arctic basins found 25% of the species observed had not previously been recorded in the Arctic (Kosobokova *et al.* 2011).

At geological time scales, the distribution of foraminifers and other biological proxies fluctuated strongly between interglacial/glacial periods, attributed to changes in productivity (see Darby *et al.* 2006 and references therein). Retreat and recolonization of cold-temperate species in the Arctic is well known to have occurred in the past during the glacial and interglacial periods, respectively (Lüning 1990 and references therein).

At shorter time scales, the removal of vast numbers of marine mammals and their associated biomass from Arctic ecosystems over a few decades to a few centuries (see Section 14.5.3) is likely to have had important implications for Arctic marine food webs. The extirpation of bowhead whales and walruses from Svalbard is believed to have had major cascading effects on the marine ecosystem, contributing to the structure of present-day ecosystems (Weslawski *et al.* 2000). Hence, planktivorous seabirds such as the little auk and polar cod probably took advantage of the abundance of zooplankton 'freed' by decreased predation from bowhead whales. The increased abundance of pelagic fish would, in turn, have provided food for piscivorous alcids and gulls, supporting the development of the large bird colonies found on Svalbard. Similarly, common eiders *Somateria mollissima* and bearded seals *Erignathus barbatus*, both benthic feeders, would have benefited from walrus exploitation (Fig. 14.8). In the same way, it is likely that pre-historic human interventions in Arctic ecosystems led to alterations of Arctic biodiversity composition and ecosystem functioning (see Meltofte *et al.*, Chapter 1).

Present-day ecosystems have evolved from past conditions and pressures on their various components. Currently, changes in the diversity and in the structure and functionality of Arctic marine ecosystems are taking place at a rapid pace, associated with local/global pressures on these ecosystems, northward shifts in pelagic and benthic assemblages, and new introductions (see previous Section). Here, we present observations of current changes and trends in Arctic marine ecosystems in relation to the stressors described above. However, it is essential to bear in mind that ecosystem responses are complex and cannot be ascribed to a single driver due to the confounding effects of multiple stressors that could be acting in synergy or in opposite directions, and at varying time scales. This is exacerbated in the Arctic where interannual climate variability (See Box 14.4) and rapid climate change combined with intensified anthropogenic pressures may simultaneously affect species (e.g. reproduction, growth), community (e.g. predation, competition) and ecosystems (e.g. type of production, food web interactions).

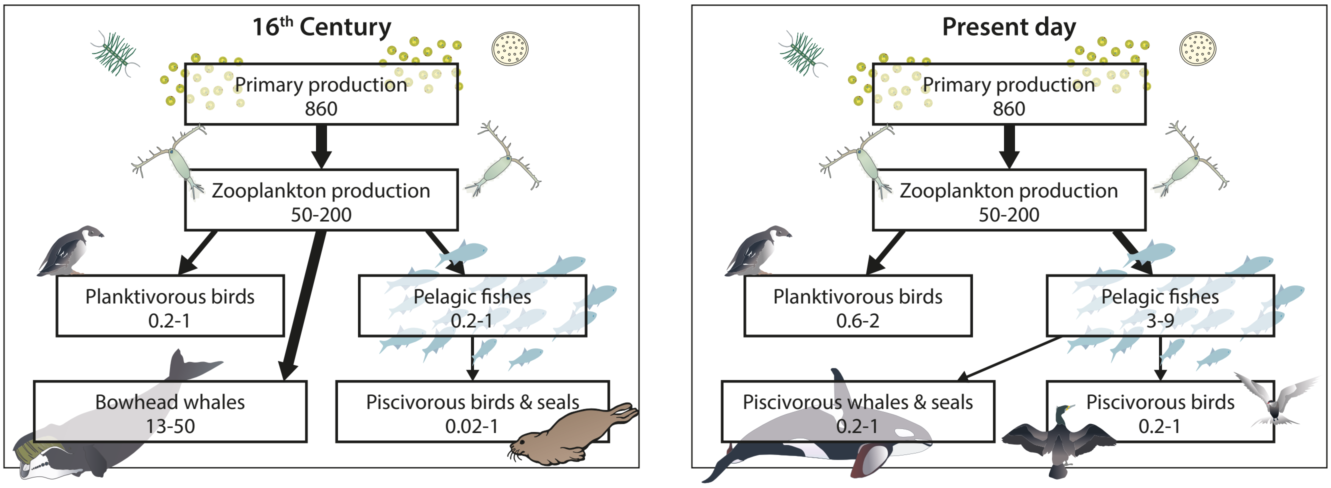
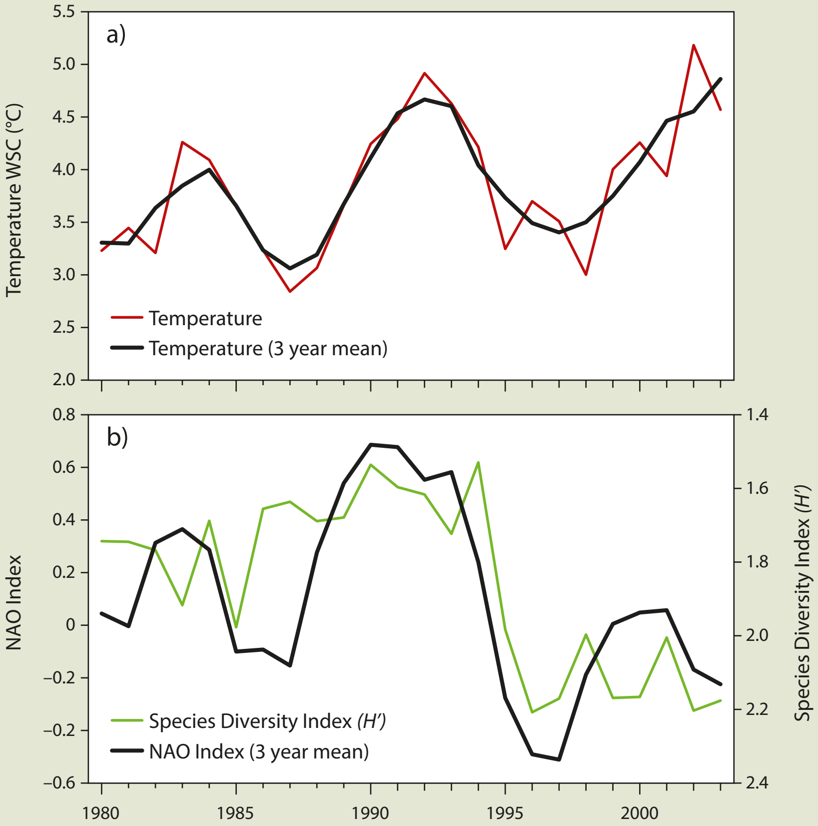


**Figure 14.8.** Schematics of historical and contemporary pelagic coastal food webs off Svalbard, assuming comparable primary and secondary production. Values are consumption in Kcal per $m^2$ per year. Thickness of arrows is relative to consumption values. (Source: Weslawski *et al.* 2000.)

## Box 14.4. How the atmosphere influences Arctic marine ecosystems

The North Atlantic Oscillation (NAO) is an important index of the interannual variability in the atmospheric circulation across the North Atlantic, with low frequency variability on multi-year to decadal time scales. It is associated with changes in temperature and the current regimes of the entire North Atlantic. The NAO index is defined by the co-variability of average atmospheric sea level pressure between the Icelandic Low and the Azores High, the major pressure systems over the North Atlantic. When both are strong (i.e. Icelandic Low lower than normal and Azores High higher than normal), the NAO index is positive and the westerly winds across the Atlantic intensify. A positive NAO phase has been associated with a stronger Atlantic inflow and temperatures higher than normal in the Barents Sea, whereas a negative NAO phase has an opposite effect (reduced Atlantic inflow and lower temperatures) (e.g. Blindheim *et al.* 2000, Ingvaldsen 2005).

The Arctic Oscillation (AO), defined by Thompson & Wallace (1998), is the dominant mode of variability of Northern Hemisphere sea level pressure. Another name for the AO is the Northern Annular Mode (Wallace & Thompson 2001). Changes in the AO impact the pattern and velocity of



**Box 14.4 Figure 1.** a) Mean autumn (August-September) temperature of the West Spitsbergen Current at about 79° N between 100 and 300 m depth. b) Correlation between the NAO Index (3-year mean calculated from September-August) and Shannon-Wiener diversity index (H'). The secondary y-axis scale (species diversity) is inverted. (Source: Beuchel *et al.* 2006.)

### 14.5.2. Observations with respect to climate-associated changes

The decline in sea ice extent directly impacts ice-associated species and food webs, as sea ice serves as habitat for a variety of species, providing feeding and reproduction areas for ice-associated fauna including ice-endemic amphipods, fishes (e.g. polar cod), seals, whales and polar bears (see Kovacs *et al.* 2011b, Vincent *et al.* 2011). On-going changes in sea ice conditions are expected to impact ecosystem biodiversity at various scales, from millimeters to hundreds of kilometers. Changes in sea ice structure directly affect the habitat of viruses, bacteria and protists that are found in abundance in Arctic sea ice and support the sea-ice associated food webs (see Lovejoy, Chapter 11). The rapid melting of ice shelves and associated loss of unique microbial habitats may also constitute an irreversible loss to Arctic ecosystem biodiversity (see Box 14.5).

Changes in sea ice surface conditions (e.g. snow cover, presence and location of ridges) impact the reproduction (e.g. ringed seals) and foraging success (e.g. polar bears) of ice-associated species (summarized in Kovacs *et al.* 2011a). Changes in snow and sea ice conditions also indirectly affect pelagic and benthic communities through changes in stratification, light attenuation and nutrient availability. There is growing evidence of a freshening and warming of surface waters in the Canada Basin, largely attributed to sea ice melt (McPhee *et al.* 2009, Proshutinsky *et al.* 2009). Associated with these physical changes, the community composition of pelagic primary producers is also changing. The abundance of small algae is increasing whereas that of large algae is decreasing as the former have a competitive advantage over the latter (Li *et al.* 2009). If this trend towards a community of smaller cells is sustained, it may lead to reduced biological production at higher trophic levels as the size structure of phytoplankton communities is a strong determinant of trophic pathways and carbon fluxes in marine ecosystems. In addition, changes in the timing of the productive period can have major cascading impacts on Arctic marine food webs since the synchronization of events is a key factor in the transfer of primary producice motion in the Arctic Ocean (Darby *et al.* 2006). Another atmospheric pattern, the Arctic Dipole (AD) anomaly (also referred to as the Arctic Rapid Change circulation pattern; Zhang *et al.* 2008) produces strong meridional winds that export sea ice from the western to the eastern Arctic. The dipole anomaly is considered a key driver of the record low summer sea ice extent observed in 2007 (Wang *et al.* 2009).

In turn, changes in sea ice patterns influence where the ice melts and ice-associated material is released, impacting ecosystem productivity and biodiversity. A study of benthic communities in Kongsfjorden, Svalbard, over the period 1980-2003 has linked changes in benthic community structure to the NAO and its local manifestations via the West Spitsbergen Current (Beuchel *et al.* 2006). Severe changes in the benthic community were observed between 1994 and 1996 coinciding with a shift in NAO from positive to negative mode (Box 14.4 Fig. 1). The change in biodiversity was accompanied by a decline of sea anemones (actinarians) and the appearance of dense carpets of brown algae (Beuchel *et al.* 2006). At higher trophic levels, regime shifts associated with the NAO have shown important effects on circumpolar murre populations, with populations in the North Pacific and NW Atlantic sectors trending in opposite directions from those in the eastern Atlantic (Irons *et al.* 2008; see Box 4.3 in Ganter & Gaston, Chapter 4).

tion to secondary producers and the efficiency of transfer of material through the food web (Michel *et al.* 1996, 2006, Leu *et al.* 2011).

Alternatively, a longer open water period has been linked to increased primary production (Arrigo *et al.* 2008, Pabi *et al.* 2008), and increased wind mixing creates favorable conditions for upwelling of nutrient-rich waters, thereby increasing pelagic (Tremblay *et al.* 2011) and sea ice (Mundy *et al.* 2009) production by large phytoplankton. These large cells are important for energy transfer to higher trophic levels in marine food webs. Since the ability of the Arctic macroalgal community to respond to nutrient input during summer is restricted to a few nitrophilic species (Gordillo *et al.* 2006), more frequent upwelling events associated with extended open water periods may not impact macroalagal communities in the Arctic.

With respect to benthic diversity, the lack of light-attenuating sea-ice cover and reduced ice-scouring

## Box 14.5. Vanishing ice shelves and melting icebergs

Mass balance estimates for the Greenland Ice Sheet indicate an overall loss of ice since the early 1990s. This loss has increased rapidly in recent years, from a yearly average of about 50 Gt between 1995-2000 to about 160 Gt between 2003-2006 (AMAP 2011). The fragmentation and loss of ice sheets and glaciers is expected to continue at an accelerated pace in a warming climate (Mueller *et al.* 2003, AMAP 2011).

The formation and release of ice islands and icebergs are important episodic events that introduce freshwater, micronutrients, dust and other particles to polar marine ecosystems (Arrigo *et al.* 2002, Geibert *et al.* 2010). In August 2010, a 40 m thick, 54 km$^2$ section of ice was released from the Ward Hunt Ice Shelf on Ellesmere Island, Canadian Arctic Archipelago (NASA observations). This ice shelf, estimated to be 3,000 to 5,000 years old, is the oldest sea ice in the Northen Hemisphere (England *et al.* 2008). During the same month, a 250 km$^2$ ice island was released from the Petermann Glacier in N Greenland. This ice island was the largest Arctic iceberg recorded since 1962. Extensive glacier melt and break-off continued in Greenland in 2012, with the release of a 150 km$^2$ section also from the Petermann Glacier. The Petermann Glacier is fed by the Greenland Ice Sheet and is replaced by ice forming upstream. However, ice shelves such as the Ward Hunt Ice Shelf are formed by centuries of accumulated snow and compressed sea ice, and are at risk of vanishing altogether as sections released into the sea are not replaced (England *et al.* 2008). A rare type of ecosystem associated with the Ward Hunt Ice Shelf was an 'epishelf' lake of freshwater that was contained by the ice of the shelf. In 2002, the fracturing of the ice shelf caused almost complete loss (96%) of the localized fresh and brackish water habitats that were known to support unique communities of organisms (Van Hove *et al.* 2001, Mueller *et al.* 2003).

Icebergs can survive for many years in Arctic waters before being exported and melting completely. While present they can impact both benthic and pelagic habitats. Their deep keels scour and carve the ocean floor. Icebergs that become grounded can disrupt local circulation, potentially becoming a physical barrier to oceanographic processes such as advection of nutrients, sea ice drift and the extent/duration of ice cover (Arrigo & van Dijken 2003). Such impacts of icebergs can significantly inhibit primary production (e.g. reductions of 40% observed in the Southern Ocean; Arrigo *et al.* 2002) thereby impacting upper trophic levels including sea birds and marine mammals.

The presence and movement of icebergs alter water column stability through mixing and the release of freshwater associated melt. These can either enhance or disrupt the productivity of the area. In the Southern Ocean, the biomass of primary producers can be > 30% higher in the wake of moving icebergs (Schwarz & Schodlok 2009) leading to increased biodiversity within the vicinity of the icebergs, including the presence of whales (Geibert *et al.* 2010).

will certainly result in new habitats available for seaweed colonization (Müller *et al.* 2009, Weslawski *et al.* 2011). In particular, the rocky Arctic islands off the Russian mainland, as well as the rocky coastlines of Kola Peninsula, Svalbard, Greenland (Baffin Bay and Greenland Sea) and the Canadian Arctic Archipelago, will experience milder environmental conditions and hence may provide new habitats for temperate seaweeds that may outcompete polar species.

Local changes in polar bear distribution, population sizes (e.g. Aars *et al.* 2009), physiological condition (Pertoldi *et al.* 2009), reproductive success and survival (e.g. Parks *et al.* 2006, Stirling 2009, Regehr *et al.* 2010) have been linked to decreases in sea ice cover extent and shorter ice-covered periods in the Arctic. The absence of summer sea ice is also seen as a key factor in the recent hybridization of polar bears and grizzly bears *Ursus arctos*. In 2006 and 2010, two hybrid 'grolar' bears were observed in the western Canadian Arctic. DNA analysis confirmed that the 'grolar' bears were hybrids between polar and grizzly bears, with a second-generation hybrid found in 2010. This indicates that there may be more interbreeding between species that do not typically co-exist, as environmental conditions change in the Arctic.

In northern Hudson Bay, an increase in the duration of the open water period has been associated with a change in the diet of marine birds, with increases in the importance of capelin, sand lance *Ammodytes* sp. and mysid crustaceans and decreases in the importance of polar cod and hyperiid amphipods (Gaston *et al.* 2009, see Fig. 4.6 in Ganter & Gaston, Chapter 4). These changes were simultaneous with an advance of about three weeks in the timing of ice break-up in the region, yet the timing of egg-laying has not advanced to keep pace with changes in ice conditions. This has resulted in lowered recruitment in years when egg-laying is late relative to ice break-up and an overall deterioration in the condition of murre chicks at colony departure (Gaston *et al.* 2009). In parallel with these changes, shifts in top predator species are expected to influence ecosystem structure by increasing competition for food resources among resident mammals (Higdon & Ferguson 2009; see Section 14.5.4).

Overall, the decrease in Arctic sea ice extent can be construed as habitat fragmentation, restraining the distribution and movement of species that use the ice for transportation (e.g. polar bear). However, an increase in first year ice at the expense of multi-year ice may provide increased habitat for some ice-associated species given that changes in the phenology of events (e.g. timing of ice melt) does not compromise key life history functions (e.g. reproduction and rearing). At the same time, the associated increase in open water area and period facilitates migration and movement of some species that avoid the ice. There is evidence that the presence of sea ice in certain areas, considered 'choke points', constrains the distribution of ice-avoiding predators such as killer whales (Higdon & Ferguson 2009). Opening of these 'choke points' with continued sea ice melt may alter the movement and distribution of whales and other 'open water' species, modifying species diversity and trophic interactions in Arctic marine ecosystems (see Section 14.5.4 and Reid *et al.*, Chapter 3).

### 14.5.3. Observations with respect to marine resources exploitation

Commercial fishing is considered a major force influencing ecosystem structure and functioning by altering community composition and species interactions within them. Fisheries impacts are documented in LMEs by using standard indicators including a marine trophic level index and estimates of the primary production required to sustain landings (Sherman & Hempel 2008). However, while these and other ecosystem indicators allow monitoring of trends, causal relationships to explain the observed changes are not yet clearly established due to the complex nature of ecosystem responses.

In W Greenland, Atlantic cod was dominant in the fisheries catch during 1950-1970, therefore the high trophic index shown in Fig. 14.9. From 1970 onward, the decrease in trophic level reflects a shift from Atlantic cod to deep-water shrimp dominance in the ecosystem (see Fig. 6.15 in Christiansen & Reist, Chapter 6). While such a trend implies 'fishing down' of the ecosystem, the shift in community structure and landing composition also coincides with a rapid change in climatic and oceanographic conditions, related to a shift in the NAO (Dickson *et al.* 2000, Buch *et al.* 2004). The drastic decline in Atlantic cod was related to a reduction in recruitment, itself related to low spawning stock biomass and temperature, whereas the growth and recruitment of shrimps would have been favored by low temperatures and reduced predation (Buch *et al.* 2004). This ecosystem shift had tremendous economic impacts as the Greenland export economy, formerly highly dependent on the cod fishery, is now almost entirely dependent on shrimp exploitation (Garcia 2007).

A decline in the mean trophic level index also occurred in E Greenland and around Iceland, somewhat similar to W Greenland. In this case, the cod-dominated fishery shifted to small pelagic fishes, mainly capelin. In the Barents Sea, the mean trophic level declined from the 1950s to the mid 1990s and showed large fluctuations thereafter (Fig. 14.9). These fluctuations are linked to the Barents Sea capelin stock, potentially the largest stock worldwide, which showed large variations and collapsed on three separate occasions over the past three decades (Fig. 14.9). Notably, a significant decline in 1986 led to the complete closure of the capelin fishery from 1994 to 1998. The causes of the large variations and decline in capelin stock have been attributed to multiple stressors including fisheries, climate and ecological interactions among species (see Section 14.5.5.2 and Fig. 1.3 in Meltofte *et al.*, Chapter 1).

With respect to commercial whaling, current observations show population recovery after cessation of activities (Box 14.6), suggesting some degree of reversibility of ecological changes with timely action.

## 14.5.4. Observations with respect to range extensions

Geographical shifts and range extensions are currently taking place in the marine Arctic in response to warming, sea ice decline and changes in water mass distribution (e.g. Wassmann *et al.* 2010).

Major distribution changes have been documented in sub-Arctic waters over the last decade. Major biogeographic changes in the biodiversity of a key zooplankton group, calanoid copepods, have been reported for the North Atlantic (Beaugrand *et al.* 2002a, 2002b, 2009). The observed rates of biogeographical expansion appear to be far greater than those in terrestrial systems, likely due to the fluid nature of the pelagic domain and the relatively short life cycles of these species (Beaugrand *et al.* 2009). Similar northward range extensions have been observed for phytoplankton (Hegseth & Sundfjord 2008), benthic invertebrates (e.g. Sirenko & Gagaev 2007) and fish (e.g. Mueter & Litzow 2008, Mecklenburg *et al.* 2011).

A warming period over the entire northern North Atlantic began during the 1920s and 1930s, with temperatures warmer than normal and enhanced Atlantic inflow in the Barents Sea during the mid-1900s (Drinkwater 2011). Associated with this warm period was a northward range extension of Atlantic cod as far north as W Spitsbergen (Fig. 14.10), with an increase in population around Bear Island that was large enough to re-establish a fishery after almost 40 years of absence. According to Drinkwater (2011), the warm temperature increased cod growth rates which, together with good recruitment, resulted in the largest recorded cod biomass in the Barents Sea. Other colder water species such as capelin and polar cod retreated northward in the Barents Sea, and haddock *Melanogrammus aeglefinus* moved eastward towards Novaya Zemlya. Herring extended their range eastward such that a Russian fishery was established off the Murman coast in the 1930s (Drinkwater 2011). (See also Christiansen & Reist, Chapter 6.)

Broad biogeographical changes of key structural seaweed species are predicted for both hemispheres due to warming of marine coastal systems (Müller *et al.* 2009). The predicted poleward shift of forest kelp seems to be in progress right now as this species has already been recorded in secluded fjords in southern Spitsbergen, Svalbard (Peltikhina 2002, Olsen *et al.* 2004). A geographi-

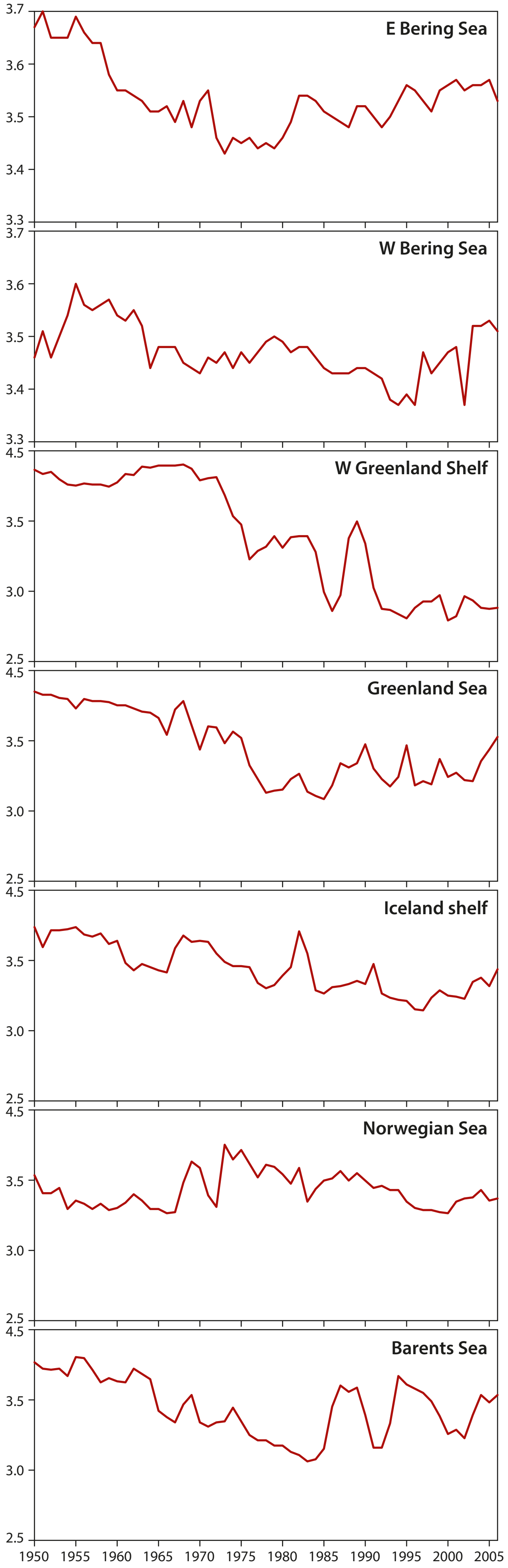
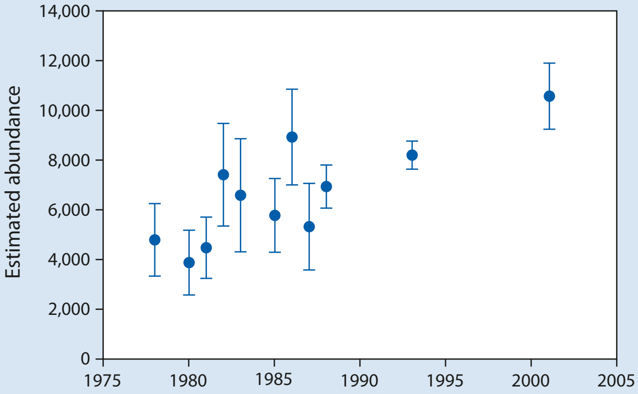


**Figure 14.9.** Mean trophic levels in seven sub-Arctic and Arctic Large Marine Ecosystems. Source: Sherman & Hempel (2008), SeaAroundUs Project (2010).

## Box 14.6. Bowhead whale population recovery

The historical population of bowhead whales in the Beaufort Sea, estimated to number between 10,400 and 23,000, was reduced by commercial whaling to about 3,000 individuals by the early 1900s, when commercial whaling of this species ceased. However, as of 2001 the bowhead whale population had recovered to an estimated 7,700-12,600 individuals, increasing at a rate of 3.4% per year between 1978 and 2001 (Box 14.6 Fig. 1; see also Reid *et al.*, Chapter 3). An increase in bowhead whale sightings in other Arctic regions is also apparent from traditional ecological knowledge:

> *…here is the place [outer Frobisher Bay] where the bowhead whales are now being spotted more frequently practically every summer, it seems that the bowhead whales are increasing in numbers every year here.*
>
> (Josie Papatsie in NWMB 2000).



**Box 14.6 Figure 1.** Abundance estimates for the western Arctic bowhead whale stock in the Beaufort Sea, 1978 to 2001. Vertical bars are standard deviations. (Source: Zeh & Punt 2005.)

cal shift of seaweed species in response to temperature fluctuations has been documented in the past (Hiscock *et al.* 2004, Hawkins *et al.* 2008). The interplay of photoperiodic responses, temperature and other interactions will not only change geographic distribution patterns but may also influence seaweed phenology (Wiencke *et al.* 2009). Similar complex interactions between environmental forcings and the responses of individual species and the interactions among species are expected to occur at multiple trophic levels, impacting Arctic ecosystem architecture and biodiversity.

Increases in several marine bird species have been reported in Arctic areas. In Hudson Bay and Hudson Strait, both razorbills *Alca torda* and great black-backed gulls *Larus marinus*, typically sub-Arctic species, have increased over the past two decades (Gaston & Woo 2008). In Spitsbergen, both great skua *Stercorarius skua* and great black-backed gull are expanding their range (Anker-Nilssen *et al.* 2000, H. Strøm pers. com.), while in the Beaufort Sea horned puffins *Fratercula corniculata* have appeared and established themselves as breeders (Divoky 1982). The first sighthings of breeding pairs of northern gannets *Morus bassanus* in northern Svalbard, 500 km north of their normal range, also speaks to impacts of a warming climate (Norwegian Polar Institute 2011). In Hudson Bay, the first documented sighting of killer whales about 50 years ago and their significant increase in recent years have been linked to reduced sea

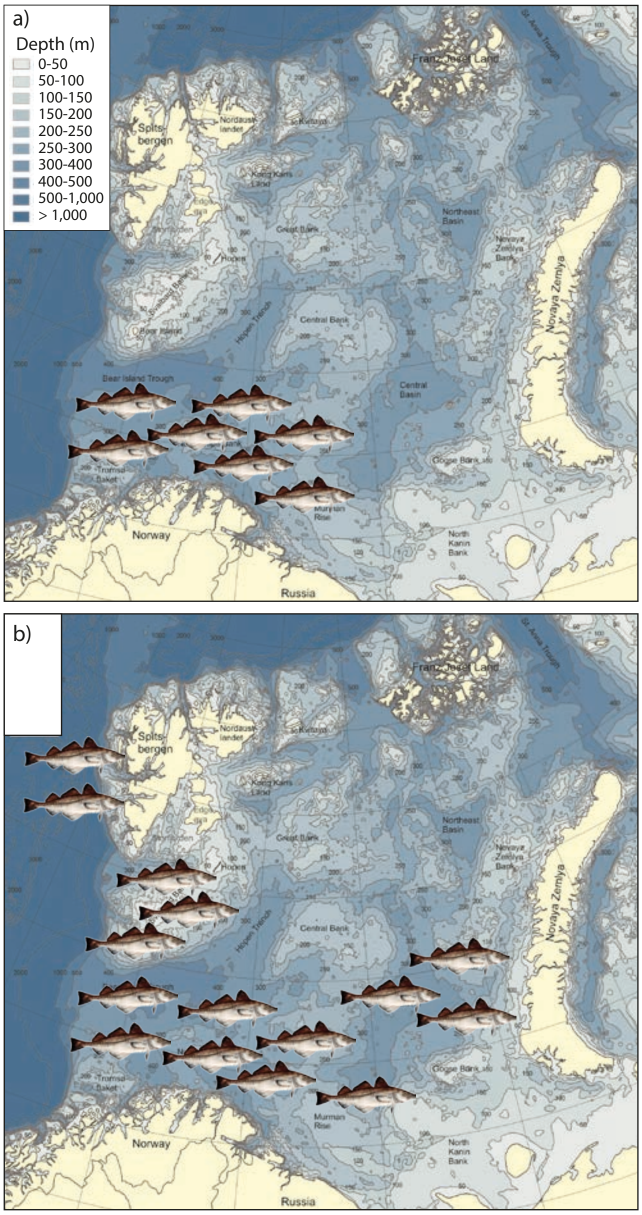


**Figure 14.10.** Schematic distribution of NE Atlantic cod *Gadus morhua* in the Barents Sea
a) prior to and b) during the 20th century warm period
(source: Drinkwater 2011).

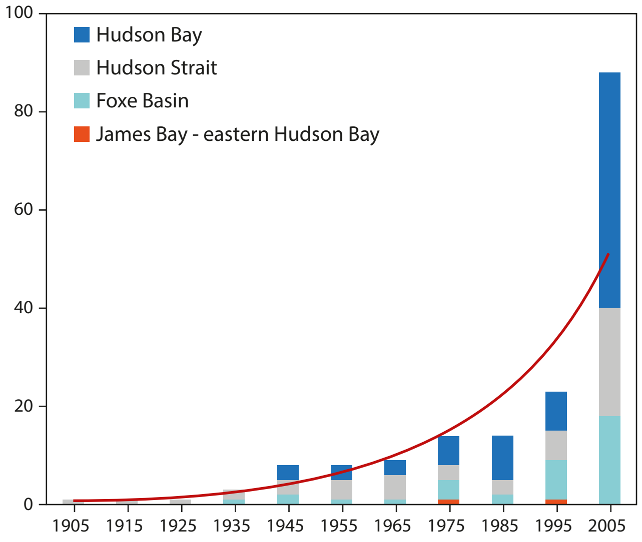


**Figure 14.11.** Trend in killer whale *Orcinus orca* observations in the Hudson Bay region, Canada (sources: Hidgon & Ferguson 2009 and Higdon *et al.* 2011).

ice cover extent (Fig. 14.11). Here, it is the change in sea ice conditions, associated with increased accessibility to open water areas, that is determinant for the range extension observed. Cascading effects on the ecosystem are expected as killer whales compete with resident marine mammals for food resources.

## 14.5.5. Case studies

### 14.5.5.1. Ecosystem regime shifts in the Bering Sea

In the past three decades, major changes have occurred in the marine ecosystem of the southeastern Bering Sea (e.g. Vance *et al.* 1998, Hunt *et al.* 2002, 2011, Schumacher *et al.* 2003). Persistent changes in the atmosphere and upper ocean fields along with corresponding shifts in the abundance and species of zooplankton and fish indicate the occurrence of climate regime shifts in 1926, 1945, 1976 and 1998 in the northeastern Pacific (Peterson & Schwing 2003). The marine ecosystem of the Bering Sea has been shown to respond to the large-scale climate regime shifts of the Pacific Decadal Oscillation (PDO), as well as the regional Aleutian Low Pressure System and Arctic Oscillation (AO), smaller-scale episodic weather events, rising global temperatures and declining sea ice (Bond & Overland 2005, Grebmeier *et al.* 2006a). The climatology and oceanography of the southeastern Bering Sea reveal a change from an ecosystem dominated by Arctic species for most of the 20th century, with a gradual replacement by sub-Arctic species in the last 30 years (Wang *et al.* 2006).

The regime shifts have impacted all levels of the Bering Sea food web and have had significant economic impacts due to changes in the abundance of salmon, crab and groundfish (NRC 1996, Schumacher *et al.* 2003). At the base of the food web, the timing and location of primary production has shifted between warm and cold years. During cold years (e.g. early 1970s), when sea-ice remains until mid-March or later, ice edge phytoplankton blooms are observed in early spring (Alexander & Niebauer 1981, Hunt *et al.* 2002) contributing significantly to total annual production. With a shift to warmer waters (e.g. > 3 °C), when sea ice is absent or retreats before mid-March, maximum primary productivity and phytoplankton biomass occurs during an open-water bloom in May or June (Whitledge *et al.* 1986, Hunt *et al.* 2002). Despite these changes in primary production regimes, there has been no significant change in total annual net primary production (NPP) over the past four decades in the southeastern Bering Sea (Jin *et al.* 2009). However, there is evidence of changes in the fate of primary producers, with more primary production reaching the benthos during cold years and more spring primary production channeled into pelagic components during warm years.

Zooplankton and fishes do not respond as quickly as primary producers to climate-associated changes. However their responses have been conspicuous, impacting predator-prey interactions and energy flow within the Bering Sea ecosystem. It was assumed that zooplankton, specifically copepods, would grow more rapidly and would graze more primary production in warm years. However, new data suggest that this assumption is incorrect. Key species such as the lipid-rich copepod *Calanus marshallae* are less abundant in warmer years, and there is no change in the abundance or biomass of small neritic species (e.g. *Acartia* spp.) between the different temperature regimes (Hunt *et al.* 2010). Understanding the response of zooplankton to regime shifts is essential, since key copepod species such as *C. marshallae*, along with euphausiids, constitute up to 70% of juvenile and adult pollock diets and are also important in the diets of juvenile salmon entering the Bering Sea (Aydin *et al.* 2007, Moss *et al.* 2009).

Regardless of the lower availability of *C. marshallae* during warm years, there is rapid growth of the small (age-0) pollock that feed during spring and early summer. Yet, increased predation by juvenile salmon, larger pollock and other fish species on age-0 pollock, due to the scarcity of lipid-rich copepods and euphausids, leads to poor survival of the small pollock (Moss *et al.* 2009, Hunt *et al.* 2011). Additionally, the reduction in the availability of *C. marshallae* and euphausiids in warm years may impact the survival of age-0 pollock directly due to energetic constraints. Recent evidence suggests that the small pollock have near or below the amount of stored lipids that they require to survive winter in years with early ice retreat and warm spring and summers (Hunt *et al.* 2011). Therefore, while the availability of lipid-rich copepods is crucial for the production of strong pollock year classes, other factors such as predation impact their survival and ultimately the pollock stocks across regime shifts (Fig. 14.12).

Pollock, specifically walleye pollock *Gadus chalcogrammus*, represent the largest major fishery in the eastern Ber-

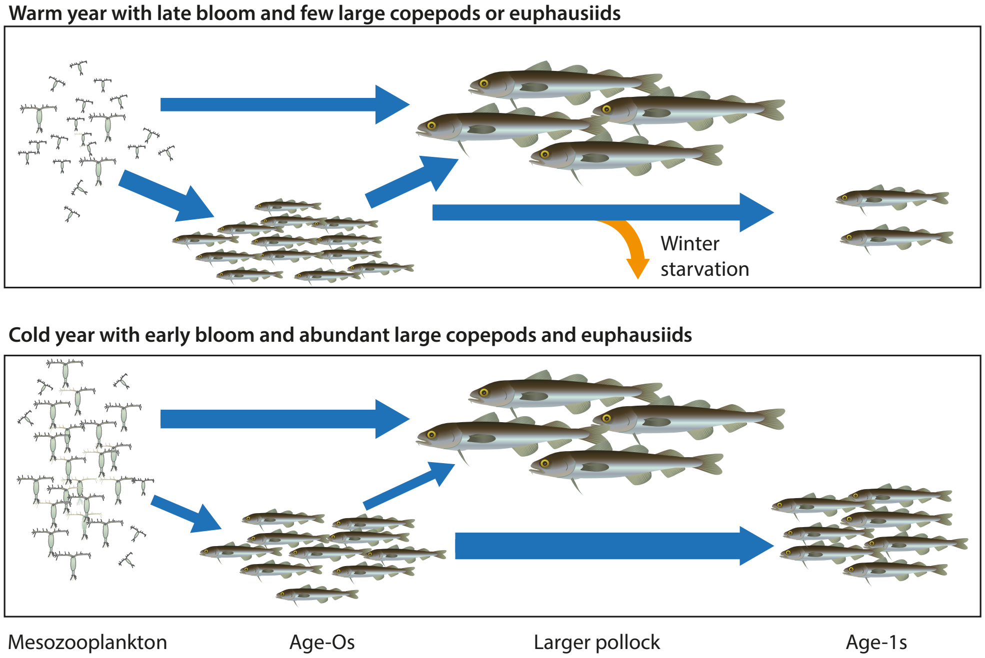


**Figure 14.12.** Differences in trophic pathways based on availability of the copepod *C. marshallae* and the euphausiid *T. raschii* on the southeastern Bering Sea shelf. When these species are not available, predation and cannibalism of age-0 pollock increases, as does overwinter mortality of age-0 pollock due to insufficient energy stores. In contrast, when the zooplankton are abundant, cannibalism and predation decrease and energy stores may increase resulting in stronger recruitment of age-1 pollock. (Source: Hunt *et al.* 2011.)

ing Sea. Increases in water temperatures were previously expected to benefit the fishery (Hollowed *et al.* 2001, Mueter *et al.* 2006). However, based on the above observations of pollock survival in regime shifts, a recent model indicates that pollock recruitment could decline 32-58% by 2040-2050 (Mueter *et al.* 2011). Extended periods of warm conditions leading to a re-occurrence of weak year classes may make fishing pressure unsustainable relative to periods with strong year classes (Hunt *et al.* 2011). These temporal considerations for fisheries management should also be coupled with considerations of shifts in spatial distributions of fishes. For example, increasing bottom temperatures may affect the distribution of fish, with warm temperatures allowing many groundfish species to extend their distribution range northward and eastward in the Bering Sea (Hunt *et al.* 2008).

### 14.5.5.2. Complex ecological interactions in the Barents Sea

The Barents Sea is an ecologically productive region with economically important commercial fisheries. It holds some of the largest fish stocks in the world including Atlantic cod, polar cod, capelin and Atlantic herring (O'Brien *et al.* 2004). These species play a critical role in the ecosystem structure of the Barents Sea. To model and predict changes in the Barents Sea ecosystem, interactions between climate change and other factors influencing species interactions must be taken into consideration. In the Barents Sea, fishing and climate change are the main stressors together with offshore oil and gas exploration, increasing marine traffic, heavy metal and organic contaminants as well as the potential for radioactive pollution. These stressors influence ecosystem food webs and habitats.

Trends and variability in the Barents Sea ecosystem are relatively well documented. Over the last few decades, fishery catches and their composition have varied significantly (see Section 14.4.2). The capelin stock has shown large variations, collapsing on three separate occasions with a > 90% reduction in stock size followed by rapid recoveries (ICES 2006, 2009, Sherman & Hempel 2008). The cause of the large variations and decline in the capelin stock have been attributed to complex interactions of multiple stressors including fisheries, climate and ecological interactions amongst species (Stenseth *et al.* 2002, Hjermann *et al.* 2004, Lindstrom *et al.* 2009).

Among the different fish species undergoing changes in their stocks, there exist strong trophic (i.e. predator-prey) interactions involving the size and distribution of different year classes (O'Brien *et al.* 2004, Lindstrom *et al.* 2009). Consequently, the impact of stressors on one species is transferable to other fish, mammals and bird species via food web interactions. In the Barents Sea, capelin are key prey items for Atlantic cod (e.g. Bogetveit *et al.* 2008) and the common murre *Uria aalge* (Bogstad *et al.* 2000) and are the most effective grazers on zooplankton in the central and northern part of the ecosystem (Gjøsæter 1998). The migration of the capelin also transfers large amounts of energy from the northern portion of the sea to other species found only within the southern and coastal regions (Hjermann *et al.* 2010). Consequently, the capelin collapses had repercussions both downward and upward in the food web (Gjøsæter *et al.* 2009). Reduced capelin abundance led to decreased predation and increased zooplankton biomass while impacting capelin's predators in various ways. Decreased growth and increased cannibalism among cod, increased mortality and recruitment failures leading to the loss of over 200,000 pairs of common murres, and food shortage and coastal invasions of harp seals *Phoca groenlandica* were all associated with the first capelin stock collapse (Gjøsæter *et al.* 2009). Ecosystem impacts were different in later collapses, likely due to increased availability of alternative food for predators (see Fig. 1.3 in Meltofte *et al.*, Chapter 1). This highlights the importance of trophic interactions and the role of functional groups in maintaining trophic pathways and food web transfers in Arctic marine ecosystems.

Multiple stressors are also impacting habitat characteristics in the Barents Sea. Of key importance are changes in water temperature and sea-ice dynamics, including the location of the marginal ice zone (MIZ). The Barents Sea has experienced warming (e.g. 1900-1920s, 1970-1980s) and cooling (e.g. 1930-1950s) periods over the last century (Ingvaldsen & Loeng 2009). The most recent warming trend continues with water temperatures increasing by 1.5 °C since the late 1970s/early 1980s (Skagseth *et al.* 2008). The currently observed warming appears to be driven by the advection of Atlantic water into the Barents Sea, which is now warmer and more saline due to increased heating and evaporation in the sub-tropics (Drinkwater *et al.* 2009). Changes in the advection of Atlantic water impact not only water temperatures but also the position of the Polar Front and the MIZ (Loeng 1991, Ellingsen *et al.* 2008; see Fig. 8.9 in Josefson & Mokievsky, Chapter 8). The Polar Front, which separates the Polar and Atlantic waters in the Barents Sea, and the MIZ are biologically productive habitats (Sakshaug & Skjoldal 1989, Roderfeld *et al.* 2008) and fertile feeding grounds for fishes such as capelin which migrate to the MIZ during summer (Hassel *et al.*1991), and immature capelin overwintering in the region of the Polar Front (Loeng & Drinkwater 2007).

Therefore, changes in habitat characteristics such as water temperature and the distribution of water masses and the fronts separating them, will impact species distribution, reproduction and ecological interactions among species. A recent model evaluating ecosystem changes in response to warming scenarios shows differential responses of zooplankton species, with a decrease in the production of Arctic *Calanus glacialis* and an increase in the production of Atlantic *C. finmarchicus* in a warmer climate (Slagstad *et al.* 2011). Past observations have shown enhanced recruitment and a northward shift in spawning for fishes during warming periods in the Barents Sea. Such trends are occurring again for fishes such as capelin and cod (Sundby & Nakken 2008, Drinkwater 2011; also see Section 14.5.4) as well as for invertebrate species. Krill biomass has increased during the last decade in response to increasing temperatures, despite heavy predation from capelin over the same time period (Eriksen & Dalpadado 2011).

Decreasing sea ice cover and the northern retreat of the MIZ is also impacting the Barents Sea ecosystem. Model results indicate that the MIZ will be displaced farther offshore in the future (Ellingsen *et al.* 2008), possibly precluding its tight association with species such as capelin, which requires shallow (< 100 m) spawning habitats. Therefore, while model simulations indicate that warming will provide more suitable habitat for temperature-sensitive fish species such as the capelin, their potential use of the newly available habitat will ultimately depend on compounded effects from exploitation, predation and competition as well as mixed factors affecting the biology and life history of the species (Roderfeld *et al.* 2008).

#### 14.5.5.3. Changes in the structure and function of the W Greenland pelagic ecosystem

Disko Bay, W Greeland, has been the site of Arctic research since 1906. Since 1992, the seasonal plankton community structure, succession and production at a 300 m deep station off Godhavn/Qeqertarsuaq has been investigated (Levinsen *et al.* 2000, Madsen *et al.* 2001, 2008a, 2008b). Disko Bay is a very productive area and is very important for commercial and recreational fishing and hunting. The bay is located at the outlet of Jakobshavn Isbræ, the most productive glacier in the northern hemisphere. Icebergs calved from the glacier float down the fjord and lie stuck on the bottom of its shallower mouth until they are broken up by the force of the icebergs behind them.

Glacier ice production and sea ice from Disko Bay substantially influence the initiation of the productive cycle of the plankton community. The intense spring phytoplankton bloom starts as the sea ice breaks up, allowing light to enter the water column, and quickly depletes surface water nitrate concentrations. The spring phytoplankton production provides a major source of nutrition for secondary producers (e.g. calanoid copepods) and is thus an essential contributor to marine food webs. Since reproduction is one of the most nutritionally demanding stages of the life cycle in *Calanus* spp., reproductive success for these copepods depends on synchronization with the phytoplankton bloom (Fig. 14.13; Madsen *et al.* 2008b) and subsequent replenishment of their lipid stores (Lee *et al.* 2006).

Traditionally, pelagic research has focused on bloom dynamics and transfers to large *Calanus* copepods. Consequently, the pelagic food web is typically modeled as a simple food chain from nutrients via large phytoplankton and copepods to upper trophic levels, whereas microbial processes are described as a simple degradation rate of detritus. However, the small species and stages of zooplankton and the diverse microbial community play a key role in determining the amount of nutrient and organic matter that is kept in the euphotic zone after the spring bloom. Studies on the succession and composition of the zooplankton community have shown that small copepods are present in the water column year round and dominate from late summer and throughout winter (Madsen *et al.* 2008a). Another group of zooplankton, the protozooplankton (ciliates and heterotrophic dinoflagellates), increases in abundance in response to reduced predation by *Calanus* spp. when the latter recede from the surface layer (Fig. 14.13). After midsummer, protozooplankton are the dominant grazer on the phytoplankton community (e.g. Levinsen & Nielsen 2002).

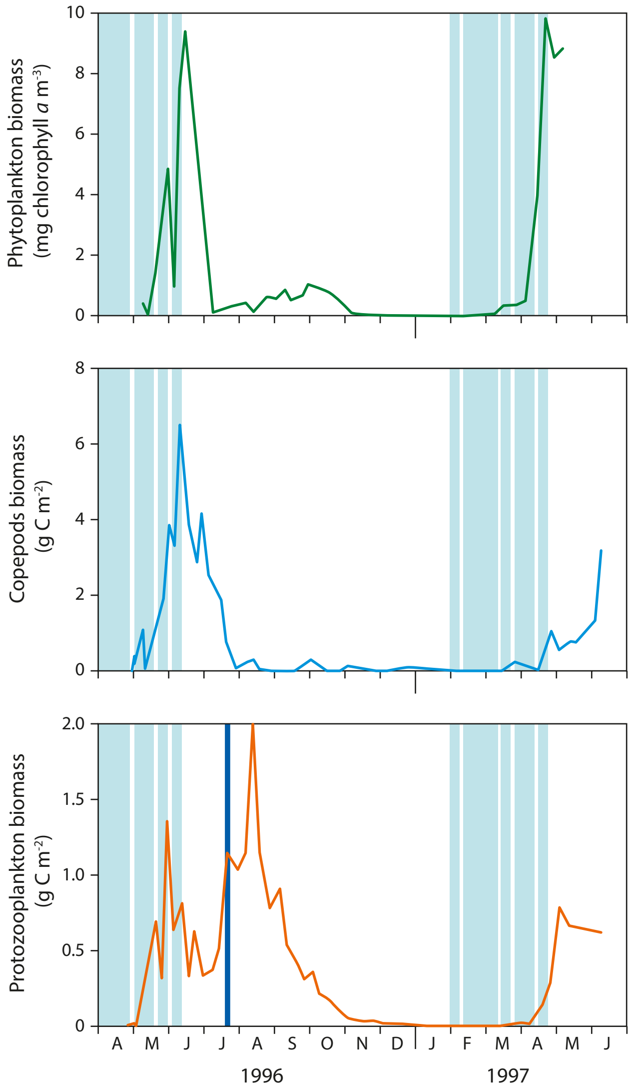


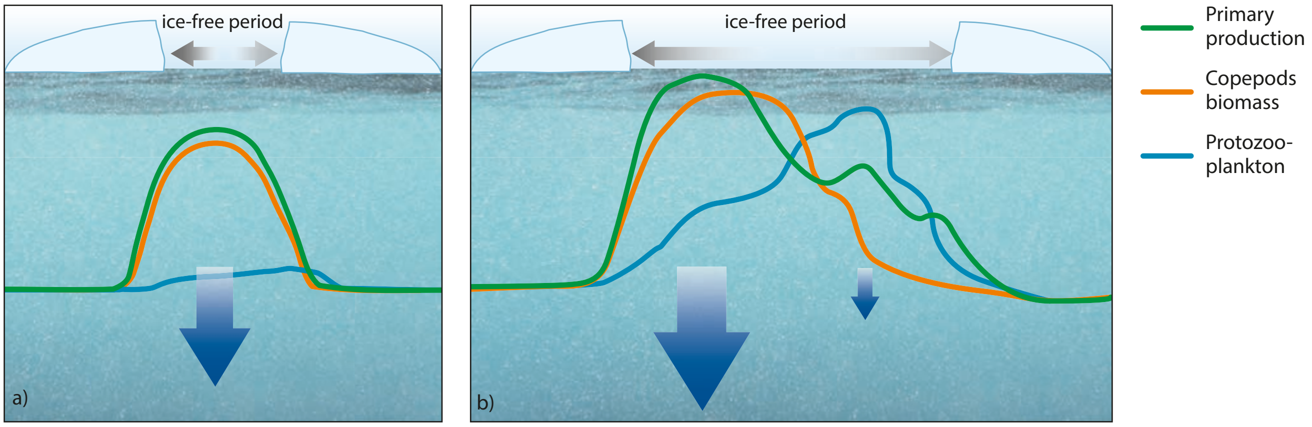
**Figure 14.13.** Seasonal succession of ice cover, phytoplankton, copepods and protozooplankton (ciliates and dinoflagellates) in Disko Bay, W Greenland, 1996-1997. Sea ice cover is represented in light blue. The vertical dark blue line indicates the time when the bulk of *Calanus* spp. biomass leaves the surface layer giving room for an additional peak in protozooplankton biomass. (Modified from Madsen *et al.* 2001 and Levinsen *et al.* 2000).

During the last decades, the open water period has extended significantly in Disko Bay. Sea ice coverage has decreased by 50% while sea ice breakup (Hansen *et al.* 2006) and the spring bloom have occurred earlier. It is unknown whether *Calanus* spp. can synchronize their ascent after winter hibernation to forage upon the earlier phytoplanton bloom (Hansen *et al.* 2003). A mismatch between these events will result in insufficient food quality and thus low reproductive success for the copepods (Madsen *et al.* 2001, 2008b, Hansen *et al.* 2003), thereby reducing the large reservoir of lipids accumulated within successful copepod populations (Fig. 14.14). Any reduction of this key lipid resource will impact the transfer of lipids through the rest of the food web.

Disko Bay is roughly the northern boundary for the reproduction of the Atlantic *Calanus finmarchicus* and the southern boundary for *C. glacialis* (Madsen *et al.* 2001). The two *Calanus* species differ in their life cycle, reproduction strategy and lipid content and may therefore respond differently to climate change. *C. glacialis* initiates spawning prior to the spring bloom with gonad maturation and egg production fueled by internal lipid reserves, most likely an adaptation to the unpredictable food conditions in the Arctic environment (Conover & Huntley 1991, Falk-Petersen *et al.* 2009). *C. finmarchicus* on the other hand, is generally dependent on foraging in order to complete gonad maturation and initiate spawning due to smaller lipid reserves (Plourde & Runge 1993).

Major changes in the *Calanus* community have been observed along W Greenland over the last decades. In the early 1990s, the three *Calanus* species (*C. finmarchicus, C. glacialis* and *C. hyperboreus*) each contributed one third of the copepod biomass in Disko bay (Madsen *et al.* 2001). However, recent investigations show that the Atlantic *C. finmarchicus* now contributes 75% while the lipid-rich Arctic species, *C. glacialis* and *C. hyperboreus*, contribute the rest (Madsen *et al.* 2008b), indicating a future trend towards a much less lipid-rich food web.

**Figure 14.14.** Conceptual model of seasonal plankton succession in W Greenland in a) current and b) future warming conditions. Blue arrows indicate sedimentation of organic material. Under warming conditions (b), an increase in primary production and in the flux of organic material to the benthos and the protozooplankton community is expected. (Adapted from Rysgaard & Glud 2007).



## 14.6. CONCLUSIONS AND RECOMMENDATIONS

### 14.6.1. Vulnerabilities, adaptation and looking forward

As primary production fuels marine food webs through its transfer to pelagic and benthic organisms, regional increases in primary production may be expected to augment the production of fish and shellfish species, some of which have commercial value. Recent increases in primary production associated with changes in sea ice cover on two geographically opposed shelves, the Beaufort and Laptev shelves, have been linked to observed/modeled increases in the sedimentation of organic material (Lalande *et al.* 2009, Lavoie *et al.* 2009). In addition, studies from Arctic areas (Svalbard) suggest that benthic biota respond to fluctuations in regional climate patterns (Beuchel *et al.* 2006). Enhanced environmental forcing leading to warmer winters with less sea ice, earlier onset of melting and increased precipitation in Kongsfjorden during the decade 1993-2004 (Svendsen *et al.* 2002) may have benefited the brown algae *Desmarestia* sp. due to the increased availability of light and nutrients (Beuchel & Gulliksen 2008). These results point to changes in marine ecosystem architecture and biodiversity on Arctic shelves, where sea ice cover is in a state of transition.

At the same time, recent studies indicate that the increased freshwater content in the Arctic Ocean, through the effect of stratification on plankton community structure (Li *et al.* 2009), decreases the efficiency of transfer of organic material in Arctic marine food webs (Kirchman *et al.* 2009, Cai *et al.* 2010). Therefore, an increase in overall production in the Arctic Ocean may not necessarily lead to more abundant harvestable species, as the composition of communities largely determines the fate of material in marine systems. Recent modelling also highlights the regional character of ecosystem responses to climatic forcing (Slagstad *et al.* 2011).

The response of Arctic marine ecosystems to on-going changes depends on complex interactions between community structure, trophic interactions, species-specific adaptation and fitness in regard to environmental conditions, superimposed upon anthropogenic stressors that often have a strong local influence. The cumulative effects of the thinning of the ice pack, its enhanced export in relation to atmospheric circulation patterns, and warmer ocean temperatures may continue to alter Arctic sea ice and associated ecosystems dramatically. How these and other emergent environmental and anthropogenic forcings will affect ecosystem biodiversity in the marine Arctic, and in downstream marine systems, is unknown.

Patterns of changing diversity will likely depend on regional characteristics and habitat types, but also on the connectivity of ocean areas with boreal/southern regions. In areas connected to boreal waters, increases in advection can result in the transport of more sub-Arctic species northward. In regions isolated from advection of boreal waters, such as the Canadian Arctic Archipelago, changes in biodiversity may be slower and mainly influenced by local changes. Trans-Arctic migrations from the Pacific to the Atlantic Ocean are likely to occur increasingly, as Arctic sea ice continues to melt and could cause restructuring of marine food webs. The presence of the Pacific diatom *Neodenticula seminae* in the North Atlantic Ocean in the late 1990s after > 800,000 years of absence, was attributed to increased transport of Pacific waters through the Canadian Arctic Archipelago (Reid *et al.* 2007). Such trans-Arctic expansions are likely to continue, reflecting the influence of the Arctic on global marine biodiversity.

Some unique habitats, species and elements of Arctic marine ecosystems are particularly vulnerable to ongoing changes. The unique habitats associated with Arctic ice shelves that have evolved over thousands of years are eroding and may be irrevocably lost in the current and predicted future climate. Multi-year ice and its associated habitats are at risk of vanishing, with major but largely unknown direct and indirect effects on Arctic marine ecosystem architecture. Ice-associated biodiversity is at risk, with species such as the polar bear exemplifying climate-related impacts on Arctic marine biodiversity.

As changes are occurring in the Arctic, marine species and Arctic residents need to adapt. Hence, much local human transport that hitherto has taken place over ice may now use ships and boats for most of the year, and hunting techniques developed for hunting on ice may be replaced by open water hunting methods. Traditional ways may have to evolve, as expressed by this Inuit hunter:

> » *A buddy of mine is into making little sleds out of aluminum, which you can use as a little kayak or boat. If you're out on the ice and you have to cross an open lead you can use that. It's one of the things that can help. I'm going to get one of those. It's combined as a little sleigh and, if you have to, you can use it as a boat. That's one way I can adapt.*
>
> (ICC 2008).

Species with more plasticity are likely to better adapt to a variable and changing environment than species with narrow tolerances and strict physiology or life history. For example, copepods and krill in the Barents Sea MIZ show marked trophic plasticity, shifting from herbivory during the bloom to omnivory when fresh material is less abundant. Predator fishes such as Atlantic cod also show high feeding plasticity, shifting their prey from fishes to zooplankton in response to changes in abundance. Such flexibility in feeding strategies may provide an advantage in highly variable environments such as the MIZ (Tamelander *et al.* 2008). Phenotypic plasticity is also expected to dominate responses of marine mammals to climate change in the short term (Gilg *et al.* 2012). Accordingly, biodiversity can offer functional redundancy and increase the resilience of marine systems to multiple stressors. However, this resilience ultimately depends on the response of each species to individual and combined stressors and the resulting trophic interactions.

Since the Arctic is at the northern limit of distribution of many species, northward range extensions due to a warming climate are likely to shift the balance of species as the sub-Arctic biome takes over the present Arctic and true Arctic species are pushed northwards or go extinct. Such changes, as exemplified by shifts in top predator species in Hudson Bay (i.e. killer whales *versus* polar bears, see Section 14.5.4), will affect ecosystem functioning and transfer pathways. In addition, extensive alterations in the physical and biogeochemical structure of Arctic marine ecosystems are currently taking place, with unknown consequences for these ecosystems and the species that inhabit them. We cannot predict the tradeoffs between the potential loss of unique ecosystems such as ice shelves and the introduction of new species via northwards range extensions and modifications in habitats.

## 14.6.2. Knowledge gaps and challenges

One of the greatest impediments to understanding the ongoing changes in the biodiversity of Arctic marine ecosystems is the fragmented nature of much of the existing knowledge and the lack of consistent and regular long-term monitoring programs in most Arctic marine regions, including unique or vulnerable ecosystems. A commitment to long-term studies is essential in this regard, and the establishment of the Arctic Marine Biodiversity Monitoring Plan supported by CAFF (Gill *et al.* 2011) is an important step towards this goal.

The effects of disturbances and stressors on Arctic marine biodiversity are not well understood. The lack of baseline information in many areas, the wide range of ecosystems and the impact of cumulative effects make it difficult to predict the direction of changes. The multiple stressors currently affecting Arctic marine ecosystems operate simultaneously at various temporal and spatial scales, emphasizing the need for local and concerted biodiversity assessment and monitoring. There is also a need to develop indicators that properly reflect the unique characteristics of Arctic marine ecosystems. For example, habitat fragmentation, used as a global biodiversity indicator, could be characterized in the marine Arctic using a variety or combination of indicators including sea ice extent and water mass distribution indices. These physical/chemical indicators could then serve as structuring elements upon which to monitor associated ecosystem biodiversity trends. Shifts in ecosystem structure, species interactions and trophic pathways need to be understood in the context of short- and long-term trends, in order to develop management strategies to maintain the diversity and sustainability of Arctic marine ecosystems. To this effect, it is essential to include biological elements in monitoring programs for the marine Arctic.

To gain new knowledge and make sensible projections about climate impacts on carbon dynamics and sequestering in Arctic marine ecosystems, key organisms from the base of marine food webs need to be considered, parameterized and included in research and modeling efforts. We also need to better understand the ecophysiology of key species to be able to better parameterize bulk processes and rates.

For example, the mismatch of formerly synchronized reproductive events and the impact of altered food quality for herbivores under climate warming are not fully understood. Similarly, the effects of ocean acidification on benthic and planktonic communities are in general poorly understood. Therefore, we need to gain knowledge on the responses of individual species and communities to elevated $CO_2$ and on underlying mechanisms and possible acclimation processes. Furthermore, we need to study the interactive effects with other environmental variables in order to predict the consequences for Arctic marine ecosystems. Much can be learned from studying and comparing spatial variation in the present-day pelagic ecosystems along climatic, latitudinal or vertical gradients, and in linking the present with past.

We still have a limited inventory and understanding of the current status of Arctic marine biodiversity, and particularly so for the small microbial communities and benthic invertebrates. There is still much to learn about the biodiversity of extreme habitats and organisms in the Arctic. For example, there is recent evidence of the widespread occurrence of cold seeps in the marine Arctic, but the organisms inhabiting these unique habitats are poorly described. Similarly, unique habitats associated with sea ice and ice shelves are poorly understood and their biodiversity is largely unknown. This special biodiversity in the Arctic presents opportunities for advancements in biotechnology, medical research and even the search for life on other planets. Deep basins of the Arctic Ocean, which were largely inaccessible, are becoming ice-free in summer, bringing new opportunities for research and exploration. As one of the last frontiers on Earth, the marine Arctic still holds many discoveries with respect to the biodiversity of its ecosystems and the species that inhabit them.

## 14.6.3. Key points and recommended actions

The marine Arctic spans a wide range of environmental conditions including extremes in temperature, salinity, light conditions and the presence (or absence) of sea ice, leading to diverse Arctic marine ecosystems. These ecosystems are experiencing rapid changes in their chemical, physical and biological characteristics together with unprecedented socio-economic pressures. Changes in the distribution and abundance of key species and cascading effects on species interactions and the structure and functionality of marine food webs are already observed.

Range extensions are taking place throughout the Arctic, with a northward expansion of sub-Arctic species and a narrowing of Arctic habitats that have existed over millions of years such as multi-year ice and ice shelves. Under current climate scenarios, the loss of these unique ecosystems could be irreversible.

Arctic marine ecosystems are influenced by large-scale processes and their connectivity to the Pacific and Atlantic Oceans. However, the strong regionality in physico-chemical conditions and in observed trends and their drivers precludes generalization of ecosystem responses to current and predicted environmental changes.

- With continued warming and sea ice decline, measures should be put in place to monitor areas of particular biological significance and uniqueness in support of preservation and protection measures. One such area is N Greenland and the northeastern Canadian Arctic Archipelago, predicted to be the last refuge where multiyear ice and its associated species will persist.
- Establishing a network of long-term biological observatories of marine ecosystems across the Arctic is highly recommended. It is essential that biological communities and ecosystem processes are characterized in conjunction with physico-chemical observations as part of monitoring activities in the Arctic.
- Pan-Arctic coordination of research and monitoring activities, using standardized methods in Arctic oceanography and taking advantage of new technologies, is encouraged in order to document and forecast trends in Arctic marine ecosystem biodiversity.
- Key species at all trophic levels and ecological processes that best allow characterization of marine food webs should be identified and included in future monitoring programs across the Arctic.
- Concerted international efforts and associated national funding programs should be dedicated to better understanding changes in the functioning of Arctic marine ecosystems, including process studies to relate these changes to individual and multiple stressors.

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*Protostrongylus stilesi*, a lung nematode typical in Dall's sheep *Ovis dalli* from the Brooks Range and Alaska Range of the western North American Arctic, and in muskoxen *Ovibos moschatus* in the Brooks Range and Arctic Coastal Plain of Alaska and Yukon Territories, Canada. Shown is the tail end of an adult male with characteristic copulatory structures which are important in diagnosis of these miniscule parasites. Photo: E.P. Hoberg.

*Chapter 15*

# Parasites

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## Contents

> » **I've seen that in caribou. Just a couple of years ago, every slice through it, you'd see about 50 little white round things. We were wondering what that was, so we checked it out, and it was a tapeworm. The whole body was completely filled with tapeworms. Yeah. It's unbelievable how they could actually still move and run and their whole body just completely filled with tapeworms.**
>
> Village elder, Sachs Harbour, Canada, as related to S.J. Kutz.

> » **He's saying that when we go harvesting caribou, moose, whatever, when we're skinning them, we really watch out for all these things. The insides, and that yellow stuff they're talking about; it's like a doctor looking at things. Like when you take the stomach out, you always look on the inside. You look at the liver; you look in the flesh. Like when they bring the meat home and when the women make dried meat, sometimes they find those little white like beans in the meat. That's what we eat, so when we skin something we have to make sure to look at everything – the heart, the lungs, the liver, the stomach, the kidney.**
>
> Village elder, Fort Good Hope, Canada, as related to S.J. Kutz.

## SUMMARY

Parasites are among the most common organisms on the planet, and represent diverse members of all biological communities. Parasites tie communities together, revealing or telling stories about critical connections established by a history of evolution, ecology (food habits, foraging behavior, interactions among host species) and biogeography (patterns of geographic distribution) for host populations, species, ecosystems and regional faunas that constitute the biosphere. As such these organisms tell us about the processes, biological (e.g. range shifts, invasion) and physical (e.g. climate variation), that have determined the patterns of diversity that we observe in high latitude ecosystems.

Parasites can have subtle to severe effects on individual hosts or broader impacts on host populations which may cascade through ecosystems. Parasitic diseases have dual significance:

1. influencing sustainability for species and populations of invertebrates, fishes, birds and mammals, and
2. secondarily affecting food security, quality and availability for people.

As zoonoses, some parasites of animals can infect and cause disease in people and are a primary issue for food safety and human health. Sustainability, security and safety of 'country foods' are of concern at northern latitudes where people maintain a strong reliance on wildlife species.

In the Arctic, we often lack baseline and long-term data to establish trends for parasite biodiversity (host and geographic distributions or numerical measures of abundance and prevalence) in terrestrial, freshwater and marine systems, even for the best known host species. Absence of biodiversity knowledge has consequences for understanding the role of parasites in an ecosystem, and patterns of emerging animal pathogens, including zoonotic diseases, at local to regional scales. There is urgent need to incorporate parasitological information into policy and management plans and to emphasize awareness of parasitic diseases to wildlife managers, fisheries biologists, public health authorities and local communities.

Parasitological knowledge can be incorporated into policy and management plans through an integration of field-based survey, local knowledge, development of baselines linked to specimens, archival data resources to assess change, and models that can predict potential spatial and temporal distribution for outbreaks of disease among people or animals. We recommend that parasites be considered particularly as they relate to biodiversity and conservation of populations, availability of subsistence food resources and concerns for food security and food safety (i.e. zoonoses and wildlife population declines caused by parasites). Further, research is necessary to demonstrate linkages among climate change, environmental perturbation, shifting abundance and range for hosts, and emergence of parasites and disease. These facets are essential to our capacity to predict future shifts in ecosystem structure over time, to develop adaptations, and to mitigate or prevent disease outbreaks among human and wildlife populations.

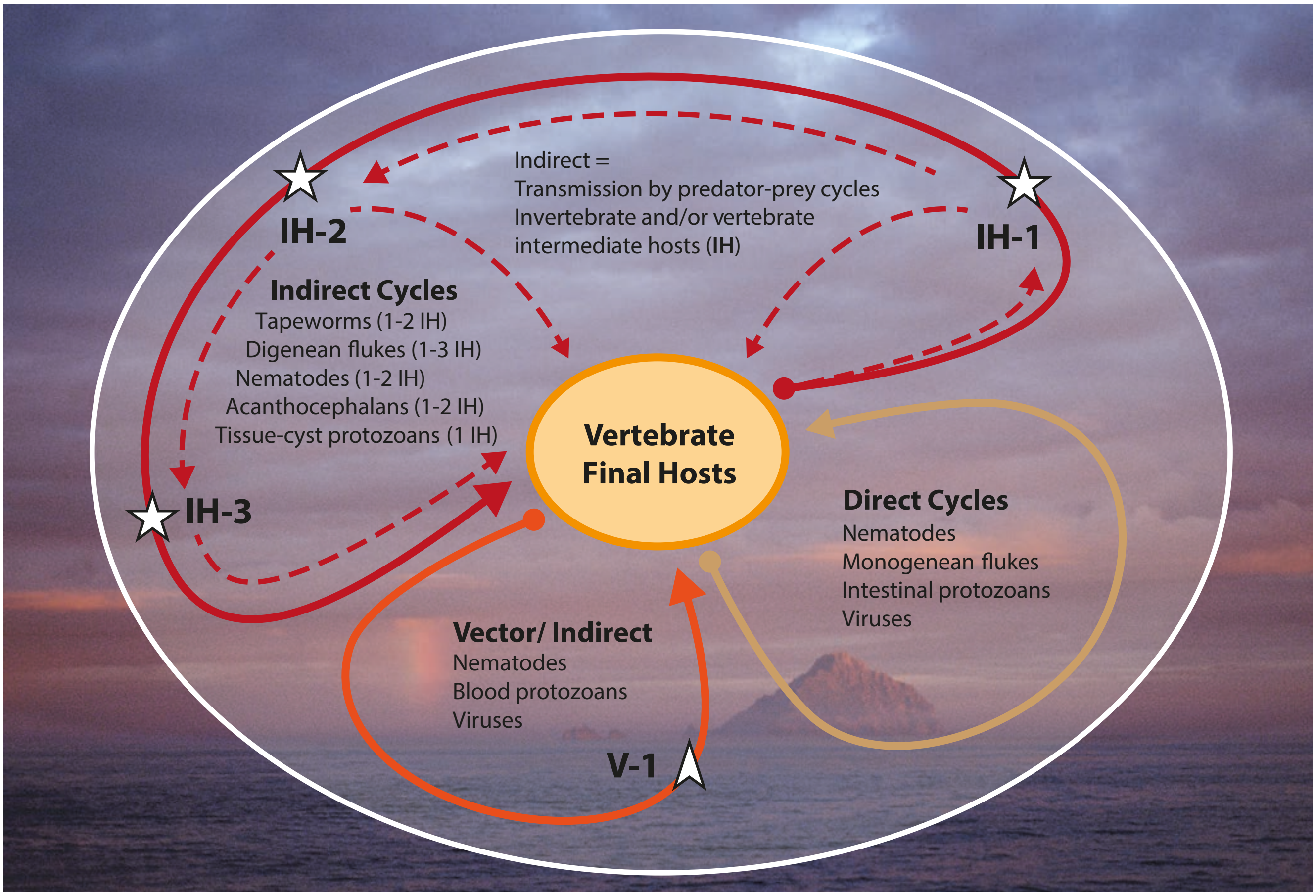
## 15.1. INTRODUCTION

Parasites represent in excess of 40-50% of the organisms on Earth and are integral components of all ecosystems (Dobson *et al.* 2008). Vertebrates and invertebrates are hosts for complex assemblages of macroparasites (worms and arthropods including insects) and microparasites (viruses, bacteria, fungi and protozoans) that shape ecosystems, food webs, host demographics and host behavior (e.g. Marcogliese 2001a, 2005, Hudson *et al.* 2006, Dobson *et al.* 2008). Surprisingly, in some ecosystems the biomass of parasites exceeds that of apex predators such as birds and fishes, and these otherwise obscure organisms have extraordinary ecological connectivity with involvement in over 75% of trophic links within food webs (Lafferty *et al.* 2006). A substantial role in nutrient cycling and trophic interactions at local to regional scales is evident for these assemblages of parasites (Kuris *et al.* 2008).

Parasites are taxonomically complex and diverse, even in high latitude systems characterized by relatively simple assemblages, and are considerably more species-rich than the vertebrate hosts in which they occur. For example, consider the 62+ described species of helminths, arthropods and protozoans, not to mention viruses and bacteria, which circulate in four species of ungulates across high latitudes of North America and Greenland (Kutz *et al.* 2012). Among 19 of 24 species of relatively specialized auks (seabirds of the family Alcidae) there are in excess of 100 species of helminths and arthropods in addition to viruses, bacteria and protozoans (Muzzafar & Jones 2004). Among the five species of loons (Gaviiformes) there are 97 species of helminths and among Holarctic grebes (three species of *Podiceps*), all of which breed at high latitudes, there are 145 species of helminths which contrasts with 244 among all podicipediforms in the global fauna (Storer 2000, 2002). Further, in a single fish species, Arctic char *Salvelinus alpinus*, there are over 100 known species of helminths and protozoans (Dick 1984, Wrona & Reist, Chapter 13). These observations emphasize the broad distribution of parasites across and within ecosystems in terrestrial and aquatic environments. Considerable complexity and knowledge gaps, however, suggest that it is currently intractable to develop a synoptic picture for trends in abundance or diversity across phylogenetically disparate assemblages of vertebrate hosts (fishes, birds and mammals) and their parasites extending from regional to landscape scales. As an alternative, we highlight a series of exemplars demonstrating the importance of parasites both conceptually and functionally as integral components of high latitude ecosystems. Our discussion explicitly explores the distribution of metazoans (helminths) and protozoans circulating in fishes, birds and mammals, and to a lesser extent some parasites that are recognized as zoonotic pathogens; we do not examine the diversity and distribution of viruses, bacteria, parasitic fungi (in animals or plants; but see Dahlberg & Bültmann, Chapter 10), or arthropods in parasitic and mutualisitc associations.

Parasites can cause disease and mortality, influence the dynamics and regulation of host populations, mediate competition among hosts which determines community structure, and in the worst case scenarios contribute to extinction events for hosts. Circulation of parasites is based on specific pathways that represent links among hosts and the environmental settings where they occur (Fig. 15.1). Some parasites have direct transmission cycles that involve passage between definitive hosts where the adult parasite develops and reproduces. Often, the infective stages will occur free in the environment, sensitive to ambient temperature, humidity, salinity and light (including ultraviolet), and are acquired by hosts through ingestion of water or forage. In contrast, indirect transmission is often related to connections established through foraging and food habits where predators (definitive hosts) are infected through ingestion of prey (intermediate hosts where the parasite develops). Significantly, trophic structure in the Arctic involves an unusually great percentage of predators and relatively fewer herbivores (Callaghan *et al.* 2004a). Predator-prey interactions are among the dominant trophic links in high latitude systems where small to medium mammalian and avian predators often specialize on voles and lemmings in terrestrial environments; many shorebirds specialize on aquatic invertebrates in either marine or freshwater habitats (most often terrestrial/freshwater in the breeding season and marine in the non-breeding season). Consequently, parasite life cycles and transmission are directly influenced by fluctuations in abundance and density for both predators and prey species. Alternatively, indirect life cycles may involve vectors, usually biting flies or other arthropods such as ticks, which disseminate the parasites among hosts. In the Arctic, the

**Figure 15.1.** Life cycles for parasites. Transmission patterns emphasize the triad of 'host-parasite-environment', thus both biotic and abiotic mechanisms and controls serve to determine the occurrence of helminths, arthropods, protozoans and viruses. Indirect cycles involving development of larval stages in intermediate hosts (☆ IH-1 to IH-3) are typical for most helminth parasites in terrestrial, freshwater and marine systems of the Arctic. The IH(s) in specific cycles are usually invertebrates (arthropods, molluscs, annelids) or occasionally other vertebrates (fishes, birds or mammals) that are important as prey for the definitive or final host. Among helminths, 1-3 intermediate hosts are often required for transmission, and the length of the cycle is characteristic of a particular parasite group. In these cases life cycles describe predictable pathways associated with trophic linkages, and thus parasites serve as ecological indicators for diet or other host activities. Indirect cycles may also involve arthropod vectors (△ V-1) that are required for development and transmission of parasites to the final host, usually for macroparasites or microparasites in the blood. Direct cycles involve transmission between definitive hosts, often with infective stages distributed in the environment. Photo: Matakiel Island, Northern Sea of Okhotsk, by E.P. Hoberg.



ambient environmental setting (temperature, humidity, seasonality, geography, host diversity, density and abundance) dramatically influences the survival, development, abundance and distribution of parasites and related disease in space and time (e.g. Kutz *et al.* 2005, Hoberg *et al.* 2008a, Kutz *et al.* 2009a, Laaksonen *et al.* 2010a, Kutz *et al.* 2012).

Parasites have predictable associations with their hosts and consequently serve as indicators of ecological structure, biogeography and history in complex biological systems (e.g. Hoberg 1996, Marcogliese 2001a, Nieberding & Olivieri 2007, Hoberg & Brooks 2008, 2010, Morand & Krasnov 2010). As succinctly outlined by Marcogliese (2001a): "… Parasites may be excellent indicators of biodiversity. This idea follows from the very nature of parasite lifecycles. Many parasites have a variety of intermediate hosts and often depend on predator-prey interactions for transmission. A single parasite in its host reflects the presence of all the hosts that participate in its life cycle. All the parasite species occurring in the host (the parasite community) reflect the plethora of life cycles represented by the different parasites and all the associated intermediate and definitive hosts. In this way parasites are indicative of food-web structure, trophic interactions, and biodiversity. … They thus reflect long-term persistence and stable interactions in the environment."

In northern systems, studies of parasite diversity directly complement our knowledge about the historical processes that have served to determine the structure of faunas, and the role of episodic shifts in climate that have influenced dispersal, isolation and speciation during the late Tertiary and Quaternary periods, approximately 3-3.5 million years ago to present (e.g. Rausch 1994, Hoberg *et al.* 2003, Cook *et al.* 2005, Hoberg 2005a, Zarlenga *et al.* 2006, Waltari *et al.* 2007a, Koehler *et al.* 2009). Contemporary diversity in aquatic and terrestrial environments has largely been determined by events that unfolded during the Pleistocene. For example, most groups of parasites now distributed in terrestrial mammals across the circumpolar region had origins in Eurasia and secondarily expanded into North America during glacial stages coinciding with lowered sea-levels that exposed the Bering Land Bridge, the primary pathway linking Siberia and Alaska (Rausch 1994, Waltari *et al.* 2007a, Hoberg *et al.* 2012). Alternating episodes of rapid climate change from glacial to interglacial cycles resulted in expansion, geographic isolation and diversification in diverse host-parasite systems, both between Siberia and Alaska, and also within North America and Greenland (e.g. Stamford & Taylor 2004, Waltari *et al.* 2007a, Shafer *et al.* 2010, Galbreath & Hoberg 2012). In parallel to terrestrial and freshwater systems, patterns of diversity are also reflected in the history and distribution of parasite faunas in marine birds, mammals and fishes that were influenced by isolation or expansion between the North Atlantic and North Pacific basins through the Arctic Ocean and Bering Strait (e.g. Polyanski 1961a, Hoberg 1995, Hoberg & Adams 2000, Briggs 2003). These observations highlight the idea that the 'past is the key to the present', with history providing a pathway or analogue for predicting how complex host-parasite systems will respond in a regime of accelerated environmental change over time (Hoberg 1997).

## 15.2. PARASITES AND THEIR IMPORTANCE IN THE NORTH

Across the North, parasites are important as evidenced by their ecological connectivity among hosts, at local landscape scales and more broadly across regional communities. Parasites can be a concern for humans as zoonotic organisms (transmissible from animals to humans often through consumption of wild food resources or 'country foods') (e.g. Gyorkos *et al.* 2003, Polley & Thompson 2009, Davidson *et al.* 2011) and as agents of disease in populations of wild fish, birds or mammals that are the foundations of subsistence foodwebs. Although parasites are important components of terrestrial, freshwater and marine systems in the Arctic, these organisms have not often been included in general assessments of biodiversity at high latitudes (Marcogliese 2001a, Hoberg *et al.* 2003, Kutz *et al.* 2009b, Gilg *et al.* 2012). This situation may reflect the insularity or isolation that separates different disciplines of the biological sciences and until recently sporadic communications among parasitologists, disease specialists and a broader community of ecologists, wildlife and fisheries biologists. Further, a sustained history for parasitological studies in high latitude systems has been limited to relatively few scientists in Europe, Russia and North America over the past century. These factors have interacted to hinder both the development of information and the subsequent dissemination of knowledge to wider audiences beyond those working directly with parasites and pathogens.

Climate change and associated ecological perturbations are modifying the structure of terrestrial, freshwater and marine systems across high latitudes of the North and globally (e.g. Callaghan *et al.* 2004a, Hoberg *et al.* 2008b, Kutz *et al.* 2009a, Burrows *et al.* 2011). These changes have an effect on patterns of distribution, timing of migrations and seasonal development of vertebrates, invertebrates and their parasites. Although we recognize and predict direct and indirect impacts to terrestrial, freshwater and marine systems, parasites and associated disease have seldom been considered in the 'equations' for environmental change (e.g. Post *et al.* 2009, Gilg *et al.* 2012). Parasites are critical components of these ecosystems, influencing the dynamics for host populations and a range of interactions from competition to predation (Marcogliese 2001a, Bustnes & Galaktionov 2004, Kutz *et al.* 2009b).

Climate and environmental change are accelerating in northern ecosystems (Callaghan *et al.* 2004a, Gilg *et al.* 2012). These perturbations (particularly in patterns of temperature in aquatic environments, and temperature and humidity in terrestrial systems) have a direct influence on the occurrence of parasites and the potential for emergence of diseases. Temperature, however, is only one of a myriad of interacting biotic and abiotic mechanisms that directly and indirectly determine the distribution, abundance and potential impact of parasites (Marcogliese 2001a).

Cumulative (long term) processes and extreme (short term) events influence the occurrence of parasites (Marcogliese 2001a, Hoberg *et al.* 2008a). Further, atmospheric-oceanic oscillations (shifts between warm and cold conditions over periods of months to years and decades) on varying temporal and spatial scales can also influence the structure of parasite and host communities and patterns of disease over broad geographic regions (Mouritsen & Poulin 2002a, Hoberg 2005b).

Many northern parasites are adapted to cold environments and have short transmission windows. Long term processes such as 1 °C increases in global temperature can reduce generation times, increase developmental rates and broaden seasonal windows for transmission. In contrast, extreme weather events can result in the explosive emergence of disease leading to morbidity and mortality at regional and local scales (Ytrehus *et al.* 2008, Laaksonen *et al.* 2010a). Amplification of parasite populations responding to either cumulative or extreme events may lead to cascading effects within ecosystems, ultimately affecting biodiversity for both free-living and parasitic species (Kutz *et al.* 2005, 2009a, Galaktionov *et al.* 2006, Marcogliese 2008). Concurrently, northern range expansion for many vertebrate species will create new opportunities for exposure of naïve host populations to an array of pathogens (Brooks & Hoberg 2006, 2007, Reist *et al.* 2006, Lawler *et al.* 2009, De Bruyn 2010, Gilg *et al.* 2012). Interacting with overall habitat change and other biotic and abiotic variables, disease is one outcome that can directly influence the availability of food resources on which northern communities depend. The role of anthropogenic introduction, establishment and invasion of parasites into the north also cannot be discounted given the degree of globalization and connectivity that now influences the distribution of free-ranging and domestic animals and their pathogens (e.g. Hoberg 2010).

Consequently, parasites must be explored in the context of

1. ecosystem function, stability and sustainability,
2. emerging pathogens that may directly influence subsistence foodwebs and food security at high latitudes under a regime of environmental perturbation, and
3. potentially threatened components of northern systems that may lack a capacity for adaptation to shifting environmental conditions, or may be eliminated through competition with new invaders (e.g. Kutz *et al.* 2004, 2009a, Tryland *et al.* 2009, Laaksonen *et al.* 2010a).

Ecosystem assessments and the role of complex interacting factors which may influence patterns of host and parasite abundance can only be explored through long-time series of biological collections and surveys at local to regional scales (e.g. Haukisalmi & Henttonen 1990, 2000, Marcogliese 2001a).

## 15.3. STATUS AND KNOWLEDGE

Knowledge of parasite diversity in the Arctic expanded in the 1800s coincidental with the earliest biological collections in Eurasia and North America. Studies were usually local and opportunistic, often with minimal samples providing an incomplete glimpse of parasite diversity among vertebrate and invertebrate hosts in terrestrial, freshwater and marine systems. A process of discovery emphasized taxonomy and the identification and characterization of diverse macroparasites (less often microparasites), but usually in the absence of an ecosystem approach or historical and biogeographic context.

A more comprehensive view of parasite diversity did not emerge until the late 1940s and 1950s as cadres of scientists began to systematically explore northern environments. These studies may be best exemplified by the relatively comprehensive attempts to document and characterize parasite diversity across Siberia and the northern regions of the former Soviet Union. For example, the series of All Union Expeditions to such areas as Kamchatka (317th) and Chukotka (318th) in the 1960s provided the basis of our initial in-depth view of parasite distributions among birds, mammals and some fishes in these regions through examination of representative and large series of host specimens (e.g. Spassky *et al.* 1962, 1963). These and other field surveys led to considerable knowledge about helminth parasite faunas circulating across tundra, nearshore and marine environments (Belogurov 1966) among shorebirds (Scolopacidae and Charadriidae) (e.g. Belopol'skaya 1953, 1980, Bondarenko & Kontrimavichus 1999) and in marine birds such as auks, gulls and seaducks (Belopol'skaya 1952, Galaktionov 1996a), which collectively dominate avian diversity at high latitudes. These further served as the basis for comprehensive monographs exploring parasite diversity in avian, mammalian and piscine taxa, particularly in the Russian literature (e.g. Bykhovskaya-Pavlovskaya *et al.* 1962, Spasskaya & Spassky 1977, 1978, Ryzhikov *et al.* 1978). In Alaska at this time, studies of parasite faunas, principally among mammals and birds, were driven by Robert L. Rausch and his colleagues and presented in a long series of papers in *Studies on the Helminth Fauna of Alaska*. For the most part, however, multi-taxon surveys that were both geographically extensive and site intensive were without counterpart in either northern Eurasia or North America until the current era of biodiversity inventory (Cook *et al.* 2005).

Coincidental with expanding interest in wildlife parasites, the implications of pathogens and disease for people were receiving attention (e.g. Rausch 1972, 1974). This focus began to examine the interaction between indigenous peoples, subsistence food chains and the cultural aspects of parasite transmission and disease (e.g. Rausch

1951, Babbot *et al.* 1961, Cameron & Choquette 1963). The role of humans in introductions and dissemination of parasites was revealed by the metazoan and protozoan faunas demonstrated on Iceland (Skirnisson *et al.* 2003).

Classical and elegant research in parasitology conducted at high latitudes has emphasized parasites transmissible to people (e.g. Rausch 1967, 1974, 2003), however, much remains to be revealed about the extremely diverse world of parasitic organisms. For example, new species and genera of macroparasites continue to be discovered across the circumpolar region. These include assemblages of tapeworms in such reasonably well studied host groups as arvicoline rodents (voles and lemmings) (e.g. Rausch 1952, Haukisalmi *et al.* 2001, 2002, 2006, 2009, Wickström *et al.* 2003, Cook *et al.* 2005, Makarikov *et al.* 2011). Additionally, among ungulates including muskoxen *Ovibos moschatus*, moose *Alces americanus* and caribou *Rangifer tarandus*, new stomach and lungworms are being identified and described (e.g. Hoberg *et al.* 1995, 1999, Kutz *et al.* 2007, Laaksonen *et al.* 2010b). Substantial new information about host and geographic distribution has also emerged reflecting recent programs for parasitological surveillance and monitoring in terrestrial systems (e.g. Kutz *et al.* 2001b, Hoberg *et al.* 2002, 2008b, Jenkins *et al.* 2005, Laaksonen 2010, Laaksonen *et al.* 2010a). These studies have demonstrated the need for broad integrated approaches which increasingly rely on both comparative morphological and molecular data to understand patterns of cryptic parasite diversity (related species of parasites that cannot be easily identified based on morphology) in the North (Hoberg *et al.* 2003, Haukisalmi *et al.* 2009, Pérez-Ponce de León & Nadler 2010). Accurate documentation of diversity (the species of parasites, how they are related, which hosts they infect, where they occur geographically and measures of numerical abundance and population genetic diversity) are the foundations for understanding and recognizing changing patterns of distribution and the emergence of disease. Further, different species of parasites behave in a variety of ways relative to hosts and environmental settings, thus clear definitions of diversity provide important information for predicting the outcomes of environmental change in these systems (e.g. Marcogliese 2001a, Albon *et al.* 2002, Kutz *et al.* 2012).

Large scale or synoptic biological collections linked to assessments of ecology, biogeography and phylogeography in some regional settings such as Beringia (the crossroads of the northern continents linking North America and Eurasia) have been ongoing over the past decade (e.g. Hoberg *et al.* 2003, Cook *et al.* 2005). Additionally, during the International Polar Year (2007-2008) a broad-based and standardized project exploring health of reindeer and caribou was initiated under the CircumArctic Rangifer Monitoring & Assessment Network (CARMA). In contrast to terrestrial systems, time sensitive inventories and baselines for parasites in marine birds (primarily auks, gulls and some waterfowl) have resulted from collections in the Arctic Ocean (White Sea), the region adjacent to Greenland and in the North Pacific/Bering Sea and Sea of Okhotsk (e.g. Belopol'skaya 1952, Threlfall 1971, Hoberg 1992, 1996, Galaktionov 1996a, 1996b, Muzzafar 2009). Some of these large collections provide the opportunity for direct comparisons of ecological conditions that characterized systems 30-50 years ago, relative to contemporary environments, and thus can reflect the results of accelerated perturbation over time. Parasites are particularly sensitive indicators of ecological conditions, migration pathways and habitat use because their transmission is often directly linked to the food habits and foraging behaviour of hosts (e.g. Dogiel 1964, Hoberg 1996, 1997, Marcogliese 2001a, Muzzafar 2009).

Similar inventories, however, are reasonably rare across Arctic latitudes. Essentially there are few comprehensive historical baselines (derived from comparable sampling standards) against which to measure trends for changing patterns of distribution, host associations or numerical occurrence of most parasites (and diseases) in free-ranging and domestic animals or in people (Appendix 15.1). Indeed, we continue to have an incomplete picture of diversity, host associations and distribution for parasites in vertebrates and invertebrates in northern regions. Faunal checklists can be assembled from a distributed literature for parasites in many species of fishes, birds and mammals, but these are not always appropriate as temporal and spatial baselines. Further, there is relatively little ongoing survey-based collecting that will allow direct comparisons with the contemporary historical records that document faunal structure during the past 30-50 years, which now appears to be a critical period with respect to environmental perturbation in northern systems. This situation heightens the need for active collaborations among field biologists, including parasitologists, vertebrate biologists, wildlife disease specialists and local communities.

## 15.4. ECOSYSTEM COMPONENTS IN THE NORTH

Assemblages of microparasites and macroparasites are associated with vertebrate host groups in terrestrial, freshwater and marine systems across the circumpolar North. Diversity and abundance of parasites is partitioned among the approximately 200 species of birds numbering more than 100 million individuals, 100 species of mammals and respectively about 127 (incl. the sub-Arctic) and 250 species of fishes in freshwater and marine systems in the Arctic (Callaghan *et al.* 2004b, Reist *et al.* 2006, Mecklenberg *et al.* 2011, Ganter & Gaston, Chapter 4, Christiansen & Reist, Chapter 6, Hodkinson, Chapter 7). In addition, a considerable array of invertebrates (among approximately 4,750 species in terrestrial and freshwater habitats, and 5,000 in marine environments) may serve as intermediate hosts. As a generality, species richness for macroparasites declines on a gradient from south to north in terrestrial (Hoberg *et al.* 2012), freshwater (Belopol'skaya 1959, Shulman

1961) and marine (Delyamure 1955, Polyanski 1961a, Rohde 2005) environments, although exceptions are apparent for some host and parasite groups that attain maximum diversity and abundance at high latitudes. This trend reflects an interaction of historical processes, ecosystem structure, host-group diversity, and patterns of distribution, abundance and density for vertebrates (and invertebrate prey and vectors) on landscape to regional scales. Migration further influences patterns of diversity, and this is manifested at varying spatial scales from landscape for rodents, to regional for some ungulates, and intercontinental for some birds. For example, among the helminth faunas associated with charadriiform shorebirds, species of parasites may be partitioned on wintering or breeding grounds or on migration corridors that extend from the Arctic deep into the Southern Hemisphere (e.g. Belopol'skaya 1953, 1959, 1963, Dogiel 1964). Thus, northern parasite faunas are characterized by low diversity and are to some degree constrained by biotic and abiotic mechanisms that define species occurrences and associations (Tab. 15.1).

In a simplistic sense, the biogeography and evolution of circumpolar assemblages of hosts and parasites reflects a history of recurrent climatological and environmental perturbation extending over the past 3-3.5 million years. The history is one of episodic geographic expansion (and contraction) in the ranges for vertebrate hosts and parasites. The processes have directly determined patterns of geographic invasion, and the potential that parasites have periodically colonized new host species or host groups (e.g. Kontrimavichus 1969, Hoberg & Adams 2000, Hoberg *et al.* 2012). The important implication here is that mechanisms that have historically served to determine parasite diversity are equivalent to those processes in ecological time that involve invasion, breakdown of ecological isolation and shifts in distribution for parasites and host-parasite assemblages (Hoberg & Brooks 2010). Northern host-parasite assemblages have origins and have diversified in a crucible defined by environmental change on evolutionary and ecological scales (Hoberg & Brooks 2008).

**Table 15.1.** Characteristics of Arctic host-parasite systems.

| **Biological characteristics: strongly influenced by Arctic environments** |
|---|
| *Relatively low diversity*; abundance and diversity for parasites are correlated with that for the host group. Levels of species richness and diversity in high latitude systems are substantially lower relative to temperate and boreal zones. This appears to be a generality across parasite faunas in fishes, birds and mammals. |
| Domination by *limited number of taxonomic groups* that may occur at high levels of abundance. |
| Numerous *migratory host species and populations*; avian species with long distance migration in terrestrial, freshwater and marine environments; some mammals particularly caribou, occasionally lemmings, some marine mammals; anadromus and diadromus fishes. |
| Often *high density aggregations* of hosts during breeding season (e.g. colonially nesting birds) and some through the year (e.g. caribou), influencing parasite abundance and transmission. |
| Some species *fluctuate in abundance on annual or longer cycles*; includes vertebrate host species and invertebrate vectors. |
| *Extreme seasonality in distribution and abundance*; brief pulses of primary/secondary productivity; prolonged winter. |
| *Short trophic links*; synchronicity in production cycles, occurrence of susceptible hosts, narrow transmission windows. |
| *Diversity influenced strongly by secondary productivity*; shifting abundance for invertebrate intermediate hosts and vectors. |
| *Diversity partitioned on spatial patterns* reflecting local to regional conditions. |
| **Historical characteristics influencing diversity** |
| *Episodic climate change* and habitat perturbation coinciding with glacial/interglacial cycles. |
| *Recurrent (episodic) expansion* (geographic colonization/range shifts), isolation, fragmentation of host/parasite populations. |
| *Spatial heterogeneity*; mosaics of suitable habitat for species persistence, driving speciation and distribution of cryptic species. |
| *Refugial effects*; residual isolation related to vagility (ability to disperse and velocity of dispersal). |
| *Complex patterns of species overlap* (sympatry) and patterns of parasite exchange (host switching) among respective groups. |
| *Prominent biotic filters*; constraints leading to loss of diversity due to limited resilience/tolerances/thresholds for development and survival in ephemeral, cold and xeric environments. |
| *Prominent abiotic filters*; constraints related to temperature, precipitation and humidity (terrestrial); temperature, ice cover, salinity, water flow and availability, circulation, UV exposure, etc. (aquatic). |
| **Adaptations in Arctic parasite systems** |
| *Rapid development* of larval-infective stages tied to seasonality (response to ephemeral conditions). |
| *Prolonged development* tied to sitting and waiting for suitable conditions (multi-year cycles); timing of development and dispersion of larval infective stages often reflects seasonal abundance of definitive hosts (migratory marine birds and shorebirds); responses to temperature with developmental thresholds and tolerances also linked to ephemeral conditions. |
| *Continuous transmission* through all seasons, reduced arrested development (ungulate nematodes). |
| *Resilience* of eggs/larvae to adverse environmental conditions. |
| *Synchronicity* in larval availability/infectivity coinciding with vulnerable spectrum of host population (e.g. nestling and fledgling birds; young of the year ungulates; pre-migratory salmonids). |
| *Long life span* as adult parasites, large size, high fecundity; multi-year infections; broad dissemination of larval stages in environment (e.g. lungworms and some gastrointestinal nematodes in ungulates). |
| *Short life span* as adults, rapid development, small size, great abundance, but low fecundity; absence of free-living larval stages; prolonged survival in intermediate hosts (e.g. trematodes including species of *Microphallus* and *Gymnophallus* and cestodes such as *Microsomacanthus* in charadriiform shorebirds, gulls and waterfowl). |
| *Geographically partitioned faunas*; specific wintering and breeding/nesting ground parasite faunas in migratory birds. |

A history of ecological perturbation and faunal interchange is an underlying theme as we summarize observations for a limited number of exemplars representing each of these systems. Our focus necessarily involves host groups of some importance in subsistence and those which may be significant for circulation of some zoonotic organisms. The exemplars also are indicative of the patchy nature of the data available for host-parasite systems at high latitudes where comparable sampling regimes are generally not available for all vertebrates throughout the circumpolar zone. Notably many records for the occurrence of parasites in fishes, birds or mammals relate only to the original description, and thus our context for understanding broader distributions is often limited. Unlike free-living fishes, birds and mammals, parasites are inherently more difficult to count and are not easily amenable to annual census activities that may define trends in populations for vertebrates. Further, not all Arctic vertebrates and free-living invertebrates have been extensively surveyed for parasites, and this gap in knowledge suggests that we still do not recognize some systems that may be particularly important indicators of environmental change in the North. Emphasis on a series of keystone species in respective ecosystems, however, serves to clearly demonstrate the substantial importance of parasites in the Arctic and highlights the need for more comprehensive surveys.

## 15.5. TERRESTRIAL ECOSYSTEMS

As mentioned above, terrestrial host-parasite systems at high latitudes are characterized by low diversity (species richness) relative to those in the boreal and temperate zones, consistent over all with a latitudinal gradient that to some degree coincides with patterns of species-richness and abundance for vertebrate hosts (Callaghan *et al.* 2004a). Due to differences in vagility, some mammalian parasite faunas appear to be more strongly partitioned geographically than those among avian hosts. Latitude, however, is only one component that serves to determine general patterns of parasite distribution.

### 15.5.1. Mammals

Across terrestrial habitats in the Arctic there are about 65 species of terrestrial mammals (Reid *et al.*, Chapter 3). Diversity of parasite faunas in terrestrial systems, particularly among mammals, is a legacy of recurrent or episodic expansion during the Pliocene and Pleistocene from Eurasian areas of origin, eastward into North America (Waltari *et al.* 2007a, Hoberg *et al.* 2012). As a consequence of geographic expansion, however, longitudinal and latitudinal gradients in diversity appear to be a further generality for many helminth groups among ungulates, rodents, carnivores and lagomorphs. Species richness within respective helminth groups is greatest in Eurasia, lesser in North America, and minimal in the Arctic; or alternatively there is a gradient with a gap at high latitudes (Appendix 15.2). The gap of minimal diversity represents those parasite groups which could not successfully colonize high latitudes, or which were secondarily eliminated historically through local or regional extinction associated with rapid climate and environmental change. Beyond these longitudinal patterns, a latitudinal gradient has been secondarily superimposed, which is consistent with north-south and south-north expansion, isolation and diversification particularly in North America during the Pleistocene and Holocene (Galbreath & Hoberg 2012). Patterns of diversity also reflect a mosaic structure resulting from recurrent episodes of geographic colonization by hosts and parasites at intercontinental, regional and landscape scales over extended time frames. Mosaics are complex admixtures of species and populations that result from invasion and faunal interchange, both general phenomena in evolutionary and ecological time (Hoberg *et al.* 2012). Collectively, diversity gradients and mosaics provide a context to understand contemporary distributions for many parasite assemblages and the possible outcomes of natural and anthropogenic disturbance in northern terrestrial systems, and may have broader generality.

#### 15.5.1.1. Ungulates

Ungulates, including caribou and reindeer are keystones of terrestrial ecosystems throughout the Arctic, and are the core of subsistence food chains in many regions (e.g. Vors & Boyce 2009). Nematode parasites are a common and dominant group among ungulates across high latitude systems, occurring in the gastrointestinal system (e.g. Halvorsen & Bye 1999, Hoberg *et al.* 2001, Albon *et al.* 2002, Kutz *et al.* 2004, 2012) or in pulmonary (lungs) and extrapulmonary sites (musculature, thoracic, abdominal, peritoneal sites) of their hosts (e.g. Lankester 2001, Hoberg *et al.* 2002, Laaksonen *et al.* 2010a, 2010b). Among these, the protostrongylids and filarioids may be most sensitive to climate change (e.g. Kutz *et al.* 2001a, 2005, Laaksonen *et al.* 2010a). These parasites interact with an array of factors including weather events, contaminants and human disturbance that alone or in concert directly influence ungulate biology (Gunn & Irvine 2003, Kutz *et al.* 2004, 2012). Consequently, development of new baselines for distribution and abundance (and a capacity to predict and monitor changes in abundance) can contribute directly to a more robust understanding of health and sustainability among ungulate populations.

Protostrongylidae is a prominent family of nematodes common in ungulates across the circumpolar region (Boev 1975). Life cycles are complex involving adult nematodes in ungulates and infective larvae in gastropod (slugs or snails) intermediate hosts (e.g. Kutz *et al.* 2001a). Development of larvae is temperature dependent occurring more rapidly under warmer conditions up to a threshold of 21 °C. For example, research on the lungworm *Umingmakstrongylus pallikuukensis* of muskoxen produced models suggesting that climate warming in northern Canada has resulted in a shift (or tipping point) for the transmission of this parasite from a two to a one year life cycle (Kutz *et al.* 2005). Concurrently, the total number of larvae available to infect muskoxen increased under these warming conditions, contributing to heightened infection pressure and parasite abundance. Further, apparent geographic expansion for this lungworm north from the central mainland onto the Arctic islands has been demonstrated by recent field collections of muskoxen (S.J. Kutz, M. Dumond & E.P. Hoberg, unpubl. data). These interacting factors for rapid parasite development, increasing levels of infection and changing geographic distribution are those often associated with emergence of disease driven by parasites in ungulate populations (Kutz *et al.* 2012).

Other protostrongylid species are expected to be affected in a similar manner under a regime of accelerated warming and environmental change (Jenkins *et al.* 2006, Hoberg *et al.* 2008a). For example, during unusually warm years in Norway, severe outbreaks of disease associated with the protostrongylid *Elaphostrongylus rangiferi* were seen in reindeer (Handeland & Slettbakk 1994). Detailed empirical data and model-based research has not been done on the majority of the other protostrongylids, but the influence of climate, and both cumulative and extreme events, on patterns of distribution and emergence are readily apparent (Hoberg *et al.* 2008a).

Despite the fact that protostrongylids are common and pathogenic parasites found in keystone ungulates, and are among the best studied parasites of large mammals, considerable knowledge gaps remain about their diversity and ecology in the Arctic. This was exemplified by the original discovery of *Umingmakstrongylus* in the late 1980s (Hoberg *et al.* 1995) and most recently by recognition of an apparently new species of protostrongylid, based on DNA sequences of larvae, in caribou, moose and muskoxen across the North American Arctic (Kutz *et al.* 2007). Adults of this previously unknown lungworm were collected for the first time in 2010, and are under evaluation (G. Verocai, S.J. Kutz & E.P. Hoberg, unpubl. data).

Filarioid nematodes in ungulates across the Holarctic include species of *Setaria*, *Onchocerca* and *Rumenfilaria*. In contrast to protostrongylids, these parasites are all transmitted by biting flies (mosquitoes and black flies) (e.g. Bylund *et al.* 1981, Nikander *et al.* 2006). In Fennoscandia, *Setaria tundra* is associated with outbreaks of disease and substantial mortality events in reindeer and Eurasian elk *Alces alces*, and is a direct threat to sustainability and food security (Laaksonen 2010, Laaksonen *et al.* 2010a); *Rumenilaria andersoni* was only recently documented in Finnish populations of reindeer (Laaksonen *et al.* 2010b), and although it may be geographically widespread at high latitudes of North America, accurate data for distribution are lacking (Kutz *et al.* 2012). Emergence of disease attributable to *S. tundra* is driven directly by climate and short-term events of extreme weather (summer temperatures averaging above 14 °C in two consecutive years and apparently in conjunction with high humidity). In North America, these parasites are known to be present among caribou and moose, but geographic ranges, specific host associations, prevalence of infection and identity of the species remain poorly resolved. In light of the significant disease associated with filarioids in Fennoscandia, and recent anecdotal reports in Alaska of individual cases of disease (K. Beckmen, pers. com.), these may be parasites of special interest that warrant enhanced surveillance under current conditions of climate warming.

Among tissue dwelling and pulmonary nematodes it appears that infections are often cumulative with age of hosts, and lifespan for individual worms may extend over periods of years (Bylund *et al.* 1981, Hoberg *et al.* 1995). Both of these factors have implications for dissemination, invasion (colonization of new geographic areas) and emergence of disease (Hoberg 2010, Kutz *et al.* 2012). Development of parasitic stages in the intermediate hosts or vectors is also strongly defined seasonally and by temperature (Bylund *et al.* 1981, Handeland & Slettbakk 1994, Kutz *et al.* 2005, Laaksonen *et al.* 2010a). The widespread distribution of both pulmonary and gastrointestinal nematodes in conjunction with patterns of life history indicates the potential for considerable effects on host populations through mortality and reduced fecundity (Albon *et al.* 2002, Gunn & Irvine 2003, Hoberg *et al.* 2008a, Kutz *et al.* 2009a, 2012, Laaksonen *et al.* 2010a). The role of parasites at the ecosystem and regional level, however, including the widespread declines in populations of Barren Ground caribou (Vors & Boyce 2009) has not been explored. Significantly, heightened thermal stress for muskoxen and caribou (Ytrehus *et al.* 2008, Campos *et al.* 2010) will coincide with conditions of increasing temperature and humidity that are suitable for rapid amplification of parasite populations linked to reductions in development time for larval stages (e.g. Hoberg *et al.* 2008b). Thus, trends for expansion of parasite populations (abundance and infection pressure), increasingly coincidental with adverse thermal conditions for hosts represent opposing trajectories where synergy between these feedback loops ultimately may pose threats to continuity for populations of muskoxen at landscape to regional scales.

A primary management implication of parasites among ungulates may be the northward expansion of free ranging species in otherwise natural ecosystems and of domestic stock in agricultural systems, both leading to eventual encroachment on Arctic environments (Hoberg *et al.* 2008a, 2008b, Kutz *et al.* 2009a, 2012). Translocations, introductions and ongoing expansion of free ranging species including reindeer and muskoxen may already have influenced parasite distribution across the Arctic (e.g. Hoberg *et al.* 1999, Hoberg *et al.* 2002). Thus, a process to identify environmental and management factors that may enhance (or reduce) transmission of parasites and diseases is needed. Knowledge of parasite diversity provides a measure for understanding the drivers for emergence of disease and predictive power that can contribute to management decisions (e.g. Laaksonen *et al.* 2010a). In this manner, parasites are integral to understanding faunal diversity across Arctic systems.

### 15.5.1.2. Rodents

Rodents are abundant components of circumpolar ecosystems, and at high latitudes the fauna is dominated by the arvicolines (voles and lemmings) which overall has 28 genera and 151 species in the Northern Hemisphere; with eight genera and approximately 20 species restricted to the Arctic (Reid *et al.*, Chapter 3). Species of *Arvicola*, *Myodes*, *Microtus*, *Dicrostonyx*, *Lemmus* and *Synaptomys* are typical of this fauna. Rodents are of critical importance in Arctic ecosystems as the dynamics and occurrence of both avian and mammalian predators are often linked to the cyclical abundance of lemmings and voles (Callaghan *et al.* 2004a). Voles and lemmings serve as both intermediate and definitive hosts for a diverse assemblage of macroparasites and microparasites (e.g. Rausch 1952, Gubanov & Fedorov 1970, Egorova & Nadtochii 1975, Ryzhikov *et al.* 1978, 1979, Shakhmatova & Yudina 1989, Yushkov 1995, Haukisalmi & Henttonen 2000, Laakkonen *et al*. 2002). For macroparasites, distinct latitudinal and longitudinal gradients for species richness are apparent (Hoberg *et al.* 2012) (Appendix 15.2). Helminth parasites in voles and lemmings are indicators of historical and ecological connections in circumpolar environments (reviewed in Hoberg *et al.* 2012). Predator-prey cycles for helminths that are mediated through voles and lemmings are also the basis for circulation of some zoonotic tapeworms, including the taeniid, *Echinococcus multilocularis*, which is the causative agent of alveolar hydatid disease in people (Rausch 1967, 1995, Shakhmatova & Yudina 1989, Yushkov 1995). The biogeographic history and contemporary dynamics of vole and lemming populations thus strongly influence the distribution of complex parasite faunas in northern environments.

Parasite distribution in arvicolines depends on internal host factors, particularly immunity, and permissive environments where conditions of temperature and humidity are suitable for development and survival of infective stages (Callaghan *et al*. 2004a). Factors of climate and weather further act as determinants of distribution and abundance of invertebrates such as soil mites, insects and gastropods that serve as intermediate hosts and are essential for transmission. Aside from intrinsic host factors, the timing of precipitation in early summer was shown to be most critical in influencing the prevalence of infection for tapeworms and nematodes infecting *Myodes* voles in sub-Arctic Finnish Lapland (Haukisalmi & Henttonen 1990).

As an example of the dynamics of rodent-parasite systems, these observations emerged from two long-term programs for monitoring of host populations in northern Finland, at Pallasjärvi in the north boreal zone and Kilpisjärvi in the sub-Arctic zone that respectively extend to 1970 and 1946. Arvicoline diversity in these areas is high, eight species occurring at Pallasjärvi (European water vole *Arvicola amphibious*, Norway lemming *Lemmus lemmus*, bank vole *Myodes glareolus*, gray red-backed vole *M. rufocanus* and northern red-backed vole*M. rutilus*, wood lemming *Myopus schtisticolor*, field vole *Microtus agrestis* and tundra vole *M. oeconomus*) and six species at Kilpisjärvi (*M. glareolus* and *M. schisticolor* are absent), providing a powerful framework for comparative parasitological studies. Although all host species have been studied for helminths since the late 1970s, efforts for extended time series have focused on *M. glareolus* at Pallasjärvi, a key indicator species in western Eurasian boreal zone (Haukisalmi & Henttonen 1990). Deep time-series data from *M. glareolus* have been the basis for assessing patterns of seasonal and long-term population dynamics of cestodes and nematodes, with particular reference to varying strategies of 'common' and 'rare' species (Haukisalmi & Henttonen 2000).

Annual and seasonal monitoring has revealed, for example, that the populations of 'common' helminths of *Myodes glareolus* are regulated interactively with host density (with a lag) and in conjunction with climatic factors, particularly precipitation (Haukisalmi & Henttonen 1990). Because the trapping sites at Pallasjärvi are situated in all main habitat types (with replicates), it has been possible to study certain spatial aspects of helminth ecology as well. One of the most interesting findings is that some of the 'rare' species occur predictably in certain spatially limited, temporally persistent 'foci' (Haukisalmi & Henttonen 1999). Additionally, they occur almost exclusively in old, overwintered (soon-to-die) animals, particularly females in mid and late summer (Haukisalmi & Henttonen 2000). Without this knowledge, they would easily be missed in normal short-term surveys. Of further significance, the composition of rodent communities has undergone rather dramatic changes (besides lemming peaks) during recent decades, with faunal turnover and replacement over periods of years (H. Henttonen, unpubl. data). Such perturbations have not had any noticeable effects on helminth faunal diversity, and parasite assemblages have to some degree been maintained continuously with little modification. An exception to this trend may be represented by the appearance of a single nematode species (the heligmosome, *Carolinensis minutus*) associated with *Microtus agrestis* at Pallasjärvi (V. Hauksalmi & H. Henttonen, unpubl. data). Such data would be hard to gather without properly designed long-term monitoring. Although these studies in Finnish Lapland are rare in the Arctic, they should nonetheless be a model for exploring the dynamics of host-parasite systems in small mammals at multiple sites throughout the Arctic.

A consequence of climate warming may be fragmentation of rodent populations through interactions with expanding ranges for arvicolines, other rodents, and their parasites from the south (Callaghan *et al.* 2004a). The dynamics for these processes may be complex, with patterns of local extinction, faunal mixing through geographic colonization and potential host switching by parasites. In this regard, ecological perturbation has been among the primary mechanisms driving changes in faunal structure and species richness in these northern faunas (reviewed in Hoberg *et al.* 2012). In both evolutionary and ecological time, phylogeographic structure, including patterns of cryptic speciation for macroparasites, has resulted from episodes of range expansion and contraction; such structure is often evident for parasites even when not reflected in the history for particular host groups or species.

Extensive collections from long term monitoring at various localities has served to confirm the outcomes of environmental perturbation during the late Pleistocene, particularly glaciations and post-glacial expansion, on the distributions of some parasites (Haukisalmi & Henttonen 2001). For example, we have been able to confirm that some of the otherwise ubiquitous helminths are missing in Fennoscandia. Throughout the Holarctic, species of *Lemmus* have four main helminths (species or a group of closely related species): *Arostrilepis* spp., *Paranoplocephala fellmani* and related species, *Anoplocephaloides lemmi* (actually two species) and *Heligmosomoides* spp. (probably two species). Of these, only *P. fellmani* occurs in the Norway lemming in Fennoscandia; *Arostrilepis* is also absent in other Fennoscandian rodents. In contrast, cestodes of the genus *Arostrilepis* are known in arvicolines (*Arvicola*, *Dicrostonyx*, *Lemmus*, *Microtus* and *Myodes*) in the region immediately adjacent to Fennoscandia including Karelia, and European Russia (Mozgovoi *et al.* 1966, Yushkov 1995).

Faunal mixing, range shifts and establishment of parasite populations are also potentially influenced by human activities in the Arctic. For example, introductions of the sibling vole *Microtus levis* to Svalbard facilitated the establishment of *Echinococcus multilocularis* for the first time in the archipelago (Henttonen *et al.* 2001). Although the tapeworm may have been present in transient Arctic fox *Vulpes lagopus*, it had not become established due to the absence of a primary arvicoline intermediate host. This example demonstrates that the distribution of this tapeworm is likely limited by that of its required intermediate hosts, rather than extensive ranges occupied by highly vagile foxes that disperse over considerable distances in the Arctic. Thus, changing abundance and distribution of voles and lemmings may contribute to a broadened range for this zoonotic taeniid.

### 15.5.2. Terrestrial birds

Birds that occupy predominantly terrestrial habitats year round are poorly represented in the Arctic. They include limited numbers of passerines, birds of prey, owls and grouses, all of which constitute groups that are widespread in the Northern Hemisphere (Callaghan *et al.* 2004b, Ganter & Gaston, Chapter 4). Most of these species are short range migrants, with occurrences in the Arctic limited to relatively narrow seasonal windows during the summer breeding season. Consequently, the affinities of parasite faunas in the assemblage of landbirds are strongly tied to boreal and temperate environments. Helminth faunas for raptors are usually linked to the cyclic abundance of lemming populations and transmission pathways involving carnivory. In contrast, the faunas circulating among other landbirds involve both direct transmission and indirect cycles using various invertebrate prey species. Thus, patterns of abundance and diversity for potential prey can strongly influence the distribution and composition of helminth faunas.

As an example of diversity, the parasite faunas of rock ptarmigan *Lagopus muta* include 40 species of microparasites and macroparasites globally. In Iceland, these are represented by 16 species of endo- and ectoparasites which contrasts with 21 and 26 found in the Nearctic and Palearctic, respectively (Skirnisson *et al.* 2012). A notable absence in Iceland is digenean flukes that require molluscan intermediate hosts for transmission and haematozoans that require blood-feeding *Culicoides* midges. Reduced diversity appears to have been further influenced by founder events related to the original colonizers of Iceland from Greenland (Skirnisson *et al.* 2012).

Currently, haematozoan parasites of birds appear to be virtually absent from high latitude (tundra) habitats, although sampling has been relatively minimal (e.g. Bennett *et al.* 1992). Their absence has been attributed primarily to the paucity of appropriate arthropod vectors and suitable environmental factors that are necessary for transmission. Although most avian hosts are migratory, seasonal arrival on the nesting grounds does not appear to be commonly associated with establishment and dissemination of vector-borne parasites in the Arctic region. In the Canadian Arctic, it appears that haematozoans are mostly restricted to areas on the periphery of forest and forest-tundra habitats, and are less abundant or absent to the north. The genus *Leucocytzoon* is an exception (Simulidae, or black-fly vectors), however, and the species *L. simondi* may be particularly abundant extending into the Arctic and substantially north of the tree-line (Valkiūnas 1997). Latitudinal shifts in the treeline may lead to northward expansion and concomitant changes in abundance and density of blood-feeding blackflies and other dipterans that are recognized vectors. Such climate-mediated shifts in habitat structure may promote invasion and dissemination of these protozoans, which are a common component of avian parasite faunas and often significant pathogens at temperate to boreal latitudes (Bennett *et al.* 1982, Valkiūnas 1997).

Loss of habitat and habitat restrictions, shifts from tundra to forest habitats and structural changes related to productivity are expected to influence the distribution of parasites at all geographic scales. Ongoing shifts in species distributions of avian hosts may be predicted to influence the ranges occupied by various host-parasite assemblages with the consequent development of new faunal associations through geographic and host colonization (e.g. Callaghan *et al.* 2004c, Lawler *et al.* 2009).

## 15.6. FRESHWATER ECOSYSTEMS

Vertebrate faunas associated with freshwater environments in the Arctic are dominated by birds and fishes, with relatively few mammals restricted to these habitats (e.g. Callaghan *et al.* 2004b, Wrona *et al.* 2006, Ganter

& Gaston, Chapter 4, Wrona & Reist, Chapter 13). Parasites in birds and fishes are represented by diverse assemblages of protozoans and helminths (and other macroparasites), with the latter often cycling through aquatic invertebrates including insects, annelids and molluscs. Overall, freshwater systems are highly sensitive to water levels, ice cover, flow rates and changing patterns of primary and secondary productivity that influence ecosystem structure and potential prey diversity and abundance for both fishes and birds (Marcogliese 2001a, Ganter & Gaston, Chapter 4). These factors are central to the continuity of parasite life cycles and potential for transmission. Climate change in freshwater systems may be manifested by a number of interacting factors (Schindler & Smol 2006) of relevance for parasite diversity among both birds and fishes:

1. shifts in development for invertebrates that involve tipping points or transitions in life history from multi-year to single year (e.g. steps of entire years, not weeks and months),
2. loss of cold-water refugia leading to extirpation of fishes when tolerances and resilience are exceeded,
3. changing distribution of wetland habitats,
4. northward extension of the ranges for many invertebrate species, and
5. higher diversity for fish and invertebrate faunas.

### 15.6.1. Fishes

Arctic and sub-Arctic freshwater systems support approximately 127 species of fishes including some species complexes, notably among the char and whitefishes (Christiansen & Reist, Chapter 6). The fauna is dominated to some degree by diadromous species primarily salmon and whitefishes that move between freshwater and marine environments; cyprinids (minnows) are also speciose whereas the fauna includes limited numbers of sticklebacks, sculpins, perches and other fishes. Parasite faunas include species of microparasites and macroparasites that circulate solely in freshwater, in addition to those that are disseminated through dispersal from adjacent coastal seas and involve fishes as both definitive and intermediate hosts (Shulman 1961, Bykhovskaia-Pavlovskaya *et al.* 1962). In the circumpolar region of Russia (either Arctic Russia or the Russian north, dependent on the extent beyond the strict definition of the Arctic in our report) in excess of 222-300 species of protozans, helminths, crustaceans and other parasites have been documented in freshwater habitats and fishes (Shulman 1961, Rumyantsev 1984). Interestingly, many species of fishes occupy broad Holarctic ranges at high latitudes, contrasting with the fish parasite fauna in which diversity is often partitioned regionally and geographically in the Palearctic and Nearctic (Shulman 1961, Carney & Dick 2000). Patterns of distribution for parasites of freshwater fishes are treated in more detail by Wrona & Reist (Chapter 13).

Parasite assemblages in freshwater fishes are influenced by changes in ecological structure linked to expansion of geographic range, habitat perturbation and/or to host switching leading to a broadened array of species infected. Such faunal modifications can come about through anthropogenic mechanisms (e.g. fisheries management, introductions and hatcheries) (e.g. Petrushevski 1961) or through expansion driven by either natural events or those facilitated through external environmental factors (e.g. Marcogliese 2001a). An example of the former is the continuing invasion of the monogenean fluke, *Gyrodactylus salaris,* in populations of Atlantic salmon *Salmo salar* from northern Norway (Johnsen & Jensen 1991). In contrast, changing water conditions (increasing temperature) in the Yukon River, Alaska and adjacent Bering Sea have been implicated in the emergence of the protozoan *Ichthyophonus* in Chinook salmon *Onchorhynchus tshawytscha* (Kocan *et al.* 2004).

Pacific salmon *Onchorhynchus* spp. are keystone species involved in nutrient cycling and transport across ecosystem boundaries, with particular importance in riparian habitats (Gende *et al.* 2002, Naimann *et al.* 2002). They are also critical in commercial and subsistence fisheries. Disruption of salmon populations by natural and anthropogenic drivers can have substantial cascading effects in aquatic and adjacent terrestrial systems. In this regard, *Ichthyophonus* spp., poorly understood protozoan parasites that infect marine and anadromous fishes across the Holarctic, may be of particular concern (Kahler *et al.* 2007). *Ichthyophonus hoferi*, a pathogen of Chinook salmon from the Yukon River drainage of North America, has rapidly emerged over the past 30 years (Kocan *et al.* 2004, Zuray *et al.* 2012). Substantial pre-spawn mortality for adult fish poses serious implications for subsistence and commercial fisheries and can ultimately limit the sustainability of salmon populations in the Yukon system (Kocan *et al.* 2004). Further, the parasite directly affects palatability and suitability of infected salmon as food. The presence of *Ichthyophonus* in the Yukon reflects either a relatively recent introduction or invasion or emergence of an endemic pathogen driven by changing environmental regimes in the Bering Sea. The origins of this parasite in salmon remain obscure, although genetic data suggest a shift from other fish species in the marine or aquatic environment (e.g. Pacific herring *Clupea pallasi*) with potential amplification in the Yukon system being linked to increasing water temperatures (Criscione *et al.* 2002). Cascading effects of this pathogen in the Yukon ecosystem may be substantial, particularly if parasites cause significant fish mortality, ultimately limiting reproductive success for salmon. Significant reductions in major populations of anadromous fishes can have substantial impacts on nutrient cycling in riparian and adjacent terrestrial habitats (Schinlder & Smol 2006). Potential consequences also include reduced ecosystem sustainability and direct influences on subsistence and commercial fisheries (Kocan *et al.* 2004, Bradley *et al.* 2005).

Current predictions suggest that fishing practices, eutrophication and temperature increases may have the most profound effects on parasite faunas among Arctic freshwater fishes (Marcogliese 2001a, 2008, Wrona

& Reist, Chapter 13). Impacts of climate change are expected to be profound and will involve both direct and indirect effects on parasite diversity, faunal structure (turnovers) and abundance and, in synergy with anthropogenic factors, can be expected to influence host populations. Northward expansion along rivers and through lakes for southern fish species (for example yellow perch *Perca flavescens*) and invertebrates of importance for transmission may lead to introductions of parasite species previously unknown in the North (Reist *et al.* 2006). In contrast, species of fishes endemic to the Arctic may undergo range reductions leading to extirpation of both hosts and arrays of parasites in sensitive biological systems (Wrona & Reist, Chapter 13).

### 15.6.2. Birds

Waterfowl, cranes, shorebirds, gulls and loons are dominant and often abundant in freshwater, wetland and estuarine habitats of the Arctic (Ganter & Gaston, Chapter 4). Macroparasite faunas among this assemblage of phylogenetically disparate birds are often diverse and to some degree specialized with host associations linked to particular avian taxa and ecological settings (e.g. Spasskaya & Spassky 1978, Wong & Anderson 1990, Storer 2000, 2002, Bondarenko & Kontrimavichus 2006).

All birds associated with freshwater habitats are migratory, and in contrast to terrestrial birds, none are residents in the North throughout the year. Further, in contrast to terrestrial birds, migration is often long-range and may involve intercontinental or global connections with passage deep into the Southern Hemisphere for some species (Ganter & Gaston, Chapter 4). Seasonal migration to overwintering areas in the South or breeding and nesting areas in the North follows traditional flyways generally using a series of historically predictable staging areas. These patterns of distribution and seasonal movement have a considerable influence on the occurrence and diversity of helminth faunas among northern birds. For example, among the helminth faunas associated with shorebirds (Scolopacidae and Charadriidae), species of parasites may be partitioned in space and time with specific assemblages linked to transmission on wintering or breeding grounds or on migration corridors (e.g. Belopol'skaya 1953, 1959, 1963, Dogiel 1964, Wong & Anderson 1990). Considerable turnover in parasite diversity may occur between wintering and breeding habitats, which for shorebirds reflect shifts from marine to freshwater/terrestrial food resources (Anderson & Wong 1992, Wong & Anderson 1993).

In the case of acuarioid nematodes and other macroparasites acquired on marine wintering and staging areas, the occurrence of these parasites in birds during passage reflects the diversity and abundance of crustaceans, polychaetes and molluscs, and consequently, the structure and ecological integrity of coastal and intertidal systems where transmission occurs. On arrival to tundra environments in the Arctic, birds exploit a broad array of dipterans, coleopterans, annelids and other macroinvertebrates in freshwater/terrestrial habitats and are subsequently exposed to a considerably different parasite fauna (e.g. Bondarenko & Kontrimavichus 2006). Thus, parasites often can be indicators of geographic origins for different species or populations of hosts at varying spatial and temporal scales (Bondarenko & Kontrimavichus 1999). Irrespective of latitudinal and geographic partitioning, many species of tapeworms and flukes have longitudinally broad ranges across the Holarctic, or at the continental scale (e.g. Belopol'skaya 1979, 1980, 1983). These patterns of distribution, particularly for breeding ground faunas would be expected to be modified by northward expansion of some species of boreal shorebirds in both Eurasia and possibly North America (Ganter & Gaston, Chapter 4). Further, northern migrants come into contact with different spectrums of parasites, which circulate independently among resident avian faunas established in tropical and Southern Hemisphere environments.

Consequences of seasonal shifts in phenology, including early migration and nesting in conjunction with geographic expansion in ranges, may be seen in perturbations in the timing and synchronicity of food availability for breeding birds and fledglings (Ganter & Gaston, Chapter 4). Synchronicity determines parasite transmission where the presence of a susceptible host population coincides with the availability of primary invertebrate prey serving as intermediate hosts (Marcogliese 2001a). Mismatches in the arrival and breeding activities for birds and the seasonal timing of production cycles that determine the critical availability of invertebrate prey may be expected to disrupt patterns of parasite diversity. This may be reflected through loss of typical parasites, or declines in their abundance and prevalence and could also extend across migration corridors and staging areas. Asynchrony may also drive shifts to alternative prey species that result in exposures to a broader spectrum of parasites. Examination of these postulated outcomes is dependent on the availability of baselines for parasite diversity at varying geographic scales (Appendix 15.1).

Migration may also play a role in the distribution of some zoonotic parasites including *Toxoplasma gondii* in the Arctic, which may have been introduced from more southerly latitudes (Prestrud *et al.* 2007). *Toxoplasma gondii* is a protozoan parasite that now occurs globally, and the disease toxoplasmosis has been reported from an extraordinary diversity of vertebrate hosts including humans (Dubey & Beattie 1988). The parasite is now well documented in terrestrial and aquatic ecosystems of the Arctic, but the mechanisms for apparent introduction and dissemination remain largely enigmatic (Jensen *et al.* 2010); both marine and terrestrial pathways appear to be involved. For example polar bears *Ursus maritimus* and their primary prey including ringed seals *Pusa hispida* and bearded seals *Erignathus barbatus* appear to have had increasing levels of infection over the past decade, and the parasite is also common in Arctic foxes, wolverines *Gulo gulo* and even some ungulates (Kutz *et al.* 2012). On Svalbard it has been postulated that the parasite may be maintained by periodic introductions associated with migratory barnacle geese *Branta leucopsis* (Prestrud *et al.* 2007). A shift in the distribution and abundance of this parasite and broad dissemination within this ecosystem may have accompanied population increases for geese and greater diversity of terrestrial birds arriving in Svalbard that serve as prey for both Arctic foxes and bears (Prestrud *et al.* 2007, Jensen *et al.* 2010).

A mosaic of trends and responses is apparent, and the avian parasite faunas at high latitudes will ultimately reflect the cumulative environmental processes that influence diversity across considerable latitudinal and geographic gradients. For migratory species (and their parasites) there will be synergy with impacts manifested at lower latitudes (Gilg *et al.* 2012, Ganter & Gaston, Chapter 4). The effects of climate change and eutrophication in freshwater habitats may be additive (Marcogliese 2001a, 2008). Loss and restrictions of habitat, particularly diminished tundra habitat for shorebirds and waterfowl, shifts from open tundra to closed and heavily forested zones, and structural changes related to productivity are among the factors that will modify complex host-parasite systems. Parasites are important components of the mosaic of environmental change. It has been observed, with respect to avian taxa, that "Species respond individualistically to environmental variables such as temperature, moderated by species assemblages, competitors, facilitators, food, pests and parasites, and potential immigrant species" (Callaghan *et al.* 2004b).

## 15.7. NEARSHORE AND PELAGIC MARINE ECOSYSTEMS

### 15.7.1. Fishes

Marine fishes in the Arctic include nearly 250 recognized species (Christiansen & Reist, Chapter 6). As with other vertebrate taxa, our knowledge of parasites of marine fishes is fragmentary and incomplete. Historically, the most complete information stems from the former Soviet Union, with very broad host species coverage, whereas in North America, the best-studied hosts are anadromous fishes.

Most of the work in the former Soviet Union has been concentrated in the Barents Sea, the White Sea and the Bering Sea, where parasites have been surveyed in at least 46 species of marine fishes. Parasites tend to be most diverse in the Barents Sea and least diverse in the White Sea, apparently reflecting its relatively young biogeographic history (Polyanski 1961a). A total of 146 parasite species have been found in the Barents Sea including 28 sub-Arctic species, 27 Arctic-boreal species, 58 boreal species, five cosmopolitan species, 10 freshwater and estuarine species, and 18 species of unknown affiliation. In contrast, in the White Sea there are 100 parasite species including 10 Arctic species, 11 Arctic-boreal species, 17 boreal species, five Pacific species, one Baltic species, two cosmopolitan species, 17 brackish and freshwater species and 37 marine species with unknown distributions (Polyanksi 1961a). Parasites provide information on their host habitats and diets, and consequently Polyanski (1961b) recognized distinct host complexes based on their parasite fauna. In the Barents Sea, fishes could be grouped into benthic and small fish consumers, littoral and coastal species, plankton feeders and migratory fishes, whereas in the Bering Sea they were categorized as exclusive planktivores, piscivores also feeding on plankton, strict piscivores and benthivores. Taxonomically different species with similar diets share parasites, while taxonomically related hosts with different diets also have different parasites. Generally, the Barents Sea parasite fauna consists of a mixture of species of Arctic origin with those from the boreal North Atlantic (Polyanski 1961a). The proportion of Arctic-boreal parasites varies geographically within the Barents Sea and also among the host complexes mentioned above. The far-eastern seas are considered a distinct biogeographic region, but at the same time the Bering Sea also shares parasites with the White Sea, the Barents Sea and the North Atlantic (Polyanski 1961a).

Perhaps the best-studied marine fish globally occurring in sub-Arctic or Arctic waters is the Atlantic cod *Gadus morhua*. As with marine fishes, few parasites are restricted to northern latitudes. These include a few ciliates, monogeneans, a cestode, a protist and a leech. However, cod are infected with numerous Arctic-boreal parasites, which do not extend into southern waters. These include 16 protists and myxozoans, four monogeneans, 11 digeneans, at least 10 nematodes, three acanthocephalans, one leech and three copepods (Hemmingsen & MacKenzie 2001). As with other hosts, certain other cosmopolitan parasites are also found in northern waters.

It has long been recognized that parasites can provide information on stock delineation (biological tags) for fisheries management (Polyanski 1961b, Margolis 1965). Consequently, our knowledge of parasites of marine fishes in North America is largely confined to the sub-Arctic, and often restricted to commercial species such as Pacific halibut *Hippoglossus stenolepis* and rockfishes *Sebastes* spp. off the Alaskan coast (Blaylock *et al.* 1998, Moles *et al.* 1998), and Greenland halibut *Reinhardtius hippoglossoides* and roundnose grenadier *Coryphaenoides rupestris* off Labrador (Zubchenko 1981, Arthur & Albert 1994). Typically, these types of studies include sub-Arctic or Arctic waters only if the range of these commercial species extends into those waters. In a geographically extensive study, Blaylock *et al.* (1998) noted a typically sub-Arctic parasite fauna in Pacific halibut from northern latitudes. In European waters, parasites have been used to examine cod stocks in sub-Arctic waters off Iceland, coastal Norway and the Barents Sea (Hemmingsen & MacKenzie 2001). In addition, parasites have been used to determine the freshwater origins of Pacific salmon (Margolis 1965, Urawa *et al.* 1998). They also have been used to separate sea-run Arctic char from freshwater forms in Norway (Kennedy 1978), Greenland

(Due & Curtis 1995) and across northern Canada (Dick & Belosevic 1981, Bouillon & Dempson 1989, Desdevises *et al.* 1998). However, Dick (1984) cautions that given the patchy distribution of Arctic char parasites, each system must be examined separately, a rather daunting task. There are some marine parasites of char, however, that are widespread with Holarctic distributions, including a number of trematodes (*Brachyphallus crenatus*, *Derogenes varicus*, *Lecithaster gibbosus*, *Prosorhynchus squamatus*), a cestode (*Bothrimonus sturionis*) and an acanthocephlan (*Echinorhynchus gadi*). All of these are generalists, infecting numerous host species in marine waters.

Anisakid nematodes are cosmopolitan parasites that infect Arctic and sub-Arctic pinnipeds and whales, with larval stages occurring in fishes in those regions as well. Members of two genera in particular are of concern to fisheries. *Anisakis* spp. are pathogens acquired from eating raw or undercooked fish, while *Pseudoterranova decipiens* is a large, visible nematode which is unappealing to consumers and reduces fish product quality. *Anisakis* spp. mature in whales, while *P. decipiens* (sealworm) uses pinnipeds as its definitive host, and both parasites are found in a large range of fish intermediate and paratenic hosts. Consequently, these parasites, especially sealworm, have been the subject of intensive investigation for well over three decades in waters off Alaska, Greenland, Norway and in the Bering and Barents Seas, with records as far back as the 1930s in Iceland (Platt 1975, 1976, Munger 1983, Shults & Frost 1988, Karasev *et al.* 1996, Ólafsdóttir 2001). As a result, these are among the only fish parasites from the sub-Arctic or Arctic for which there are long-term data to evaluate trends over time. For example, in Iceland, there has been a declining trend in the abundance of sealworm in cod between 1980 and 1999, paralleling reduction in population size for gray seal *Halichoerus grypus* definitive hosts, but this trend is not significant (Ólafsdóttir 2001). Seal numbers alone do not account for high intensities in fishes, and other ecological and environmental factors likely are important. Across the North Atlantic sub-Arctic waters, sealworm is more abundant in Icelandic cod compared with those from Greenland and northern Norway, and this may in part be due to the location of Iceland at the interface of warm and cold water masses (Ólafsdóttir 2001). A series of studies in cod from the Barents Sea found no difference in abundance or prevalence of *Anisakis simplex* between the early 1970s and late 1980s, despite major ecosystem changes over the same time period (Hemmingsen & MacKenzie 2001). Rokicki (2009) suggests that anisakid nematodes may further increase in abundance as a result of climate change. Temperature increases due to climate change could extend the growing season and enhance development rates of eggs and larval stages (Marcogliese 2001a, Rokicki 2009). These responses, however, may vary with parasites and their relative adaptation to warm or cold waters (Marcogliese 2001b).

Clearly, only limited baseline data exist in many parts of the Arctic and sub-Arctic, and much basic survey work is required to prepare for climate change and its effects on parasitism and disease in these regions. As recognized by Polyanski (1961b) and still true today: "The study of the life cycles of parasites and their seasonal and age dynamics, requires the organization of permanent 'fixed stations' which can be sampled and investigated directly at sea. To do this it is necessary to set up specialised parasitological laboratories at our marine biological stations. ... Ecologo-parasitological investigations should constitute an inseparable part of the general plan of studies of the biology of the sea."

### 15.7.2. Seabirds

Birds are prominent and highly visible residents of pelagic, nearshore and intertidal ecosystems around the Arctic basin, often occurring as apex predators in these marine environments. Although species diversity is relatively low compared with temperate latitudes, certain groups including seaducks and other waterfowl, gulls, auks, calidrid sandpipers and their allies attain their maximum diversity in the sub-Arctic and Arctic (Ganter & Gaston, Chapter 4). Complex assemblages of digenean trematodes (flukes), tapeworms and nematodes circulate though birds, molluscan (marine snails, bivalves and cephalopods), crustacean (crabs, amphipods, euphausiids, etc.) and fish intermediate hosts in the pelagic, intertidal and upper subtidal zones, where parasites often serve to structure coastal communities (e.g. Galaktionov 1996a, 1996b, Mouritsen & Poulin 2002b, Kuris *et al.* 2008). In these avian assemblages, generally pelagic (oceanic) birds such as some auks, a few gulls (e.g. the two kittiwake *Rissa* species) and tubenosed seabirds support faunas of lower diversity compared with those in loons, grebes, seaducks and most gulls and terns, which are usually found on neritic (over the continental shelf) and littoral (nearshore and shoreline) habitats (Hoberg 1996). These patterns reflect differences in vagility, narrow versus eclectic foraging habits, and for gulls, grebes and loons, components of the parasite fauna derived from terrestrial/freshwater systems. Spatially, diversity is influenced by a dilution effect of the marine environment, where oceanic and continental islands represent foci for parasite transmission and species richness diminishes with distance as a trend into pelagic systems (Hoberg 1996).

The main biodiversity in Arctic seas is associated with insular and mainland coastal waters. The rich and abundant fauna of marine organisms in intertidal and upper subtidal zones attracts huge numbers of marine and coastal birds that feed on these animals. The proximity of all these organisms promotes transmission of complex parasite life cycles involving coastal invertebrates, fish and birds as intermediate and final hosts. The fauna of the coastal ecosystems of the Arctic seas is especially rich in helminths (trematodes, cestodes, nematodes and acanthocephalans) of seabirds. In the areas with a relatively milder climate (the White Sea, the Norwegian Sea, the southwestern part of the Barents Sea, the nearshore zone of Iceland and the north of the Sea of Okhotsk) trematodes predominate among these helminths, as they do in the boreal regions. In the regions with a more Arctic climate, there is a clear tendency towards a lower species diversity of trematodes, up to their total disappearance in the high Arctic. This may be conditioned on severe environmental conditions in the Arctic coastal zone which impede transmission of trematode free-living (miracidia and cercariae) larval stages (Galaktionov & Bustnes 1999).

Trematodes that lack free-living larvae in their life cycles, such as microphallids of the 'pygmaeus' group, advance further into the Arctic. A representative of 'pygmaeus' microphallids, *Microphallus pseudopygmaeus*, is the only trematode species recorded in seabirds from the high Arctic archipelagoes of Novaya Zemlya (northern island) and Franz Josef Land (Galaktionov *et al.* 1993, Kuklin & Kuklina 2005). It should be emphasized that the life cycles of cestodes (Tetrabothriidea, Dilepididae and Hymenolepididae) and acanthocephalans (*Polymorphus*, *Corynosoma*) parasitizing Arctic seabirds also lack free-living larval stages.

Apart from climatic conditions, expansion of seabird trematodes into the Arctic was hindered by the circumstance that most of them use molluscs belonging to the boreal and Arctic-boreal faunal complex (*Littorina*, *Hydrobia*, etc.) as first and second intermediate hosts. These molluscs do not penetrate into the high Arctic. Cestodes and acanthocephalans, whose intermediate hosts are crustaceans, are in a different situation. The abundance of crustaceans in nearshore ecosystems of the high Arctic enhances successful transmission of these parasites. Though species composition of cestodes and acanthocephalans is lower than in boreal regions, the infection indices are high. For example, at Franz Josef Land the infection intensity of cestodes *Microsomacanthus* spp. and the acanthocephalan *Polymorphus phippsi* in the common eider *Somateria mollissima* reaches 200,000 and 1,200, respectively, in individual hosts. As these parasites are pathogenic for seabirds (for review see Galaktionov 1996b) they must influence considerably the dynamics of their host populations in the Arctic. This effect was demonstrated in the population of the common eider in the White Sea in a monitoring ornithological and parasitological survey of 1935-1985 (Kulatchkova 1979, Karpovich 1987).

The Arctic is crossed by migratory routes of many species of shorebirds and waterfowl nesting along the coasts of the polar seas and in the tundra. Each year millions of birds migrate along the coasts and across the open areas of the Arctic seas (Johnson & Herter 1990, Webster *et al.* 2002, Alerstam *et al.* 2007, Ganter & Gaston, Chapter 4). This promotes a broad trans-Arctic transmission of parasites, whose scale is now difficult to assess due to the scarcity of parasitological data from the areas of the Siberian seas, the coastal waters of Alaska and the Canadian Arctic Archipelago. At the sites of mass aggregation of migrating birds, local foci of helminth infection may arise. This was shown in some areas of the southeastern part of the Barents Sea (Pechora Sea) (Galaktionov & Marasaev 1986). Especially dense aggregations of waterfowl, such as the king eider *Somateria spectabilis*, the black scoter *Melanitta nigra*, the long-tailed duck *Clangula hyemalis*, the velvet scoter *Melanitta fusca* and the Steller's eider *Polysticta stelleri*, are constantly observed there at the shallows near Dolgii Island during the molting period and migration to wintering places (Krasnov *et al.* 2004, Sukhotin *et al.* 2008). The diet of these birds is based on mussels *Mytilus edulis*, other subtidal molluscs and crustaceans, the intermediate hosts of the helminths parasitic in these birds. Near Dolgii Island these invertebrates are heavily infected by the larvae of helminths, such as the trematodes *Micropallus pseudopygmaeus*, *Tristriata anatis*, *Gymnophallus somateria* and *Renicola somateria*, cestodes *Microsomacanthus* spp. and acanthocephalan *Polymorphus phippsi* parasitic in seaducks (K. Galaktionov, unpbl. data).

Formation of such local foci of invertebrate infection by the larvae of seabird helminths is characteristic of the coastal waters of the Arctic seas. The sites of high concentrations of the final hosts (bird colonies, migratory aggregations etc.) alternate with vast areas only sporadically visited by birds. It is worth noting that human activity may have an indirect effect on the increase of the infection level in coastal invertebrates. This is associated with the anthropogenic concentration of bird populations. For instance, in northern Norway, gulls often gather in fishing ports and fishing farms to feed on offal. This leads to a concentrated distribution of the final hosts, which may, in turn, lead to increased transmission of parasites between hosts. Examinations of intertidal molluscs and crustaceans conducted on the coast of northern Norway revealed a higher infection prevalence of helminth larvae in gulls in places with human activity (fishing ports, fish industry complexes, fish farms) as compared with places untouched by human activity (Kristoffersen 1991, Bustnes & Galaktionov 1999). Here, populations of invertebrates are constantly subjected to parasitic pressure which may result in detrimental effects. Moreover, the invertebrates inhabiting these sites are also subject to heavy anthropogenic influences such as pollution with hydrocarbons, everyday wastes etc. Consequently, there is a double pressure (both parasitic and anthropogenic), which obviously strengthens pathogenicity at the organismal level and can provoke degeneration of coastal ecosystems near settlements (Bustnes *et al.* 2000).

Species composition and indices of the birds' infection with parasites are dynamic and subject to long-term fluctuations. The latter are determined by changes in marine ecosystems caused both by natural and by anthropogenic causes. An illustrative example is provided by the studies of parasites of colonial seabirds at the sub-Arctic Seven Islands Archipelago (eastern Murman, Barents Sea, 68° 45' N, 37° 25' E) where the largest bird colonies in the eastern end of the Kola Peninsula are situated. Parasitological studies were carried out there in 1940-41 by M.M. Belopol'skaya (1952) and in 1991-2000 by a team of researchers (Galaktionov 1995, Kuklin & Kuklina 2005). Over the past 50 years, since Belopol'skaya's studies, the numbers of seabirds at the archipelago and their food composition have changed due to anthropogenic influences. Due to fishery activities, the proportions of Atlantic herring *Clupea harengus* and capelin *Mallotus villosus* have dropped sharply whereas the proportion of sandeel *Ammodytes tobianus* and also Atlantic cod, redfish *Sebastes* spp., goby *Myoxocephalus scorpius*, plaice *Pleuronectes platessa* and lumpfish *Cyclopterus lumpus* have increased in the food composition of fish-eating seabirds (Krasnov *et al.* 1995). The consumption of molluscs, mainly blue mussels, decreased 2-3-fold. Shifting prey selection coincided with a dramatic decrease in the abundance of mussels (> 90%) in the Barents Sea, reflecting either changing patterns of larval recruitment controlled by advection from the Norwegian Sea, or by shifts between cold and warm water mass regimes.

Most striking in the comparison of the results of 1991-2000 survey with those of 1940-41 is the decline in the species composition of trematodes. In 1991-2000 trematodes in the Seven Islands Archipelago seabirds were represented by six species, as compared with 11 recorded by Belopol'skaya in 1940-41. It should be emphasized that the life cycles of only four of these six species are associated with marine ecosystems; the trematodes *Diplostomum spathaceum* and *Plagiorchis laricola* use freshwater invertebrates and fishes as intermediate hosts. From the richest (nine species, 1940-41) trematode fauna, which was that of the herring gull *Larus argentatus*, such common species as *Microphallus similis* and *Renicola murmanica* have disappeared. A sharp decrease of *Gymnophallus deliciosus* prevalence and the total absence of *Renicola* and *Himasthla* is likely to be determined by the above-mentioned decrease of bivalves, the intermediate hosts of these trematodes, in the diet of these birds. A similar explanation does not, however, apply to *Microphallus similis*, which in Eastern Murman uses the crabs *Hyas araneus* as the second intermediate host (Uspenskaya 1963). The tendency concerning *Cryptocotyle lingua*, a common parasite of gulls, is also obscure. An increased consumption of fish (young cod, redfish, goby and plaice), which enter the intertidal and upper subtidal zones, should have resulted in an increased prevalence of *C. lingua* in gulls, as the aforementioned fishes are intermediate hosts of this parasite. Instead, *C. lingua* prevalence in gulls was much lower in 1991-2000 than in 1940-41.

Decreased species diversity and prevalence of trematodes in seabirds appears to have been promoted also by the reduction in the number of the principal final hosts of these parasites – the herring gulls, great black-backed gulls *Larus marinus* and common gulls *Larus canus* in the archipelago area (Krasnov *et al.* 1995). Eastern Murman is the northeastern boundary of the known distribution area of most aforementioned trematodes. Their prevalence in the first intermediate host (molluscs) in this area is thus extremely low in comparison with the western parts of the Barents Sea coast (Galaktionov & Bustnes 1996). Its further decrease in the archipelago area, as a result of the decrease in the main species of final hosts, should lead to an even greater decrease in the possibility of infection of the second intermediate hosts. Correspondingly, the probability of the second intermediate host (fish, crustacean, mollusc) containing the infective larvae being eaten by the final host (seabird) is infinitesimal.

In contrast to trematodes, Eastern Murman is not a boundary for the distribution of the majority of the cestode species observed in the Seven Islands Archipelago seabirds. They have been found in the gulls and auks of Greenland, Novaya Zemlya, Franz Josef Land and in the North Pacific basin and Bering Sea (Markov 1941, Baer 1956, Galaktionov *et al.* 1993, Hoberg 1996). Changes recorded in the cestode fauna of the archipelago seabirds were not so conspicuous and can be attributed mainly to changes in their diets. For example, disappearance of *Tetrabothrius jaegerskioeldi* and the decrease in the prevalence of the common species *T. erostris* in gulls may be attributable to shifting abundance of fish species. At the same time, the tetrabothriid fauna of kittiwakes was supplemented by *T. immerinus* and *Tetrabothrius* sp. I, whereas the great black-backed gull was demonstrated for the first time to be a host for *T. cylindraceus* and *Tetrabothrius* sp. I. The increase in the proportion of small crustaceans (Mysidacea, Euphausiacea, Calanoidea) in kittiwake diet may have caused an increase (from 41% to 69%) of infection with *Alcataenia larina*. At the same time, this species disappeared from the herring gull helminth fauna, whereas *Wardium cirrosa* appeared and infection with *Alcataenia micracantha* and *Microsomacanthus ductilis* increased. Most probably, these latter shifts were linked to an increase in intertidal and upper subtidal crustaceans (intermediate hosts for the above cestodes) in herring gull diets, as compared with 1940-41.

To sum up, the changes in the helminth fauna composition of the Seven Islands Archipelago seabirds can be to a great extent explained by the changes in the numbers of seabirds and in their diet. To some extent, marine birds forage opportunistically, and prey selection and its relationship to parasites reflects shifts in abundance for fishes or invertebrates that may be available as prey. Consequently, in these cases parasites directly indicate the structure of foodwebs and the intricate connections between birds and forage resources (Hoberg 1996, 2005b).

Concurrently, considerable shifts in the structure of host-parasite assemblages in the Arctic seas may also be driven by climatic changes, including variation in oceanographic conditions, current regimes and range shifts for certain crustacean intermediate hosts, particularly euphausiids. For example, shifting abundance of species of *Alcataenia* tapeworms has been linked to differential exploitation of euphausiid prey by thick-billed *Uria lomvia* and common murres *Uria aalge* and kittiwakes in the North Pacific and Bering Sea, and oceanic regime shifts (from warm to cold conditions linked to the Pacific Decadal Oscillation) were implicated as determinants of parasite distributions (Hoberg 1996, 2005b). New current regimes and watermass structure through the Arctic basin were identified as drivers in an apparent range expansion from the North Pacific to the North Atlantic of another species of *Alcataenia* in murres (Muzaffar *et al.* 2006, Muzzafar 2009). Oceanic colonization was apparently mediated by an expanding range for euphausiid crustacean intermediate hosts of Pacific origin. Establishment of these tapeworms appears to have coincided with a substantial restructuring of the parasite fauna of these pelagic birds relative to conditions documented in the late 1960s (Threlfall 1971, Muzzafar 2009). As in the Seven Islands Archipelago, it was the presence of a large scale historical baseline established through prior collections that allowed exploration of faunal change over time in these pelagic systems.

These studies clearly indicate that parasites are powerful adjuncts to studies of food habits and foraging ecology among diverse assemblages of hosts. Such is particularly evident in the detailed investigations of parasite faunal structure among marine birds in the White Sea region and North Pacific basin. Studies of food habits are often temporally limited providing a brief glimpse of food selected by birds at a particular moment in time. In contrast, parasites that circulate among apex predators such as murres and other seabirds facilitate a more nuanced exploration of trophic ecology. Parasites reveal the underlying oceanographic conditions and regime shifts that determine distributions of euphausiids, fishes and cephalopods (e.g. Ganter & Gaston, Chapter 4) that are the foundations for intricate links involved in transmission and completion of life cycles. Parasites found in a host are the sum of foraging activity spread over some period of time, but generally within a definable spatial sphere related to prey abundance and distance to colony sites (e.g. Hoberg 1996). Thus, knowledge of parasites directly complements more targeted studies designed solely to reveal the spectrum of prey selected by various vertebrate species.

Climatic effects are also manifested in relatively short term events that may represent responses to incremental change over time. The process of parasite development in intermediate hosts, mostly cold-blooded animals, the release of the parasite larvae into the environment and the process of the host animals' infection are greatly influenced by the temperature of the environment (Galaktionov *et al.* 2006, Poulin 2006, Poulin & Mouritsen 2006, Koprivnikar & Poulin 2009, Studer *et al.* 2010). A highly relevant circumstance in this respect is the fact that parasite transmission in the Arctic regions is confined to a very short time period, the so-called transmission window. Recent studies in the coastal zone of the White Sea demonstrated that climate change and long-term warming of intertidal systems can drive the amplification of parasite populations in both birds and molluscan hosts (Galaktionov *et al.* 2006).

Intensified transmission for flukes represents an unfolding cascade in intertidal systems where

1. the seasonal window for infection of molluscan intermediates will be prolonged,
2. higher numbers of infected molluscan hosts will drive expansion of parasite populations in invertebrates and fishes that are primary prey for birds, and
3. prevalence and abundance of parasites in birds is predicted to increase coincidentally with patterns of atmospheric warming and increasing sea temperatures, leading to heightened levels of infection for molluscs.

These feedback loops will be further enhanced as the duration for residency by shorebirds in intertidal zones of the sub-Arctic and Arctic broadens seasonally in response to ameliorating conditions linked to climate change (Lehikoinen *et al.* 2004). The ultimate outcome of these cascades may be collapse of intertidal communities as parasitism and mortality in molluscan, crustacean and piscine hosts disrupts food-web dynamics (Marcogliese 2008). It is essential that monitoring programs be developed throughout the Arctic basin to follow the development of this process that can have profound effects on the structure of nearshore ecosystems (Galaktionov *et al.* 2006).

### 15.7.3. Marine mammals

Marine mammals are characteristic inhabitants throughout global seas and include approximately 13 species of baleen whales, 71 species of toothed whales, 34 species of pinnipeds (seals and sea lions), polar bear, sea otter *Enhydra lutris* and the sirenians (Evans & Raga 2001). Among these, there are 313 species of macroparasites, relatively few protozoans, but a considerable diversity of viruses and bacteria (Aznar *et al.* 2002). Marine mammals are locally abundant in circumpolar seas extending from the northern North Atlantic to the Bering Sea where overall the fauna is characterized by 22 species of cetaceans (whales), nine pinnipeds (walrus *Odobenus rosmarus* and seals), and the polar bear (Reid *et al.*, Chapter 3). At high latitudes, helminth parasite faunas include over 30 species of tapeworms, flukes, nematodes and thorny-headed worms that have distributions through the Arctic Ocean, with a minimum of 26 in pinnipeds and six in cetaceans (Delyamure 1955). Consistent with latitudinal gradients, this contrasts with boreal seas (North Atlantic and North Pacific Oceans) where approximately 35 species parasitize pinnipeds and 49 are known in cetaceans. Patterns of diversity reflect species richness and abundance for respective host groups.

Original recognition of these gradients has been augmented by recent studies. For example, in waters of the North Pacific and eastern Arctic Ocean, baseline survey data exist for macroparasites in phocids including harbor seal *Phoca vitulina*, largha *Phoca largha*, ringed seals and ribbon seals *Phoca fasciata* (Adams 1988, Shults & Frost 1988, Hoberg *et al.* 1991, Measures & Gosselin 1994) and otariids including the Steller's sea lion *Eumetopias jubatus* (Shults 1986). Additionally, among cetaceans, twenty-two species of helminths are now known from the blue whale *Balaenoptera musculus*, of which 20 occur in the Arctic (Measures 1993).

Prominent in these faunas are tapeworms of the genera *Diphyllobothrium* and *Anophryocephalus* (e.g. Hoberg 1995, Hoberg & Adams 2000, Rausch 2005) and anisakine nematodes including species of *Anisakis*, *Pseudoterranova*, *Contracaecum* and *Phocascaris* (Rokicki 2009). Lungworms (*Acanthocheilonema spirocauda*, *Otostrongylus circumlitus*) and heartworms (*Filaroides gymnurus*, *Parafilaroides arcticus*) also have been surveyed in ringed seals from the Canadian Arctic (Bergeron *et al*. 1997, Gosselin & Measures 1997, Measures *et al*. 1997). Species of *Diphyllobothrium*, *Anisakis* and *Pseudoterranova* are recognized as zoonotic parasites in people, and larval stages are acquired from consumption of infected fishes, with anadromous species having a prominent role (Rausch & Adams 2000). Historic records for the distribution anisakines tend to be strongest for *Pseudoterranova* spp. in seals, especially in Iceland, because this parasite has been a continuing problem for commercial fisheries (Ólafsdóttir 2001).

In contrast to pinnipeds and cetaceans, polar bears have remarkably few macroparasites other than *Trichinella* nematodes, despite relatively deep temporal origins and expansion into marine environments since the late Miocene about 4-5 million years ago (Miller *et al*. 2012), and a specialized diet of pinnipeds and marine carrion. As polar bears are increasingly displaced from ice-edge habitats and stranded on shore, shifts in foraging behaviour may be anticipated to lead to exposures for a broader spectrum of parasites derived from intertidal zones (e.g. Laidre *et al.* 2008). Such dietary shifts may be indicated by an array of digenean flukes that circulate through molluscs and crustaceans in shallow coastal seas (Rausch *et al*. 1979).

Decreases in sea ice in the Arctic Ocean are predicted to have a pervasive effect on ecosystem structure and the biology of ice-associated marine mammals, including polar bears, walruses, some other pinnipeds and whales that have considerable importance in subsistence foodwebs (Moore & Huntington 2008). Changes in oceanic regimes, currents and water-mass structure, associated ice conditions, freshwater melt and salinity will drive modifications in behavior and diets for marine mammals as distribution and species composition for invertebrate and vertebrate prey species respond to new environmental conditions (Marcogliese 2001a, Laidre *et al.* 2008). The degree of sympatry and seasonal overlaps in distributions for cetaceans and pinnipeds are predicted to increase, suggesting heightened opportunities for the exchange and dissemination of parasites and pathogens (Burek *et al.* 2008).

Concurrently, accelerated warming in the Arctic may modify the diversity and abundance of parasites associated with these mammals, resulting in greater levels of exposure for people to zoonotic helminths such as *Trichinella nativa*, anisakine nematodes and species of *Diphyllobothrium* tapeworms and protozoans including *Toxoplasma gondii*, species of *Giardia* and possibly *Cryptosporidium* (Marcogliese 2001a, Hughes-Hanks *et al.* 2005, Rausch *et al*. 2007, Burek *et al.* 2008, Jensen *et al.* 2010).

Although infection pathways through zooplankton and fishes are well defined for anisakines and *Diphyllobothrium*, circulation of *Trichinella* and either intestinal or tissue-cyst forming protozoans like *Toxoplasma* are poorly understood in marine environments (Forbes 2000, Jensen *et al*. 2010). Other disease agents recently detected in northern marine mammals include *Brucella* sp. and morbillivirus, the latter similar to phocine distemper virus in walrus (Forbes *et al*. 2000, Nielsen *et al*. 2000).

## 15.8. TRADITIONAL ECOLOGICAL KNOWLEDGE ON PARASITES IN THE NORTH

> » *Liver – if liver good, animal healthy, if bumps on liver animal is discarded. … You use common sense; you eat what is good for you. If it doesn't look good you don't eat it. Won't eat liver if they see something on it.*
>
> *If we start getting disease in all the wildlife what's going to happen? Our age group is still living off the land. Younger generation won't know anything like that. Go to the store and buy wieners and sandwiches. They don't eat the same food as we do.*
>
> *In the old days there was no study on the animals like caribou and moose, but when the elders killed a moose or caribou, they ate the meat and nobody ever got sick from the animal in the old days. They never saw dead animals anywhere. He said you guys are studying animals now, but in the old days they had no study on the animals. But he said that when they see animals or they shoot at animals, they know if it's good or bad, because their ancestors used to tell them how to see, so they never did any studies on the animals, but they know what is good and what is not. They just knew it by heart. If the animal was fat and good to eat, they knew it by heart. If the animal was not good to eat, skinny, they knew it.*
>
> *Alfred just mentioned that from Alberta and in the North we're different because we always have cold weather all the time, and they have the warm weather and those kinds of spiders (ticks) can go on anything, can go onto the animals. But here we have cold weather and we don't see that much in the summertime.*
>
> (Village elder, Aklavik, Canada, as related to S. J. Kutz).

Traditional knowledge held by indigenous peoples about parasites in wildlife used for food and materials can directly complement scientific baselines (Brook *et al*. 2009). Considerable knowledge is evident in some regions and for some wildlife species, often reflecting an understanding of potential food safety risks associated with a subsistence diet. For example, traditionally in Alaska meat from bears is not consumed raw but is always cooked due to the threat of infection and disease posed by *Trichinella* nematodes (e.g. Rausch 1972).

A more general knowledge about disease processes and the impact of parasites is also apparent as demonstrated in the NWT of Canada through focus groups and interviews about ungulates (Kutz 2007). Participants included elders and mature hunters and women who had handled hide and meat for numerous years. Those among this cohort were familiar with many of the common parasites of caribou, muskoxen and moose. Observations by hunters brought an apparently unknown emerging disease – "slimy green/yellow wet stuff under the skin" – affecting caribou to the attention of biologists (Kutz 2007). Later reports from the field documented the increasing incidence of this syndrome in harvested caribou (Kutz *et al.* 2009a). Parasitic infection was suggested based on the structure of the lesions, but the cause remains to be determined. In some cases, the liquefied lesions were found in association with the protozoan *Besnoitia tarandi* and dead larvae of the warble fly *Hypoderma tarandi*; nematodes were not demonstrated. In Finland a similar syndrome is known in semi-domestic reindeer and in Eurasian elk, observed in conjunction with subcutaneous infections of the filarioid nematode *Onchocerca*, where in some areas 100% of animals are affected (S. Laaksonen, unpubl. data).

The recent invasion into the northern boreal forest of the NWT by the winter tick *Dermacentor albipictus* was further confirmed by local hunters who had no prior traditional knowledge of this arthropod parasite in the region (Kutz *et al.* 2009a). Interestingly, hunters from several communities indicated that parasitism was normal in the animals and kept them healthy, but that animals with numerous visible parasites were often "skinnier" than those without parasites.

Results from these interviews demonstrated that there is considerable traditional knowledge and local expertise on the occurrence of specific parasites and disease syndromes. It is urgent that such local insights about northern systems be recorded, given an ageing population and the continuing transition away from lifestyles linked directly to the environment. Documenting personal histories and observations from community elders and others should be a collaborative process between social scientists and biologists who are conversant with parasites and wildlife diseases (e.g. Kutz 2007). Local knowledge provides valuable historical baselines, particularly in regions and localities lacking scientific collections, surveillance or monitoring, as well as a methodology for contemporary tracking of infectious diseases in wildlife (Henri *et al.* 2010).

Similarly, in aquatic habitats, subsistence fishermen were the first to recognize an expanding disease syndrome in Chinook salmon on the main stem of the Yukon River in Alaska (Kocan *et al.* 2004). Infections by the enigmatic protozoan *Ichthyophonus hoferi* were unknown prior to 1980 in Pacific salmon and were apparently absent from the Yukon River system. The parasite is now abundant and well established and constitutes a direct influence on the availability, suitability and palatability of salmon as food (Bradley *et al.* 2005).

## 15.9. CONCLUSIONS AND RECOMMENDATIONS

### 15.9.1. New tool development

Knowledge of parasite diversity, particularly definitive identification, geographic distribution and host association, is critical as a foundation for understanding the potential for pathogen dissemination and disease (Brooks & Hoberg 2000, 2006, Hoberg 2010). Achieving this goal requires field-based research, networks with local capacity, scientific and local community engagement, coordination and collaboration to facilitate collections, plus methodologies that provide timely or rapid identification of parasites. Parasite collection and identification has often been a laborious process dependent on special expertise and knowledge of specific taxonomic groups. Collections were often logistically difficult (e.g. ungulates or marine mammals) where the necessity of field-based necropsy to recover adult parasites often limited the geographic scope and numbers of host specimens that could be examined. Molecular-based methods increasingly complement microscopic identification, and such approaches for the first time provide a means for geographically extensive and site-intensive sampling for parasite diversity that does not always have to rely directly on necropsy (e.g. Jenkins *et al.* 2005, Kutz *et al.* 2007). These and other non-invasive, 'field-friendly' methods enhance data and sample collection and storage by hunters, substantially increasing the capacity to rapidly assess diversity and epidemiology of parasites across large landscapes and regions (e.g. blood filter paper (Curry 2009), and fecal sampling for parasitic eggs and larvae in conjunction with DNA amplification and sequencing (Jenkins *et al.* 2005, Huby-Chilton *et al.* 2006, Kutz *et al.* 2007, DeBruyn 2010)). Additionally, definitive identification of many microparasites such as species of *Giardia*, *Toxoplasma*, *Besnoitia* and others is not feasible in the absence of molecular methodology (e.g. Criscione *et al.* 2002, Polley & Thompson 2009). The latter is increasingly important in identifying the sources and pathways for human infection from stages of parasites acquired through water or food contamination mediated by wildlife (Polley & Thompson 2009).

Documentation of parasite diversity is a continuum that includes:

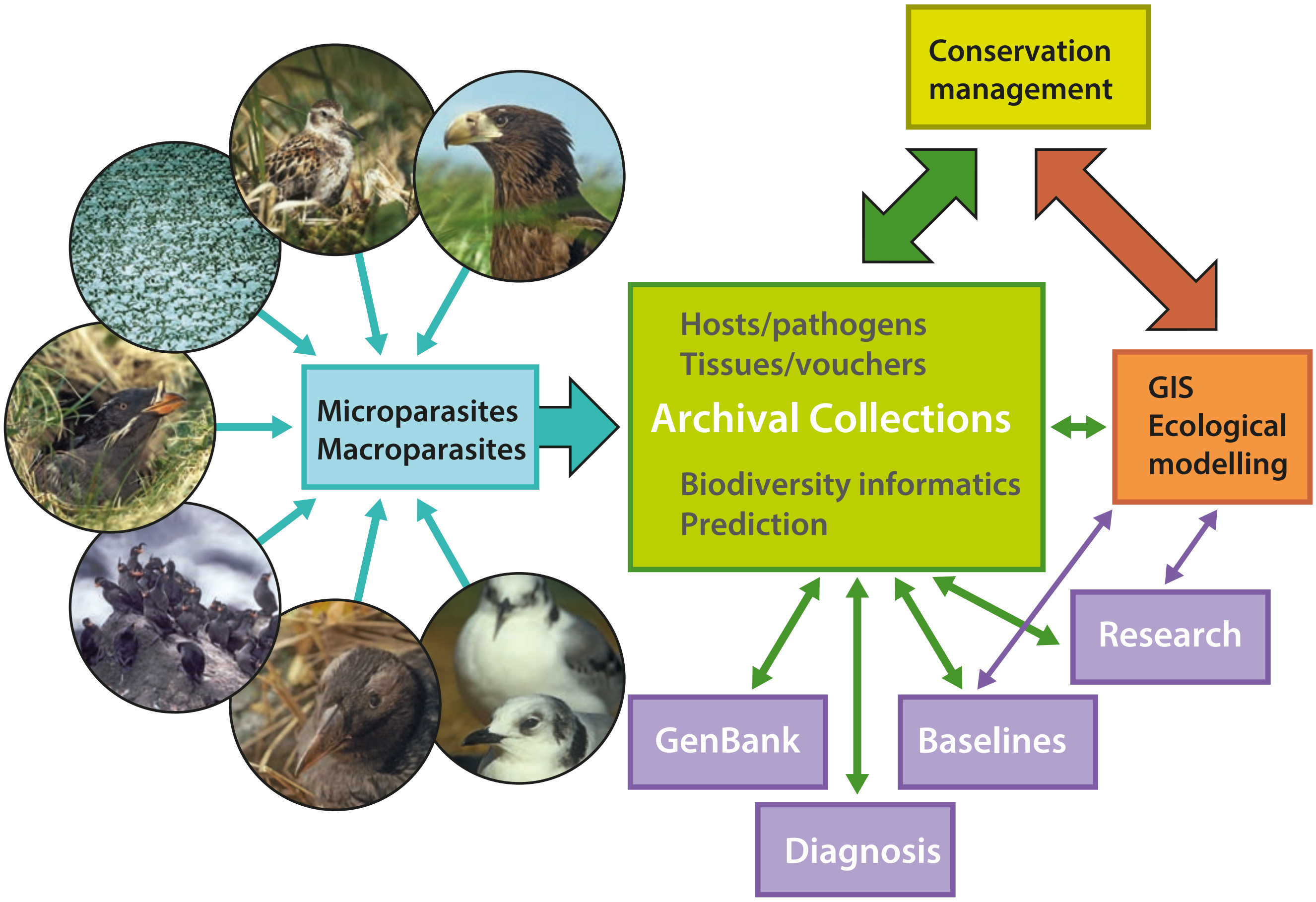
1. targeted taxonomic studies on single parasite species and simple case reports in individual hosts,
2. surveys for parasites in single host species at a limited spectrum of localities,
3. survey and inventory at the ecosystem level based on standardized and comprehensive sampling protocols implemented on broad geographic scales, and
4. integrated inventory for hosts and parasites with application of population genetic approaches and phylogeography to explore relationships at fine temporal and spatial scales (see Cook, Chapter 17).

Ecosystem approaches for survey (and surveillance) are necessary as the distribution of a parasite is generally broader than the distribution of disease (Audy 1958), and outbreaks may represent geographic (and host) mosaics that are ephemeral in space and time (Thompson 2005, Hoberg 2010). Geographic coverage from local landscapes to regions is thus a foundation for establishing patterns of abundance and circulation for parasites. Further, such surveys should contribute directly to the development of archival biological collections (parasites, hosts, tissues and biodiversity informatics) held in museum repositories as a baseline for diversity and faunal structure (Fig. 15.2) (Brooks & Hoberg 2000, Hoberg *et al*. 2003, 2009).

The Beringian Coevolution Project (BCP), initiated in 1999, represents a primary model for integrated survey and inventory of northern fauna (Hoberg *et al.* 2003, Cook *et al*. 2005). The BCP was designed to:

1. provide a detailed and geographically widespread resource of museum specimens from key high-latitude areas that had not been inventoried,
2. develop a comparative framework for Beringia to examine the history of host-parasite systems that are phylogenetically and ecologically disparate, providing the basis for detailed studies in coevolution and historical biogeography,
3. explore large-scale physical (climate variation) and biotic forces that have structured high-latitude biomes, including drivers of intercontinental faunal exchange across the North, and
4. build a spatial and temporal foundation at fine scales for investigations of Arctic biodiversity by identifying regions of endemism and contact zones between divergent lineages while exploring fundamental mechanisms that determined faunal diversity within complex biotic systems.

**Figure 15.2.** A model for integrated survey and inventory to explore diversity in northern host-parasite systems. Ecosystem and multi-species approaches rely on field-based collections of macroparasites and microparasites that result from collaborations among parasitologists, wildlife biologists, ecologists and local communities. Specimens are deposited in archival collections, where geo-referenced data are linked to tissues and vouchers for hosts and parasites, along with their definitive identifications. Biodiversity information becomes the focal point for diagnostics, development of temporal and spatial baselines, and diverse research activities including ecological modeling and prediction in a regime of environmental change. Archives representing specimens and informatics become the baselines to define faunal diversity and against which environmental perturbations may be assessed. As a limited example of integrated and ecosystem level survey in the Bering Sea, counter-clockwise from the top: Steller's sea eagle *Haliaeetus pelagicus*, rock sandpiper *Calidris ptilocnemis*, short-tailed shearwaters *Puffinus tenuirostris* and lesser numbers of sooty shearwaters *Puffinus griseus*, rhinoceros auklet *Cerorhinca monocerata*, crested auklet *Aethia cristata*, tufted puffin *Fratercula cirrhata* and black-legged kittiwake *Rissa tridactyla*. Photos: E.P. Hoberg.



The BCP has resulted in extensive archival collections of host and parasite specimens, including whole vouchers, tissues and DNA products from approximately 18,000 small mammals (primarily rodents, soricomorphs, lagomorphs and mustelids representing 80 species and 31 genera, with additional materials from high latitude ungulates) across 250 sites spanning > 100° longitude and > 25° latitude in Siberia, Alaska and Canada. Specimens and information are housed in permanent museum repositories including the Museum of Southwestern Biology, University of New Mexico, the University of Alaska Museum of the North and the US National Parasite Collection (Cook *et al.* 2005). A crucial foundation and unique baseline of information for hosts and parasites is emerging and under current evaluation for basic research and conservation in the face of changing climate and increasing anthropogenic impacts at high latitudes (Arctos 2012).

In parallel, the International Polar Year (2007-2008) provided the opportunity to focus on health, status and population trends for caribou and reindeer through the CircumArctic Rangifer Monitoring & Assessment Network (CARMA). From 2007 to 2009, this network developed and implemented standardized sample and data collection protocols to evaluate the body condition, demographics and health of multiple herds in North America, Greenland and Russia. CARMA also built on existing programs (Brook *et al.* 2009) to develop training materials to facilitate hunter-based health monitoring for caribou. Development of locally supported, effective and efficient monitoring programs that can provide long-term data are dependent on assessing protocols and by adapting methods that are most appropriate at the community level across region.

Another mechanism for ongoing parasite monitoring is through local programs. For example, due to food safety issues, the Nunavik Trichinellosis Prevention Program was established in Kuujjuaq, Quebec (formerly Fort Chimo) by the Nunavik Research Centre (Proulx *et al.* 2002). This program serves to monitor prevalence, intensity and geographic distribution of *Trichinella* in walrus from Nunavik. Such a program may have general applicability across the Arctic given ongoing perturbation at the ecosystem level and projected changes for the distribution of *Trichinella* in marine mammals (Rausch *et al.* 2007).

The importance of efforts to improve methodologies that facilitate sample and data collection in the field cannot be overestimated. The Arctic continues to be a logistically challenging region for field biology and assessment of pathogens and the distribution of disease. As much as is possible, knowledge of parasite diversity should be linked directly to specimen-based information. The primary cornerstone will be integrated survey and inventory supporting surveillance (active systems designed to discover general patterns of abundance, prevalence or incidence) and monitoring (ongoing assessments of health status of specific animal populations) (Salman 2003) that contributes to archival collections (parasites, hosts and tissues) as a permanent record of environments in dynamic change (e.g. Hoberg *et al.* 2008b, Cook, Chapter 17). Such archival resources, as self-correcting records of biodiversity, will be increasingly important in the arenas of ecosystem sustainability, human health and conservation (Hoberg *et al.* 2003, Koehler *et al.* 2009, MacDonald & Cook 2009).

### 15.9.2. Anticipated important host-parasite assemblages and processes

The presence of diverse assemblages of parasites is indicative of a healthy ecosystem (Marcogliese 2005, Hudson *et al.* 2006). The presence of parasites is an indicator of ecosystem stability and the connections that fishes, birds, mammals and invertebrates have within and across complex foodwebs in aquatic and terrestrial environments (Lafferty *et al.* 2006, Amundsen *et al.* 2009). Following from this complex web of interactions, parasites tell stories about where host individuals, populations and species have been (in migration), what they eat and where they spend their time. Consequently, perturbations in ecosystems are often reflected in the diversity and spectrum of parasites that occur at landscape to regional scales (Hoberg 1996, Marcogliese 2001). These relationships serve to indicate the importance of understanding parasite diversity in space and time (Hoberg 1997, Brooks & Hoberg 2000).

The biodiversity crisis is not simply an issue of ecosystem perturbation and species loss, but also one of emerging infectious diseases in both wildlife and people (Daszak *et al.* 2000, Brooks & Hoberg 2006). Fundamental to either an invasion or emergence of parasites is breakdown in environmental structure or ecological isolation driven by natural or anthropogenic processes (e.g. Elton 1958, Hoberg 2010). Ecological disruption with the development of new borderlands or ecotones is also central to the process for expanding host and geographic ranges for assemblages of parasites. Analogues based on historical processes for episodes of climate change can serve to inform us about how complex host-parasite systems in the Arctic have been structured by events in the Quaternary Period during the last 2.6 million years (e.g. Rausch 1994, Hoberg *et al.* 2003, 2012). Dispersal, range shifts, colonization of new geographic regions and switching of parasites among host species and within ecosystems are fundamental characteristics of northern systems, and these mechanisms are equivalent in evolutionary and ecological time (Hoberg & Brooks 2008, Hoberg *et al.* 2012). The nature of invasion and emergence, however, suggests that it not always simple to predict how assemblages of hosts and parasites will respond to transitional conditions, particularly those associated with accelerated climate change in contemporary northern systems (Marcogliese 2001a, Hoberg *et al.* 2008a, 2008b, Kutz *et al.* 2009a, 2012, Hoberg 2010, Gilg *et al.* 2012). These factors heighten the need for comprehensive surveys to establish baseline faunal associations for poorly known hosts or among host-groups identified as keystones within specific ecosystems (Appendix 15.1). Application of model-based approaches, particularly ecological niche modelling, in conjunction with detailed records from archival collections can also contribute to an understanding of the consequences of environmental change on the distribution of parasites and disease (e.g. Waltari *et al.* 2007b, Waltari & Perkins 2010).

Establishing baselines for diversity is central to identifying the role of parasites in an ecosystem, among host groups, host species and populations (Appendix 15.1). Baseline data provide a way to identify trends in host and geographic distribution or abundance, which may reflect changing ecological conditions. There is a distinction between numerical trends (difficult to acquire), versus faunal trends, or evidence of range shifts and development of new host-parasite associations. Both may be indicators of shifting patterns of abundance for host organisms where host density is a factor that directly influences the potential for expansion and successful establishment by parasites (Skorping 1996, Marcogliese 2001a, Hoberg 2010). Consequently, our recommendation is that field biologists exploring populations of fishes, birds or mammals incorporate parasitology as an integral component of their research and management programs. If vertebrate populations are worthy of monitoring because of their perceived and real value, then parasites should concurrently be of equal importance because of what they reflect about the state of the biosphere.

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Appendix 15: www.abds.is/aba-2013-appendix-15

An increasing number of human-introduced species are becoming established in the Arctic and putting indigenous species under pressure. Many more potentially disruptive alien species are found in the sub-Arctic and will probably be able to spread northward in a warming climate. One such species is Nootka lupin *Lupinus nootkatensis* spreading extensively in Iceland and also found in S Greenland. Photo: Sigurður H. Magnússon.

## Chapter 16

# Invasive Species: Human-Induced

**Authors**
Dennis R. Lassuy and Patrick N. Lewis

## Contents

> » **Mink have spread and become more and more common. I believe they come here both from south [of Finland] and from Norway. Minks are real pests; they eat fish from creeks and ptarmigans and whatever they can catch.**
>
> Late Saami reindeer herder Ilmari Vuolab, Finland;
> Helander *et al.* 2004.

## SUMMARY

As human society has become more mobile, the transfer of species beyond their native ranges has similarly increased. Human-induced biological invasions now occur around the world and are a leading cause in the loss of biodiversity. While few invasions are currently known from the Arctic compared with lower latitudes, changes in climate and patterns of human use are likely to increase the susceptibility of Arctic ecosystems to invasion. Much of that increased risk of invasion may come from increased shipping, energy development, mineral exploration and associated shore-based developments such as ports, roads and pipelines.

Because future change will be best understood when measured against a credible baseline, much more work is needed to define the current status of native and invasive species populations in the Arctic. The development of cost-effective early detection monitoring networks will be a challenge, but can be informed by Traditional Ecological Knowledge and may benefit from engaging a network of citizen scientists. There also needs to be increased and targeted prevention efforts to limit the influx of non-native species (e.g. ballast water treatment and the effective cleaning and treatment of ship hulls and drilling rigs brought in from other marine ecosystems).

## 16.1. INTRODUCTION

As humans and their goods and services have become increasingly mobile, the intended and unintended transfers of species have also increased. In many cases, the intended benefits of species movement (food, fiber, recreation) have been realized. In other cases, both unintentional and intentional introductions have had harmful results (OTA 1993). The term ‘invasive species’ is used here to refer to species that are not native to a given ecosystem (i.e. when a species is present due to an intentional or unintentional escape, release, dissemination or placement into that ecosystem as a result of human activity) and which may cause economic or environmental harm (including harm to subsistence species and activities) or harm to human health. This definition includes species that disperse secondarily from a site of introduction. It should be noted that even non-native species considered to pose no invasive threat at the time of introduction may exhibit explosive population growth long after their initial establishment in a new environment (Sakai *et al.* 2001), leading to invasive impacts despite initially being considered benign.

Biological invasion is widely recognized as second only to habitat alteration as a factor in the endangerment and extinction of native species and may be the less reversible of the two (Lassuy 1995, Wilcove *et al.* 1998). Indeed, many now consider invasive species and climate change to be among the most important ecological challenges facing global ecosystems today (Vitousek *et al.* 1997, Clavero & Garcia-Berthou 2005, Mainka & Howard 2010, IUCN 2012). The combined effects of invasive species and climate change on biodiversity and ecosystem function can be far reaching; for example, altering community composition, community structure, trophic pathways, trophic interactions, native species distribution, habitat structure and even the evolutionary trajectory and fitness of native species (Mooney & Cleland 2001, Hellman *et al.* 2008, Rahel & Olden 2008). The impacts of invasive species are also not limited to ecological harm. A subset of just 16 of Canada’s over 1400 identified invasive species has had an estimated annual economic impact of $13-34 billion CAD (Colautti *et al.* 2006). In the United States, economic impacts of invasive species have been estimated to be in excess of $138 billion USD per year (Pimentel *et al.* 2000).

Impacts of invasive species on cultural systems are harder to define, but two things are clear: (1) as native biodiversity is lost, so too are the potential human uses of that biodiversity, and (2) a warming climate will increase the likelihood of immigration into the Arctic of warm adapted species (e.g. Weslawski *et al.* 2011), including those mediated by human activities. The combination of these two factors, plus the use by many Arctic residents of native flora and fauna for subsistence, suggest that biological invasions are a critical and complex issue requiring further study and action. For example, invasive species may force traditional knowledge to adapt and new harvesting patterns to be developed.

## 16.2. STATUS AND TRENDS

Biological invasions are known from around the globe, but fewer are known from the Arctic compared with lower latitudes. Perhaps the best known Arctic invasion examples are American mink *Mustela vison* in Iceland and northern Scandinavia (Birnbaum 2007), Nootka lupin *Lupinus nootkatensis* in Iceland (Magnusson 2010) and Pacific red king crab *Paralithodes camtschaticus* in the Barents Sea (Oug *et al.* 2011). In the case of the American mink, its introduction has been cited as a factor in population declines of ground nesting birds and small mammals, as well as the decline of the native European mink *Mustela lutreola* (Bevanger & Henriksen 1995, DAISIE 2012).

The pattern of fewer invasive species at high latitudes may in part reflect that there have been fewer Arctic studies, but it is also consistent with the findings of de Rivera *et al.* (2005) whose work on marine ecosystems found a pattern of decreasing diversity and abundance of non-native species with increasing latitude. For terrestrial plants, M. Carlson (pers. com.) suggests a range of potential mechanisms that may contribute to this reduced pattern of non-native species invasion at high latitudes:

- Increasing proportion of widespread species at higher latitudes (i.e. less regional endemism translates into fewer species that *could* show up as new);
- Some Arctic and sub-Arctic habitats were recently disturbed by glaciations and are colonized by highly ruderal species already;

- Movement of propagules in the circumpolar region appears to be facilitated by ice, winds and currents (Abbott & Brochmann 2003); and
- Densities of people, roads and substrate disturbance decreases with increasing latitude.

This does not mean the Arctic is not susceptible to invasion. In fact, changes in climate and patterns of human use are likely to increase that susceptibility. For example, de Rivera *et al.* (2011) suggest that several marine invasive species, such as European green crab *Carcinus maenas* introduced to the US West Coast, have the potential to secondarily expand into sub-Arctic and Arctic waters even under moderate climate change scenarios. Similarly, Ruiz & Hewitt (2009) concluded that "environmental changes may greatly increase invasion opportunity at high northern latitudes due to shipping, mineral exploration, shoreline development, and other human responses." Christiansen & Reist (Chapter 6) suggest "the high potential for negative effects on native species" from introduced fish species (e.g. from aquaculture and translocations) warrants a heightened concern, a finding generally consistent with observations at lower latitudes (Lassuy 1995). To this list of potential Arctic invasion sources we can certainly add tourism, both land- and ship-based, as an increasingly important pathway. Each of these could increase the numbers and dispersal patterns of invasive species or their propagules.

The introduction of invasive species complicates ecological interactions that are already responding to northward expansion of naturally occurring species (Cheung *et al.* 2009). Ruiz *et al.* (2000) found that the rate of marine invasion is increasing; that most reported invasions are by crustaceans and molluscs; and, importantly, that most invasions have resulted from shipping. Other studies (Lewis *et al.* 2003, 2004) found that the external hull and ballast tanks of vessels operating in ice-covered waters can support a wide variety of non-native marine organisms. The combined findings of these studies have a great deal of relevance for future marine invasive risks to Arctic waters, especially in light of a recent analysis of current Arctic shipping (Arctic Council 2009) and the expansion of shipping being observed along both the Northeast and Northwest Passages as the Arctic becomes increasingly ice free (Fig. 16.1; ENR 2011, Ware *et al.* 2013). There are many other potential vectors of aquatic invasive species introduction (marine debris; translocated piers, docks and pilings; aquarium dumping; scientific and industrial instrumentation; and so on) but most of these, except perhaps the instrumentation, are not yet very prevalent in the Arctic.

To date, many fewer non-native terrestrial plants have been recorded in the Arctic than in the more highly altered and invaded ecosystems of lower latitudes. However, Nootka lupin has invaded disturbed sites and heathland vegetation in almost all of Iceland and also occurs in SW Greenland, where it has apparently not yet spread into the tundra vegetation (Daniëls *et al.*, Chapter 9). Even in the high Arctic, a number of non-native terrestrial plant species have been recorded. In Svalbard, Elven & Elvebakk (1996) reported that 15% of the flora from a survey was non-native, and Gederaas *et al.* (2012) describe nine species as actively reproducing. Here, Coulson *et al.* (2013) also found numerous non-native invertebrates, apparently largely brought in with soil for greenhouses. Similarly, over a dozen non-native plant species are already known from both the Canadian low and high Arctic ecozones and many more occur in the sub-Arctic (Canadian Food Inspection Agency 2008).

In Arctic Alaska, 39 taxa of non-native plants (7% of its total Arctic flora) have already been reported (Carlson

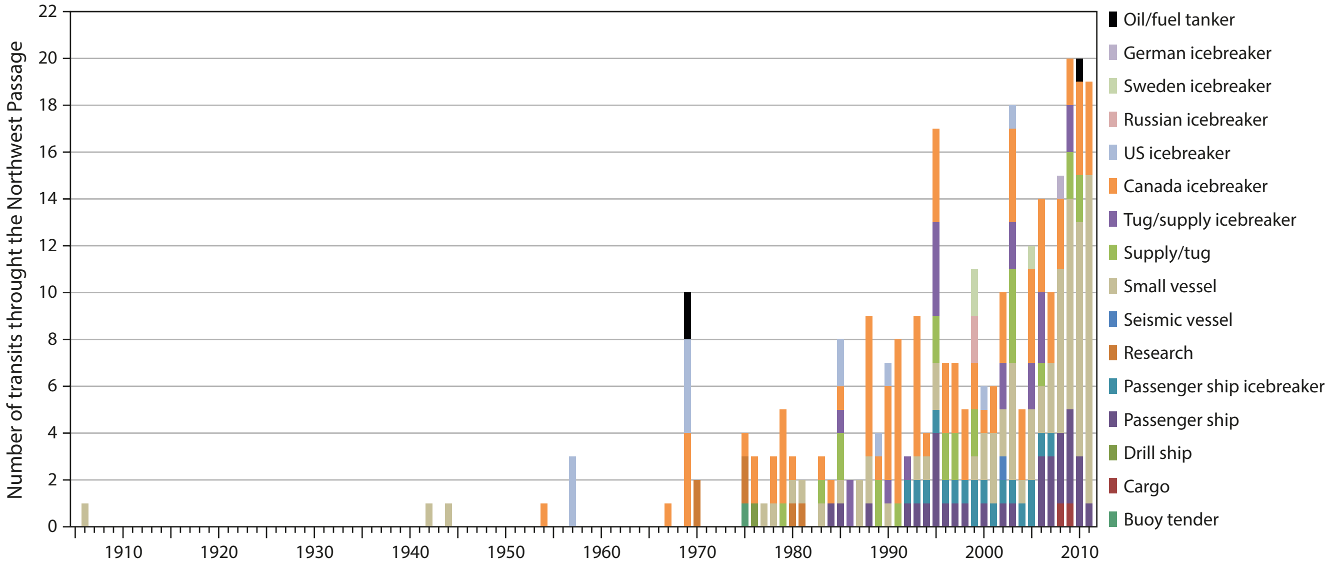

**Figure 16.1.** Ship transits of the Northwest Passage 1906-2011. From the NWT State of the Environment report (ENR 2011) with data from NORDREG updated to 2012.

*et al.* 2008), and the rates of introduction and establishment in natural systems in Alaska are accelerating (Carlson & Shephard 2007). Among the known non-natives are several highly invasive grasses and clovers. For example, white sweetclover *Melilotus alba*, which was extensively used as a forage crop for cattle and a nectar source for introduced honeybees, has now spread up the road system to the sub- and low Arctic in both United States and Canada (Oldham 2007). This nitrogen fixing invader has the potential to alter soil chemistry and has been shown to increase mortality of co-occurring plants, potentially altering successional pathways on floodplains (Spellman & Wurtz 2011).

In the Alaskan sub-Arctic, over 75 invasive plant species have been recorded with a dozen of them ranked as 'highly' or 'extremely' invasive (AKEPIC 2012). In addition to white sweetclover, other extremely invasive plant species include spotted knapweed *Centaurea stoebe*, reed canarygrass *Phalaris arundinaceae* and ornamental jewelweed *Impatiens glandulifera*. Among the highly invasive non-native plant species are orange hawkweed *Hieracium aurantiacum*, western waterweed *Elodea nuttallii* and cheatgrass *Bromus tectorum*, all of which are well documented as being capable of dramatically altering ecosystem function. With climate change enabling invasive species range expansion and resource development intensifying and expanding invasion pathways, the susceptibility of the Arctic to non-native species invasion, particularly from the neighboring sub-Arctic zone, is certainly increasing.

## 16.3. CONCLUSIONS AND RECOMMENDATIONS

As climate change alters Arctic ecosystems and enables greater human activity, biological invasion in the Arctic is likely to increase. Arctic terrestrial ecosystems may be predisposed to invasion because many invasive plants are adapted to open disturbed areas (Hierro *et al.* 2006), and Arctic habitats are characterized by extensive freeze-thaw cycles and other disturbances. If fire frequency and intensity increase with climate change (Hu *et al.* 2010), this may further enhance invasion susceptibility. Areas of human disturbance and those located along pathways of human activity (e.g. shipping and road corridors) are the most likely sites of invasion for Arctic habitats. For example, Conn *et al.* (2008) noted the susceptibility of gravel-rich river corridors to white sweetclover dispersal from bridge crossings.

The ability for a warming climate to directly enhance invasion through altered recruitment timing and growth dynamics has been demonstrated for marine tunicates (Stachowicz *et al.* 2002). The spread of invasive marine tunicates to the Arctic could interfere with access to benthic food sources for already at risk marine mammals like benthic-feeding whales and pinnipeds. There are similar concerns regarding the effects from the introduced red king crab on benthic communities in northern Norway and the Kola Peninsula (Oug *et al.* 2011). Further introductions may contribute to accelerated and synergistic impacts (Simberloff & von Holle 1999). Range map scenarios developed for 16 extremely or highly invasive plants either occurring in or at risk of invading Alaska (Bella 2009) also paint a sobering outlook for the future. Fig. 16.2 depicts the potential expansion of one well-known invasive aquatic plant, the waterweed *Hydrilla*, northward into the aquatic ecosystems of Arctic Alaska and far eastern Russia.

Because future change will be best understood when measured against a credible baseline, much more baseline survey work similar to that of Ruiz *et al.* (2006) is needed. Due to the distribution of resources in the Arctic, the development of cost-effective early detection monitoring networks will be a challenge. However, Arctic residents possessing traditional knowledge may greatly assist information gathering and monitoring design by offering observations and evaluations of changes. Engaging a network of citizen scientists, for example through school systems and other public involvement mechanisms, may also offer low-cost and sustainable enhancements to conventional monitoring approaches. The increasingly widespread use and adaptability of tools like smart phones and software applications may also help. The key to an effective citizen as well as professional science network will be strong integration and information flow to and from central repositories, for example the European Network on Invasive Alien Species (NOBANIS 2012) and the Alaska Exotic Plant Information Clearinghouse (AKEPIC 2012). However, even these valuable data repositories could additionally benefit from improved collaboration on standards for databases, reporting and access. The existence of a credible baseline, combined with cost-effective early detection monitoring and information sharing networks (particularly at invasion-susceptible locations like roads, airports and harbors), will also enhance rapid response capabilities for more environmentally and economically efficient eradication early in the invasion process.

In addition to valid baselines and improved monitoring, there will need to be increased and targeted prevention efforts to limit the influx of non-native species (e.g. effective cleaning and treatment of ship hulls and drilling rigs brought in from other marine ecosystems, and ballast water treatment consistent with the recommendation of the Arctic Marine Shipping Assessment; Arctic Council 2009, 2011). Such measures should be complemented with targeted management plans for activities known to present a high risk of introduction (Ware *et al.* 2013). For example, petroleum drilling rigs have been identified as a significant risk for modern marine introductions, and the increase of petroleum extraction in the Arctic should be accompanied by stringent cleaning and monitoring requirements (NIMPIS 2009). For all invasive species, terrestrial and aquatic, there should be more consistent use of basic prevention tools such as Hazard Analysis & Critical Control Points (HACCP)

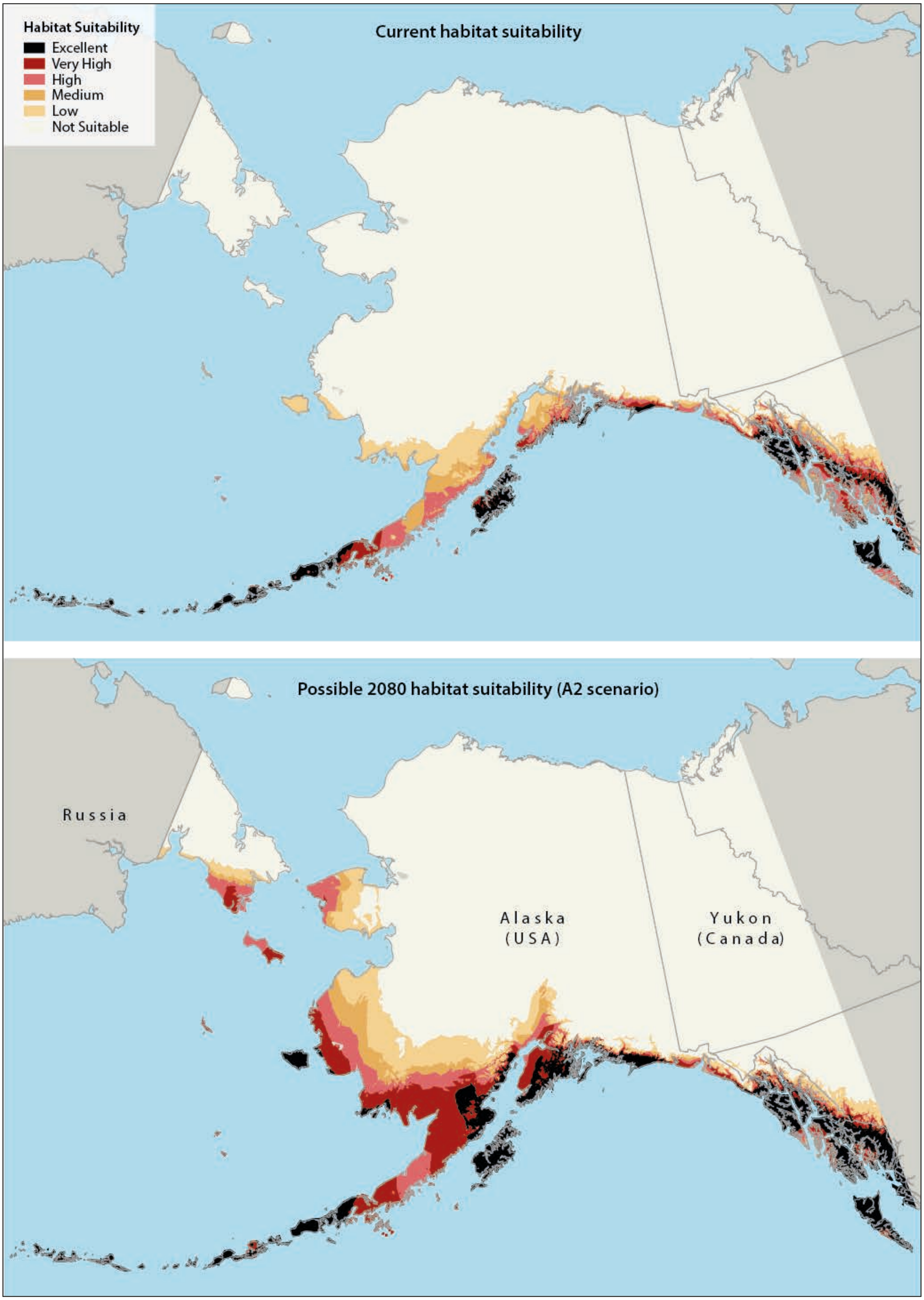

**Figure 16.2.** Current potential range of non-native aquatic plant hydrilla *Hydrilla* spp. if it invaded Alaska today and projected potential range with climate warming. (Adapted from Bella 2009).

planning (ASTM 2009) and more attention to pathway risk assessment. Snyder & Anions (2008) provide an excellent example of the use of a pathway-based approach for invasive plants and insects in Northwest Territories, Canada. Chown *et al.* (2011) provide another excellent example of a pathway-based risk assessment in Antarctica, with some interesting comparisons of tourist versus scientist visitors as vectors of plant propagules.

Two additional future Arctic risks that may accompany climate change are: (1) invasive species, much like climate change, can decrease stability and increase uncertainty in ecosystem function and the evolutionary trajectories of species, and (2) as more temperate ecosystems feel the effects of these climate-induced uncertainties, there may be a push to resort to using Arctic ecosystems as refugia at the receiving end of well-intended but risky efforts to 'assist' species in the colonization of new habitats (Ricciardi & Simberloff 2009). Since species' ability to successfully invade will vary with their physiological capacities and dispersal ability (both natural and susceptibility to human transport), much work is also needed on basic biology and life history traits of potential Arctic invaders in order to effectively assess Arctic vulnerabilities and risks. Finally, we recognize there are many other invasive species such as insects and pathogens that are of potential concern for Arctic ecosystems and people, but these are beyond our expertise and are, at least in part, covered in other sections of this report.

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The lesser snow goose *Chen c. caerulescens* shows an approximate east-west cline in their Nearctic breeding distribution in frequency of pale or dark morphs, with blue morphs most common in the east. Although studies of fitness components failed to uncover any adaptive advantage associated with either morph, geese show strong mating preference based on the color of their parents, leading to assortative mating. Queen Maud Gulf Bird Sanctuary, Nunavut, Canada. Photo: Gustaf Samelius.

*Chapter 17*

# Genetics

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## Contents

> **Knowledge exists, we live it. But I do not think about that ever. It is just there. We still follow the old ways. Naturally. This is our way.**
>
> Isak Påve, a Saami reindeer herder from northern Sweden; Hiltunen & Huovari (2004).

## SUMMARY

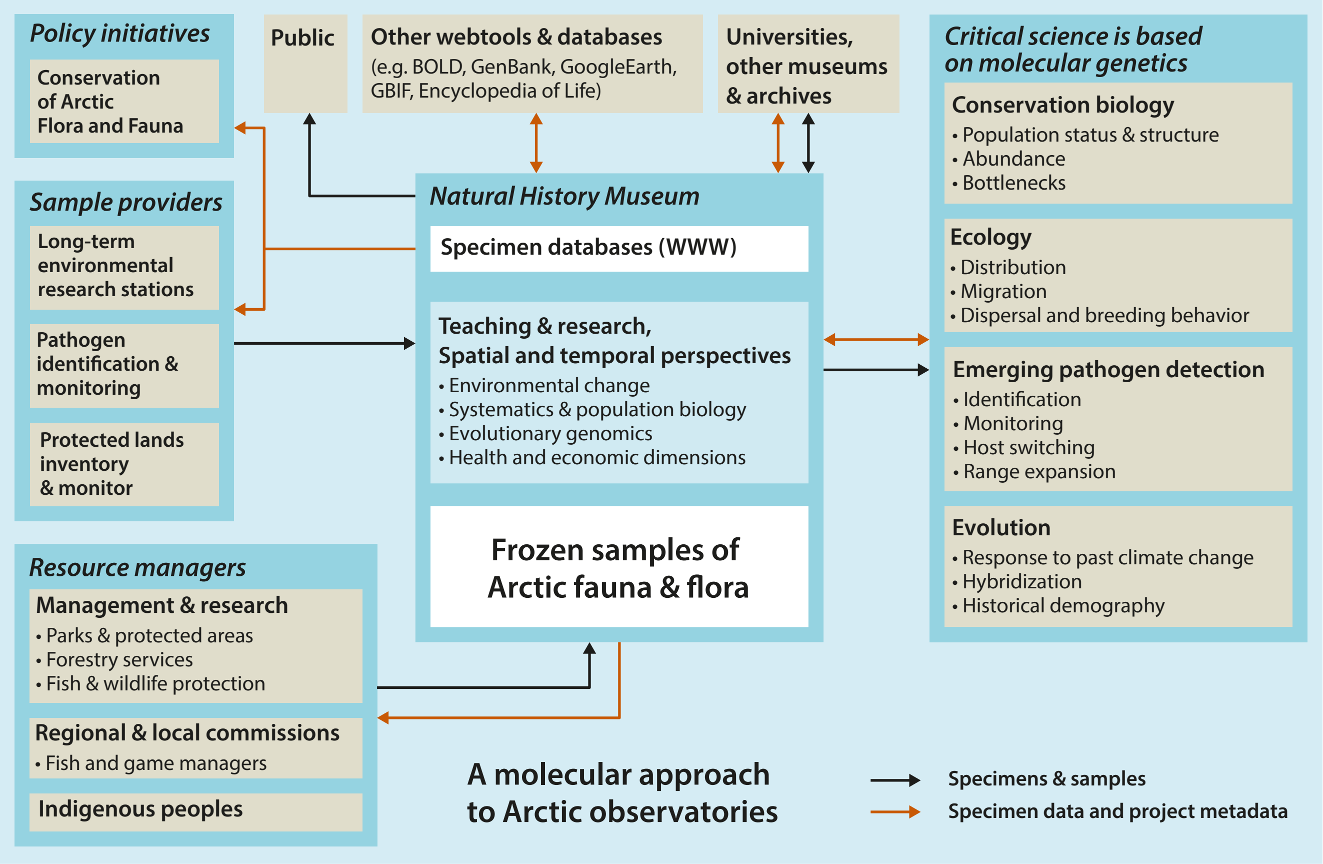
The impact of climate warming on Arctic organisms is complex, and its interpretation will require a concerted effort. To mitigate the impact of climate-induced perturbations, an essential first step is to develop an understanding of how high latitude species and ecosystems were influenced by past episodes of dynamic environmental change. One of our best views of past change in Arctic populations is through molecular genetics (e.g. DNA studies). DNA-based views provide a basis for forecasting how biomes and individual species will respond in the future and thus are a key component of an advanced early-warning system for natural environments of the Arctic.

Species typically adapt to new conditions or shift into new areas, but a number of Arctic species are now experiencing a reduction in their distributions, abundance and ability to exchange individuals among populations. Molecular genetic approaches are used in a wide range of studies to provide comprehensive assessments of how species interact with their environments. Important insights have been gained related to the conservation status of high latitude species of concern, but because Arctic environments are remote and difficult to access, only limited information is available about most essential factors for organisms (e.g. contemporary genetic diversity, evolutionary history, modes of reproduction). A coordinated investment in biological infrastructure is needed now (similar to that already in place for monitoring the physical environment) if we are to apply and realize the powerful insights provided by molecular genetics.

## 17.1. INTRODUCTION

Maintaining genetic variation in wild populations of Arctic organisms is fundamental to the long-term persistence of high latitude biodiversity. Variability is important because it provides options for species to respond to changing environmental conditions and novel challenges such as emerging pathogens or invasive species. As individual species decline in abundance and their geographic distributions shrink, genetic variability is also often eroded. It is important to realize that we have not yet developed a basic understanding of how genetic variability is partitioned across space or time in the Arctic. Furthermore, we lack information on how genetic variation, and the related concept of evolutionary potential, is generated and maintained for most Arctic organisms, whether free-living or parasitic. Fortunately, new technologies and analyti-

**Figure 17.1.** An Arctic Observatory showing the centrality of a natural history museum to multiple research, teaching, management, policy and outreach initiatives in the Arctic. Of particular importance for molecular genetic analyses is the availability of an archival repository of biotic samples that allow a rapid and rigorous response to emerging natural resource questions. Critical science in several fields related to Arctic biodiversity is now based on molecular genetic approaches and depends on temporally deep and spatially extensive archives for many organisms. Through the development of databases for these archives that are now accessible via the internet, the specimens become central to attempts to connect research to policy and the general public.



cal approaches now afford the possibility of much more comprehensive and refined views of genetic variation, but realizing the potential of these new approaches will foremost require a renewed effort to inventory and rigorously document Arctic diversity at all levels (Fig. 17.1). A revitalized effort to explore diversity will provide the foundation necessary for a variety of theoretical and applied endeavors, ranging from uncovering the history of diversification and extinction of organisms, to tracking and mitigating emerging pathogens and invasive species, to developing robust projections for the long-term security of subsistence or traditional foods in the Arctic.

Traditional ecological knowledge (TEK) should also be an integral part of Arctic biodiversity assessment (Usher 2000). In particular, this knowledge can help determine how to more effectively study Arctic fauna and flora. For example, rural coastal villages in Alaska have been instrumental in providing unprecedented sampling of marine mammal populations through subsistence harvests. In Canada, populations of the northern Dolly Varden *Salvelinus m. malma* are found in the western Arctic region (i.e. tributaries of the Mackenzie River largely along its western bank), and these are of tremendous significance to indigenous peoples of the region. The subspecies was recently assessed as a taxon of Special Concern by Canada's Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2011). A key feature of the biology of this fish is habitat located within overwintering sites characterized by groundwater upwelling that maintains ice-free habitat, and where fish congregate in large numbers. Despite the vast extent of occurrence of the subspecies' distribution across the western sub-Arctic (e.g. ~ 227,000 km$^2$), these essential overwintering sites number fewer than 20 and have a combined area of less than 1 km$^2$. The locations and the limited numbers of these key habitats were obtained in large part from TEK which was, therefore, critical to the status assessment and subsequent derivation of a conservation management plan.

This chapter does not tackle the thorny issues related to bio-prospecting and commercialization of Arctic genomic resources or introduction of genetically modified organisms. Instead, we provide an overview of not-for-profit approaches to studying genetic diversity in the Arctic emphasizing that an understanding of the influence of deeper (evolutionary) time in structuring diversity is essential to predicting future responses and persistence of the incomparable fauna and flora of the northern high latitudes of our planet.

## 17.2. SYSTEMATICS, PHYLOGENETICS AND PHYLOGEOGRAPHY

### 17.2.1. Systematics

More than any other approach, systematics integrates across all other sub-disciplines of the biological sciences by establishing the evolutionary map necessary for discovering, categorizing and interpreting biological diversity. Without this map it is impossible to even ask pertinent questions related to change in Arctic environments. Aside from the more 'charismatic' species, our knowledge of the systematics of the vast majority of Arctic organisms remains poor. We emphasize two particular aspects of systematics that are closely interlinked, *phylogeny* (evolutionary relationships) and *taxonomy* (species delimitation and a standard nomenclature) of Arctic organisms. A strong commitment to these fields is required, if we hope to explore and effectively document diversity and ultimately mitigate the impact of environmental change on the outstanding natural environments of the North. Concurrently, this knowledge contributes to the broader issues of food security as well as sustainability, viability and availability of critical biological diversity, which is the cornerstone of subsistence food webs. Systematics is, therefore, an integral facet of ecosystem management and wildlife conservation across the Arctic (e.g. Kutz *et al.* 2009a).

#### 17.2.1.1. Phylogenetics and taxonomy

*Phylogenetics* is the study of the relationships among various groups of organisms, based on evolutionary similarities and differences. Above the population level, phylogenetics becomes a history of speciation, with species viewed as independent lineages (i.e. they are on different evolutionary trajectories). Phylogenetic trees reveal history and constrain explanations about the origins and distribution of biotic diversity. *Taxonomy* is the theory and practice of classifying organisms (Mayr 1969). Early taxonomic studies relied almost exclusively on morphological variation, but now new ways of probing diversity based on molecular genetics are providing more refined views of geographic variation. Limitations imposed by a poorly developed taxonomic framework can have disastrous conservation consequences (Mace 2004). Taxonomy provides the classification system for organisms that is the basis for rigorous project design and efficient prioritization of funding. More than just providing a universally accepted name or common language for scientists and managers, though, a taxonomic framework should accurately reflect the evolutionary relationships among organisms. Systematics and taxonomy places history on the table and provides the direct connections linking evolution, ecology and biogeography. This predictive framework then allows us to rapidly investigate and identify emerging threats such as the presence of pathogens and disease (Vapalahti *et al.* 1999, Brooks & Hoberg 2006, Dragoo *et al.* 2006, Kang *et al.* 2009).

#### 17.2.1.2. Systematics and phylogenetics in Arctic species

In general, incomplete taxonomic information and discrepancies in identification between studies have severely hampered efforts to quantify the number of extant species globally and to delineate their respective ranges. The Arctic is no exception. There are large gaps in our knowledge of Arctic biodiversity for certain groups, such as the marine, terrestrial and freshwater invertebrates (Hardy *et al.* 2011, Hodkinson, Chapter 7). However, even for better-studied groups of Arctic organisms, such as vertebrates and vascular plants (Appendix 17.1), the ability to identify important forces shaping biodiversity is complicated. Vascular plants exemplify this complexity.

Next to vertebrates, vascular plants represent the most-explored group of Arctic organisms in terms of systematics. Progress towards a unified Arctic-wide taxonomy for vascular plants has long been hampered by widely different traditions among European, Russian and North American plant taxonomists (see Daniëls *et al.*, Chapter 9). Inherent problems in the Arctic flora persist, including notorious taxonomic complexities due to hybridization, reticulate evolution, inbreeding/asexuality and occurrence of very widespread species with complex morphological variation. Nevertheless, recent progress has been made in the production of the first consensus checklist for all Arctic vascular plant species (VPAF-The PanArctic Flora Checklist; Elven 2011), in which many plant groups are revised based on recent molecular studies. Approximately 2,200 species and subspecies are listed in VPAF, but only about 1,000 of them are part of the regular Arctic flora; the remainder are mainly boreal taxa that only have occasional Arctic occurrences. Only 106 taxa can be classified as Arctic endemics, i.e. with their ranges limited to the Arctic (Daniëls *et al.*, Chapter 9).

The Arctic flora, considered young in evolutionary terms, is inferred to have formed only 2-3 million years ago when continuous Tertiary forests gave way to the tundra ecosystem in response to a colder climate. The flora is composed of a mixture of lineages resulting from immigration from southern mountains, dispersal across Beringia, *in situ* Pleistocene speciation and probably *in situ* survival of some Tertiary forest elements (Murray 1995, Ickert-Bond *et al.* 2009). Evidence suggests that some Arctic plant species, such as mountain sorrel *Oxyria digyna* and Iceland purslane *Koenigia islandica* are probably very old (Murray 1995), while others, such as purple saxifrage *Saxifraga oppositifolia*, netleaf willow *Salix reticulata*, black crowberry *Empetrum nigrum*, bog blueberry *Vaccinium uliginosum*, Arctic white heather *Cassiope tetragona* and mountain avens *Dryas octopetala*, are thought to have colonized the Arctic approximately 3 million years ago, most often from Beringia (Bennike & Böcher 1990, Matthews & Ovenden 1990, Abbott *et al.* 2000). Molecular data for several other Arctic plant groups show major episodes of speciation that occurred recently, probably within the period of the major ice ages (< 1million years; Brochmann *et al.* 2003, 2004, Brochmann & Brysting 2008). Phylogenetic reconstruction and DNA barcoding (Hebert *et al.* 2004) in many Arctic plant groups demonstrate little within-genus variation or none at all (Appendix 17.1), suggestive of recent speciation in spite of conspicuous morphological divergence (Carlsen 2007, Sønstebø *et al.* 2010).

Pleistocene speciation in Arctic plant groups occurred both at the diploid level and via polyploidization (genome doubling), which in most studied cases originated after hybridization between divergent lineages. Recent, recurrent polyploid evolution in plants, associated with climate shifts and postglacial colonization (reviewed in Brochmann *et al.* 2004) appears to be positively correlated with latitude. As much as 73% of Arctic specialists are polyploids; more than half of these are hexaploids or higher. Although there is no clear-cut association between the frequency or level of polyploidy and degree of glaciation, for Arctic specialists with restricted distributions, the frequency of diploids is much higher in unglaciated Beringia than in the heavily glaciated Atlantic area. This suggests that polyploids are more successful at colonizing after deglaciation. Polyploidy results in highly heterozygous genomes buffering against inbreeding depression and loss of genetic variability following long-distant colonization and through periods of climate change. A polyploid combines and preserves, in modified form, the genomes of all of the original diploid progenitor species. The average ploidy level of the 1,000 taxa in the regular Arctic flora is pentaploid. These Arctic plant species thus represent many more species (perhaps some 2,500) in terms of genetic or 'ancestral species' diversity. Also, there is a link between polyploidy and genetic diversity in Cladocera (Hodkinson, Chapter 7).

There is abundant molecular evidence for recurrent formation of Arctic polyploids from more or less divergent diploid or low-polyploid progenitors, and this may be an important means of incorporating several alleles at each locus. The high frequency of self-pollinating and asexual reproductive systems (Brochmann & Steen 1999), and reshuffling of populations during the glacial cycles has resulted in taxonomically intricate and high-polyploid species complexes in many plant groups. New genetic and analytical approaches can disentangle ancestral sub-genomes, making it possible to demonstrate recent and dynamic evolution of Arctic polyploid species complexes (Brysting *et al.* 2007; Appendix 17.1). These approaches can also be used to identify cryptic variation in Arctic species.

### Identifying cryptic variation

Research on cryptic species has increased over the past two decades, largely fueled by increasing availability of molecular data, including large-scale campaigns to generate and catalog DNA sequence data (DNA 'barcoding') that have revealed divergent groups not previously detected using morphological analyses (Appendix 17.2). Biological species diversity in the Arctic may be higher than the number of currently recognized species. While biodiversity in the Arctic is likely underestimated in poorly-known species (Hardy *et al.* 2011), previously unidentified genetic diversity has been uncovered there in invertebrates that had been assessed with traditional morphological approaches (Hodkinson, Chapter 7) and even in the most well-studied taxonomic groups, such as vertebrates and plants (Appendix 17.2). For example, the depth of mtDNA phylogenetic splits in two genera of Arctic lemmings suggests that continuous vicariant separation by glacial barriers over several glacial-interglacial cycles resulted in cryptic speciation across the Holarctic (lemmings: *Lemmus*; Fedorov *et al.* 1999a, 2003, *Dicrostonyx*; Fedorov & Goropashnaya 1999). Coincidentally, substantial cryptic diversity has been demonstrated for parasites circulating among assemblages of Arctic mammals (e.g. Cook *et al.* 2005). For avian species, DNA barcodes have uncovered Arctic species with deep intraspecific divergence (Kerr *et al.* 2007) that is thought to result from vicariant separation over several glacial cycles (Appendix 17.2). For Arctic plants, selfing provides instantaneous isolation from other lineages, thereby facilitating the accumulation of hybrid incompatibilities. For example, in Arctic withlow grasses *Draba* spp., rapid development of sterility barriers resulted in numerous but cryptic biological species within single diploid taxonomic species, to an extent unknown in other floras or plant groups (Brochmann *et al.* 1993, Grundt *et al.* 2006). Their recent Pleistocene origin suggests that cryptic speciation was rapid and possibly facilitated by genetic drift (Grundt *et al.* 2004, 2006, Skrede *et al.* 2008).

#### Coevolution of parasites and hosts: Examples from mammals

More than 40-50% of the organisms on the planet are parasites. Terrestrial, aquatic and marine systems all support diverse faunas of worms, arthropods, protozoans, bacteria and viruses dependant on vertebrate and invertebrate hosts. Parasites are not passive players, and interactions among parasites and their hosts shape ecosystems and food webs (Hudson *et al.* 2006, Dobson *et al.* 2008, Hoberg & Kutz, Chapter 15). Elegant research in parasitology has been conducted at high latitudes, particularly studies focusing on parasites transmissible to people (termed zoonoses) (e.g. Rausch 1951, 1967, 2003), but in many ways we still are only beginning to explore the extremely diverse world of these organisms. New studies emphasize the power of integrated survey and inventory involving geographically extensive and site intensive field collections in conjunction with molecular approaches to understanding diversity in complex biological systems in the North. Across the Arctic, for example, arvicoline rodents (e.g. *Microtus*, *Myodes*, *Lemmus, Synaptomys* and *Dicrostonyx*) share long coevolutionary histories with two groups of parasitic tapeworms: the anoplocephalines, *Anoplocephaloides* spp. & *Paranoplocephala* spp., and hymenolepidids *Arostrilepis* spp. (Rausch 1952, Haukisalmi *et al.* 2006, 2008, Haukisalmi 2009, Hoberg *et al*. 2012a). Both the host and parasite faunas appear to harbor substantial cryptic diversity that is just now being revealed through application of genetic tools to a large series of newly available samples from across the Arctic (e.g. Haukisalmi *et al.* 2001, 2002, 2004, 2008, Hoberg *et al.* 2003, Wickström *et al.* 2003, 2005, Cook *et al.* 2005). Similar cryptic lineages have been observed among nematodes in free-ranging ungulates, pointing toward considerably broader host and geographic ranges for pathogenic parasites in caribou (named reindeer in Eurasia) *Rangifer tarandus*, moose *Alces americanus*, wild sheep *Ovis* spp. and muskoxen *Ovibos moschatus* (e.g. Jenkins *et al.* 2005, Kutz *et al.* 2007, Hoberg *et al.* 2008) than previously described. Comparisons of host and parasite DNA-based phylogenies reveal complex histories of geographic colonization, host switching and varying degrees of cospeciation that provide substantial insights for conservation in the Arctic (e.g. Hoberg & Brooks 2008, 2010, Koehler *et al.* 2009).

## 17.2.2. Phylogeography – setting the stage for interpreting changing environmental conditions

Assessment of the spatial distribution of genealogical lineages within species is called phylogeography (Avise 2000, Knowles 2009, Hickerson *et al.* 2010), a relatively new field that bridges phylogenetic (macroevolution) and population genetic (microevolution) analyses. Phylogeography enables us to develop fundamental insights about evolutionary origins, biogeographic barriers, refugia, historical demography, concordant genetic patterns of different species within a single ecosystem, temporal niche conservatism, and evolutionarily significant units (ESUs). Ultimately, these biotic and abiotic attributes allow a range of future responses of species to be predicted.

### 17.2.2.1. Influence of dynamic climates on structuring Arctic diversity

The contemporary distribution of genetic diversity in Arctic organisms points to potential areas of long-term persistence of populations, possible directions of colonization, and areas where distinct biotic communities may come into contact and exchange pathogens (e.g. Koehler *et al.* 2009). The Arctic is an exceptional system for examining the influence of climatic events on the patterns and processes of genetic differentiation and prospects for long-term persistence among diverse organisms. A fundamental question is whether different species are responding to climate change in much the same way, or is each species independent (i.e. are there idiosyncratic signals across multiple species)? Furthermore, how do their responses influence population structure and life history? How does this view of history then feed into predictions about dynamic change in these systems?

### 17.2.2.2. Contact between divergent populations or species

Locales where different species or distinctive populations come together or contact each other are of special interest to biologists and can be studied using molecular genetic techniques (Hewitt 2011). If multiple species show similar patterns of contact, then these sites may represent suture zones (Remington 1968) and may be especially important to conserve. Are contact zones spatially and temporally contemporaneous across species? Although warming environmental conditions should be detrimental for many Arctic species, others may experience increased genetic variability, if contact occurs between previously separate populations or species (Box 17.1). When divergent Arctic populations of the same species or of closely related species contact and interbreed, the contact may lead to hybrid vigor and increased evolutionary potential, allowing organisms to cope with

## Box 17.1. Contemporary contact zones

A zone of secondary contact between two divergent groups of *Lemmus* lemmings likely reflecting recurrent isolation by the North American ice sheets was recently detected in central-eastern Alaska and Yukon (Fedorov *et al.* 2003). Phylogenetic division between these two groups was consistently supported by sequence variation in three independent genetic markers: mtDNA, X and Y chromosome introns (Fedorov & Goropashnaya 2009). Variation in these markers across the secondary contact zone revealed a limited number of introgressants (17%) of largely one hybrid type, suggesting that reproductive isolation in these lemmings may be the result of separation by continental ice sheets during Pleistocene glacial advances. This newly characterized contact zone contains the highest genetic diversity in these lemmings, and is situated in protected national parks (Wrangell-St. Elias, Yukon-Charley and Gates of the Arctic). This lemming hybrid zone provides an impetus for similar analyses in other species from this region, with implications for multi-species or community-level conservation strategies to ensure the maintenance of high levels of genetic variability.

## Box 17.2. Historic contact zones

Fish may experience the most extensive losses of genetic variability among vertebrate species. For example, two species of char (genus *Salvelinus*) come into contact in the Arctic basins of eastern Asia and western North America. Dolly Varden *S. malma* are distributed in the western and eastern portions of the Arctic in the Pacific Basin. Arctic char *S. alpinus* exhibit a wider, Holarctic distribution throughout northern Europe, Asia and North America (see Fig. 6.3 in Christiansen & Reist, Chapter 6). The two species are broadly sympatric at least in the western Arctic basin of North America. Genetic and morphological analysis of contact zones in two lakes in western Alaska suggest the two species exhibit strong habitat partitioning in sympatry (Dolly Varden in streams, small ponds and rivers; Arctic char in larger lakes), and show little evidence of contemporary hybridization. Mitochondrial DNA analysis, however, suggested that the species have undergone hybridization historically, presumably under different environmental conditions, suggesting that changing climates may impact their level of genetic and ecological interaction (Taylor *et al.* 2008).

altered environments. In some situations, contact may be detrimental by causing the disruption of coadapted gene complexes, extinction by hybridization (Rhymer & Simberloff 1996, Taylor *et al.* 2006), opportunities for host-switching by pathogens, or possible rearrangement of pathogen genomes that increases virulence. Instances of past contact can be uncovered with molecular genetics (Box 17.2).

### 17.2.2.3. Comparisons across species – influence of episodic expansion and isolation on structuring diversity

Repeated changes in climate during the Pleistocene caused Arctic species to move, adapt or go extinct. During the late Pleistocene, the Arctic megafauna experienced significant changes in geographic distribution and composition. Some Arctic large herbivores, such as mammoth *Mammuthus primigenius* and woolly rhinoceros *Coelodonta antiquitatis* became extinct, while others, such as saiga antelope *Saiga tatarica*, caribou and muskox survived into the present, but not necessarily at high latitudes (Appendix 17.3, Box 17.3 and 17.4). The causes of the late Pleistocene megafaunal extinctions are not totally understood, but changes in the climate, the arrival of humans, or a combination of these events may have served as triggers (Barnosky *et al.* 2004, Guthrie 2006). The survival strategy of large herbivores was different. For example, the nearly circumpolar Pleistocene distribution of the nomadic saiga antelope shifted to the dry steppe and semi-desert regions of Europe and Central Asia after the tundra-steppe ecosystems were replaced by taiga forests after climate amelioration during the Pleistocene-Holocene transition (Sokolov & Zhirnov 1998). Some herbivore species, such as caribou, retained their circumpolar range, while others experienced dramatic range contraction (Box 17.3 and 17.4). Such shifting patterns of sympatry and abundance have been considered as primary drivers for parasite faunal structure among Holarctic ungulates (e.g. Hoberg 2005, 2010). Investigations of the phylogeography of these species, especially those comparative studies that include both modern and ancient DNA, are helping to establish the reasons for widespread extirpation or extinction of elements of the megafauna, and can also provide insight into more contemporary patterns associated with domestication (Box 17.3).

We gain insight into how species in the Arctic will respond to future conditions by examining how they responded to past environmental changes. Molecular markers, along with fossils, provide that window into the past (e.g. Dalen *et al.* 2007). For species that moved, repeated contractions and expansions influenced evolutionary processes and left genetic signatures (Hewitt 2004, Excoffier *et al.* 2009) within species now inhabiting the Arctic. Species were fragmented into localized populations by glacial advances (e.g. many terrestrial species) or contractions (e.g. marine species) during the Ice Ages. Some of the cold-adapted Arctic species persisted during warm interglacials in northern refugia, expanding their ranges southward during glacial periods (e.g. Markova *et al*. 1995). Some cold-adapted species persisted to the south of continental ice sheets (lemmings, pikas *Ochotona* spp.) and then shifted northward (Fedorov & Goropashnaya 1999, Fedorov *et al.* 2003, Lessa *et al.* 2003). In some cases, species persisted in multiple refugia and

## Box 17.3. Genes reflect the history of domestication

Phylogeography provides the evolutionary framework for studying the history of domestication in caribou that allows us to identify the number of reindeer domestication events. Phylogeographic relationships within caribou/reindeer reflect historical patterns of fragmentation and colonization rather than clear-cut relationships among extant populations and subspecies. Analyses of mitochondrial DNA has revealed that the three subspecies of small-bodied, high Arctic caribou had multiple, independent origins (Flagstad & Røed 2003). The three major genetic groups presumably represented three separate populations during the last glacial: the largest of these populations represented an extensive and continuous glacial population across Beringia and far into Eurasia; a smaller, more localized population was isolated and restricted to a refugium resulting from ice expansion in western Eurasia; and several discrete populations were distributed in glacial refugia presumably located south of the ice sheet in North America (Flagstad & Røed 2003).

In Eurasia, domestication of the reindeer is considered to be in the early phases, with wild and domestic herds still coexisting widely across the region (Baskin 2000, Reimers & Colman 2006, Reid *et al.*, Chapter 3). About 50% of the approximate 3 million Eurasian reindeer are wild, and many of their herds coexist with domestic reindeer in the same areas (Baskin 2005). Analyses of DNA markers have revealed at least three independent origins of domestic reindeer in Eurasia.

Genetic differences among reindeer show that the Saami people of Fennoscandia domesticated their own reindeer independently of the indigenous cultures in western Russia. Augmentation of domestic reindeer herds by crossing with wild animals has been common in most parts of the range, but absent in some localities. These data do not support the single origin hypothesis that posited that domestic reindeer first appeared a few thousand years ago east of the Urals in the southern part of the Siberian taiga and then spread to other regions (Røed *et al.* 2008). Such a finding has immediate implications for the genetic management of these herds, especially in terms of genetic restoration efforts (Hedrick 2005).

## Box 17.4. Genes reflect changes in distribution and abundance

Unlike caribou, the muskox was relatively abundant during the Pleistocene, but endemic populations are now restricted to Greenland, the central Canadian Arctic and the Arctic archipelago; re-introduced populations are present in Alaska, Canada, Russia and Fennoscandia. Analyses of mtDNA variation reveal that muskox genetic diversity was much higher during the Pleistocene than at present (MacPhee *et al.* 2005, Campos *et al.* 2010a, 2010b). Campos and coauthors have shown that there were multiple expansions and contractions of the species range over the past 60,000 years. Their genetic analyses demonstrate that population dynamics of muskox are better explained by nonanthropogenic causes, a hypothesis supported by historic observations on the sensitivity of the species to both climatic warming and fluctuations. In northeastern Siberia, which held a large diverse population until local extinction at ≈ 45,000 radiocarbon years before present (14C YBP), genetic diversity and presumably population size increased about 30,000 14C YBP, contracted about 18,000 14C YBP, and finally recovered in the middle Holocene. The arrival of humans into relevant areas of the muskox range did not affect levels of mitochondrial diversity (Campos *et al.* 2010a). It is thought that reduced genetic diversity in muskoxen may render these ungulates particularly sensitive to exotic parasites and pathogens (e.g. Kutz *et al.* 2004).

Remarkable distribution and abundance changes have also been demonstrated in the saiga antelope. Prior to the Holocene, the range of this mammal spanned from France to the Northwest Territories of Canada, but subsequently contracted to the steppes of SE Europe and Central Asia, where historical records indicate that it remained extremely abundant until the end of the Soviet Union. After that, its populations were reduced by over 95%. Phylogenetic analyses of mtDNA of ancient and modern saiga specimens revealed the existence of two well-supported, and clearly distinct, clades of saiga. The first, spanning a time range from > 49,500 14C YBP to the present, comprises all the modern specimens and ancient samples from the northern Urals, middle Urals and NE Yakutia. The second clade is exclusive to the northern Urals and includes samples dating from between 40,400 to 10,250 14C YBP. Current genetic diversity is much lower than that present during the Pleistocene. The observed data are more compatible with a drastic population size reduction (c. 66-77%) following either a demographic bottleneck in the course of the Holocene or late Pleistocene, or geographic fragmentation (followed by local extinction of one subpopulation) at the Pleistocene/Holocene transition (Campos *et al.* 2010b).

then expanded from multiple sources (collared lemming *Dicrostonyx torquatus*; Fedorov & Stenseth 2002, common eider *Somateria mollissima*; Sonsthagen *et al.* 2011). Multicellular organisms also survived glacial periods in refugia beneath ice sheets as reported for two endemic groundwater crustaceans, *Crangonyx islandicus* and *Crymostygius thingvallensis*, recently discovered in Iceland (Kornobis *et al.* 2010). Identifying this complex history of expansion and contraction lays a foundation for predicting how species will respond in the future and thus for focusing conservation efforts.

### Terrestrial taxa

The phylogeographic history of some Arctic terrestrial species and species complexes are now known in some detail (Appendix 17.3). Some terrestrial species, such as hemispherical draba *Draba subcapitata*, alpine rockcress *Arabis alpina*, glacier buttercup *Ranunculus glacialis*, king eider *Somateria spectabilis*, Arctic fox *Vulpes lagopus*, polar bear *Ursus maritimus* and snowy owl *Bubo scandiacus* (Paetkau *et al.* 1999, Schönswetter *et al.* 2003, Pearce *et al.* 2004, Dalen *et al.* 2005, Ehrich *et al.* 2008, Marthinsen *et al.* 2009, Skrede *et al.* 2009) show little genetic diversity and/or structuring across the Arctic (Appendix 17.3), due in part perhaps to repeated bottlenecks during postglacial colonization coupled with low philopatry and high levels of dispersal. However, many terrestrial species show some degree of genetic structuring (e.g. Cladocera, carabid beetles, butterflies; Hodkinson, Chapter 7) with identifiable populations or distinct genetic groups. Some plants harbor considerable genetic diversity in addition to that associated with polyploidy. Large-scale phylogeographic patterns exist in the Arctic (Eidesen 2007, Waltari *et al.* 2007), and it is clear that Pleistocene glaciations had a major impact on overall genetic diversity and its distribution over Arctic landscapes. For many species, gene flow in the Arctic is severely hampered by longstanding physical barriers, including the Atlantic Ocean, the Bering Strait, the Greenlandic Ice Cap, the Ural and Mackenzie Mountains, and the lowlands between European Arctic and southern alpine areas. For Arctic plants, high mobility appears to be a clue to understanding diversification within species and as a driver of speciation. In Arctic plants, long-distance colonization occurs at a much higher rate than previously thought. Although physical barriers such as oceans have hampered gene flow in the Arctic relative to continuous land-masses, recent cross-oceanic dispersal has occurred in many species (Alsos *et al.* 2007), including mountain avens and bog blueberry.

The boundaries of evolutionary groups within many different terrestrial Arctic species are concentrated near mountain ranges that were formerly glaciated. For example, birds (e.g. dunlin *Caladris alpina*) and rodents (*Lemmus*, *Dicrostonyx*, *Microtus oeconomus*) share suture zones where distinct evolutionary groups come together, and these correlate to the western (Kolyma Mountain uplands) and the eastern (Mackenzie River/eastern Alaska Range) borders of Beringia (Hewitt 1996, Wenink *et al.* 1996, Fedorov *et al.* 1999b, 2003, Fedorov & Stenseth 2002, Brunhoff *et al.* 2003, Galbreath & Cook 2004). Genetic studies of Arctic species showing overall high levels of genetic diversity have verified the role of Beringia as a major refugium (Hultén 1937, Abbott & Brochmann 2003). In addition, these studies led to the discovery of additional northern refugia (Fedorov & Stenseth 2001, 2002, Worley *et al.* 2004, Waltari & Cook 2005, Loehr *et al.* 2006) that are further supported by paleoecology (e.g. Kullman 2008) and ecological niche modeling (Hope *et al.* 2010, Galbreath *et al.* 2011). Cold- and ice-adapted Arctic species should see more fragmentation and greatly reduced ranges as climate warms. Thus, genetic diversity of cold-adapted Arctic species may have been influenced by warm climatic events during interglacials and the Holocene differently from temperate taxa (Box 17.5).

During glacial maxima, many species apparently occupied southern refugia (Stewart *et al.* 2010), recolonizing northward following the retreat of the Fennoscandian ice sheet in Europe (Hewitt 1996, 2001, Schmitt 2007) and the Laurentide and Cordilleran ice sheets in North America (Runck & Cook 2005, Weckworth *et al.* 2010). Much of eastern Europe, Siberia and North America, however, remained virtually ice-free. Beringia was a large refugium during glacial advances, and multiple plant species recolonized the Arctic from refugia after the ice sheets receded (Hultén 1937). Due to isolation from other populations, different refugia typically harbor divergent lineages of species, suggesting that ice age refugia promoted diversification at high latitudes (Fedorov *et al.* 2003).

In addition to its role as a cradle that generated new species, Beringia and the Bering Land Bridge acted as a crossroads between Eurasia and North America during glacial periods allowing for the transcontinental migration of plants and animals (e.g. Waltari *et al.* 2007). The influence of the Bering Strait often is not reflected in genetic analyses of terrestrial organisms suggesting that this oceanic divide between Asia and North America (most recently formed 11,000 years ago) has minimally influenced divergence within Holarctic mammals (Brunhoff *et al.* 2003, Galbreath & Cook 2004) and some birds, including migratory species (Pearce *et al.* 2004, 2005, Reeves *et al.* 2008). In a number of avian species (Zink *et al*. 1995, Wenink *et al*. 1996) and terrestrial mammals that are ecologically associated with dry environments, however, this barrier delineates significant genetic breaks (Fedorov & Goropashnaya 1999, Fedorov *et al.* 1999b, Wickström *et al.* 2003). Some species that share habitats and distributions show idiosyncratic histories with regard to expansion out of high latitude refugia, and thus are sensitive to different barriers (Box 17.6). Similarly, the Bering Land Bridge acted as a dispersal filter for transcontinental migration of some plant taxa, while other plant species never crossed the Bering Strait (DeChaine 2009, Ickert-Bond *et al.* 2009).

Range shifts following climate change in some species have not, however, followed the classical temperate model of genetic depauperation through repeated bottlenecks

### Box 17.5. Cold-adapted species respond differently than warm-adapted

Arctic-adapted collared lemmings demonstrate low genetic diversity in northern regions affected by northward forest expansions in the Eurasian Arctic during the Holocene climate warming. The low genetic diversity and timing of population expansion suggest that populations of the collared lemming went through reduction in effective population size due to range contraction during warming events (Fedorov 1999). This hypothesis that cold adapted species will see a reduction in population sizes was recently supported using ancient DNA analyses when a drastic reduction in effective population size during Late Pleistocene and Holocene warming events was demonstrated in one population of the collared lemming in the northern Pre Urals (Prost *et al.* 2010).

### Box 17.6. Barriers to transcontinental movement

Two high latitude trans-Beringian migratory passerines, the Arctic warbler *Phylloscopus borealis* and the eastern yellow wagtail *Motacilla tschutschensis* are both asymmetrically distributed across Beringia, with extensive range in the Palearctic, and a limited occurrence in the Nearctic. Both species occupy mixed habitats along streams and rivers, and birds in breeding populations of both species in eastern Beringia winter in the Palearctic. Phylogeographic studies (Reeves 2008, Reeves *et al.* 2008) show that both species are characterized by shallowly-diverged clades that sorted geographically. The Beringian clade of the Arctic warbler is found in both eastern and western Beringia, and the clade does not overlap with Palearctic clades. Conversely, the Beringian eastern yellow wagtail clade shows stronger affinity to eastern Beringia, while the Alaskan and Asian clades overlap geographically. Reeves (2008) found that the Arctic warbler displayed a divergence zone at the Lena-Kolyma barrier, but the barrier for the eastern yellow wagtail correlated with the Bering Strait. Furthermore, the wagtail colonized eastern Beringia earlier than the Arctic warbler.

during colonization (Hewitt 1996). Many cold-adapted Arctic plant species may have shifted their large distributions in response to glacial cycles (Hewitt & Nichols 2005). Many of these species were probably more widely distributed during cold periods, rather than restricted to smaller refugia (e.g. dwarf willow *Salix herbacea*; Appendix 17.3). In some Arctic plants, northern populations are more variable than southern ones, where they are restricted to refugia under the current climate (nodding saxifrage *Saxifraga cernua*, mountain avens, bog blueberry; Appendix 17.3). These species apparently proliferated in vast tundra populations during most of the Pleistocene with high genetic diversity found not only in areas little affected by the major Pleistocene ice sheets, such as Beringia, but also in areas that were colonized postglacially by several distinct lineages (mountain avens; Appendix 17.3). In some cases (e.g. purple saxifrage; Abbott *et al.* 2000, Abbott & Brochmann 2003), genetic data support Hultén's (1937) suggestion that Arctic plants radiated east- and westward from Beringia and reached a full circumpolar distribution prior to the onset of the Pleistocene glaciations. During Pleistocene glaciation cycles, the circumpolar range repeatedly fragmented into (and then was recolonized from) several refugia. However, the genetic patterns differ for other Arctic plant species. For example, Arctic white heather *Cassiope tetragona* ssp. *tetragona* (Eidesen *et al.* 2007) demonstrates low genetic diversity consistent with a much more recent history of Beringian origin, westward expansion one glacial cycle ago, and eastward expansion possibly as recent as the Holocene. Similar multiple expansions out of Beringia are demonstrated in cloudberry *Rubus chamaemorus* (Ehrich *et al.* 2008) and alpine brook saxifrage *Saxifraga rivularis* (Westergaard *et al.* 2010), although details vary.

#### Truly Arctic marine and freshwater taxa

Relatively little is known about the levels of genetic diversity in truly Arctic marine organisms, except for a few mammal (e.g. walrus *Odobenus rosmarus*, beluga *Delphinapterus leucas*, bowhead *Balaena mysticetus*) and fish species. For those taxa that do not depend on the coastal zone, the Arctic represents a relatively continuous environment where no essential subdivision is expected, and a uniform gene pool should be the rule, but this pattern has been observed even for coastal Arctic species (e.g. the opossum shrimps *Mysis oculata*, *M. nordenskioldi*, *M. segerstralei*; Audzijonyte & Väinölä 2006, 2007). Such homogeneity contrasts with clearer subdivision in similar amphi-Atlantic comparisons of boreal taxa that retain signatures of distinctive stocks (i.e. trans-oceanic endemism) that survived on opposite trans-oceanic coasts (e.g. Wares & Cunningham 2001). In some species, the role and effects of post-glacial dispersal from refugia across the current Arctic is reflected in decreasing genetic variation as distance from putative refugial areas increases, most notably Beringia (cladoceran crustaceans [Weider & Hobæk 2003], freshwater and anadromous salmonid fish [Stamford & Taylor 2004, Harris & Taylor 2010]). The effects of Arctic climate on intraspecific genetic structure are also observed in the predominance of shifts from sexual to clonal modes of reproduction (apomixis or automixis), such as in freshwater Cladocera (Hebert *et al.* 2007).

#### The Arctic Basin as a migration corridor and contact area of Atlantic-Pacific marine lineages

For the principally Arctic marine taxa, the Arctic Basin may represent a single pool. Many other marine species are mainly sub-Arctic and often extend to the boreal zone. This overall distribution is often discontinuous, with broad gaps in the central Siberian and Canadian coastal and archipelago sectors, and between disjunct sub-ranges on the Atlantic and Pacific (Bering Sea) fringes. These discontinuities reflect the post-glacial expansion from Pacific and Atlantic 'refugial' sources and indicate that trans-Arctic connections existed during climatically favorable periods. Genetic structure is often reflected in a trans-Arctic vicariance of Atlantic and Pacific sister taxa or lineages. Molecular data indicate significant variation across taxa in this amphi-boreal/amphi-sub-Arctic relationship and in structuring Arctic genetic diversity. For a number of species, exemplified by the sea urchins *Strongylocentrotus* spp., patterns of haplotype sharing between Atlantic and Pacific populations indicate effectively continuous exchange across the Arctic (Palumbi & Kessling 1991, Addison & Hart 2005). For others, the presence of distinct lineages points to effective isolation for 3 million years, since the fundamental cooling of the climate and origin of the Arctic environment. This longer isolation is reflected in the morphology of some taxa, but remains cryptic in others (e.g. Ortí *et al.* 1994, Taylor & Dodson 1994, Nikula *et al.* 2007). In some taxa, vicariance across the Arctic has probably been important in driving subsequent speciation within the Atlantic and Pacific sub-Arctic basins. For example, these patterns have been explored in complex assemblages of tapeworm parasites among seabirds and marine mammals, although these systems have yet to be explored based on phylogeographic approaches (Hoberg 1992, Hoberg & Adams 2000). Additionally, the rockfish genus *Sebastes*, for instance, consists of a species flock of about 110 species in the North Pacific and only four species in the North Atlantic (Love *et al.* 2002). The latter probably stem from speciation following trans-Arctic dispersal from the North Pacific (Johns & Avise 1998).

It is also clear that alternating episodes of isolation and connection between freshwater habitats across marine barriers (e.g. repeated opening and closing of the Bering Land Bridge/Strait) has been important in structuring species dispersal and phylogeographic patterns. The Arctic grayling *Thymallus arcticus* probably originated in the eastern Siberia (Froufe *et al.* 2003, Weiss *et al.* 2006). Both the European *T. thymallus* and the Arctic grayling dispersed widely to the west from this presumed area of origin, and the Arctic grayling also dispersed east into Arctic regions of North America as far as Hudson Bay (Stamford & Taylor 2004). Such dispersal in a primary freshwater fish must have taken place in freshwaters of the Bering Land Bridge (the Arctic grayling is also present on St. Lawrence Island within the Bering Sea). Interestingly, mtDNA and microsatellite DNA evidence suggest that some secondary dispersal of Arctic grayling back into Siberia has occurred historically (Stamford & Taylor 2004).

In the Arctic, genetic structure of marine species, exemplified by capelin *Mallotus villosus* (Dodson *et al.* 2007) and bivalves (*Macoma balthica* and *Mytilus* spp.; Nikula *et al.* 2007, Rawson & Harper 2009) often reflects both deep subdivision traceable to inter-oceanic isolation during glaciations, and subsequent dispersal to the Arctic basin with ameliorating climates followed by secondary contact and then occasionally mixing of genomes (Appendix 17.3). Particularly, in *M. balthica* such contact along the Arctic margins of the Barents and White Seas, as well as the Baltic, have led to amalgamation of diverged genomic origins into widespread hybrid swarms. These can be seen as newly evolved taxa with extraordinary levels of genetic diversity that entered new habitat in the Arctic-boreal marginal seas during the Holocene (Strelkov *et al.* 2007, Nikula *et al.* 2008). In the future, the frequency of dissolved isolation barriers and genesis of qualitatively new diversity should increase as a consequence of the changing climate and human-assisted trans-Arctic dispersal. Such contacts of Atlantic (boreal) and trans-Arctic (Pacific origin) lineages in the northeastern European sub-Arctic are known from morphological evidence for a number of fish taxa (i.e. the Pechora/White Sea populations of Atlantic/Pacific herring, *Clupea harengus*, *C. pallasii* and smelt; *Osmerus eperlanus*, *O. dentex*; Berger 2001). Such trans-Arctic vicariant events also apply to within-basin distributions (McAllister 1963, Ilves & Taylor 2009), with the potential for similar losses of isolating barriers among more recently diverged lineages and at smaller spatial scales.

#### Arctic marine – freshwater vicariance ('glacial relicts')

A number of fish, seal and crustacean taxa typical of Arctic estuaries occupy vicariant ranges in the cold waters of deep boreal lakes, the Baltic Sea and even the Caspian Sea and Lake Baikal, and are known as 'glacial relicts' or the 'Arctic element'. Their genealogical relationships (who descended from whom, and when) are a subject of long-lasting speculation (e.g. Segerstråle 1976). Genetic data contributes to our understanding of these relationships, indicating long-standing independence of the main boreal populations (i.e. Caspian and Baikal inland taxa in Asia and inland taxa in North America) from Arctic populations (Väinölä *et al.* 2001, Audzijonyte & Väinölä 2005, Audzijonyte *et al.* 2005, Palo & Väinölä 2006). In contrast, lake populations on northern coasts do not differ from adjacent Arctic estuarine lineages (e.g. shrimp *Gammaracanthus* and opossum shrimps *Mysis*; Väinölä *et al.* 2001, Audzijonyte & Väinölä 2006). Still, in several cases there is a close relationship of particular boreal lake populations to the Arctic main range, indicating recent 'relict' status for these lake populations (Ferguson *et al.* 1978, Audzijonyte & Väinölä 2006). In still other cases, such as sculpins within the genus *Myoxcephalus*, the depth and inferred time of divergence of freshwater populations from the ancestral Arctic fourhorn sculpin *M. quadricornis* appears to differ between North American deepwater sculpins *M. (q.) thompsonii* and European freshwater populations of fourhorn sculpin *M. q. quadricornis* (Kontula & Väinölä 2003). Likewise, the ice-breeding ringed seals *Pusa hispida* of the Baltic Sea and Fennoscandian lakes are true post-glacial 'Arctic relicts' isolated from the main stock that now occupies the Arctic in large numbers. Some of these marginal populations show signs of extreme depletion of genetic variation in post-glacial time (Palo *et al.* 2001, 2003).

## 17.3. CONTEMPORARY PROCESSES

### 17.3.1. Demography

#### 17.3.1.1. Population fluctuation

It is axiomatic in conservation biology that the ability of a population to respond to current ecological and evolutionary forces is partially dependent upon the maintenance of genetic diversity. Populations that undergo large reductions in the number of effective breeders are expected to exhibit reduced levels of genetic variation. Extinction risk increases in small, isolated populations due to negative effects associated with genetic drift, such as the erosion of quantitative genetic variation required for adaptive evolution (Westemeier *et al.* 1998, England *et al.* 2003) and inbreeding depression (Mills & Smouse 1994, Saccheri *et al.* 1998). These expectations have been corroborated empirically. Spielman *et al.* (2004) report that 74% of threatened avian species demonstrate lower levels of heterozygosity than non-threatened sister taxa, and that threatened populations demonstrate a 35% reduction in heterozygosity vs. non-threatened populations (see Frankham *et al.* 2002 for review). Prior knowledge that a population has endured a recent, severe population decline can help managers anticipate problems, such as decreased reproductive fitness, reduced survival and increased susceptibility to disease, even though current population size may not suggest risks. Because past fluctuations in population numbers are often undetectable, genetic data can help to infer how both recent and historical demographic, ecological and genetic histories of species interact to affect persistence. Such assessments are crucial to management prescriptions applied to recovering populations of endangered species (Brown-Gladden *et al.* 1997), such as the widely distributed but likely never abundant peregrine falcon *Falco peregrinus* (Johnson *et al.* 2010). Some populations of this species recently recovered from severe declines in the Arctic and elsewhere during the last half of the 20th century, due to effects associated with the bioaccumulation of chlorinated hydrocarbons.

#### 17.3.1.2. Effective population size (homozygosity and heterozygosity)

Populations of Arctic organisms, especially those in isolated populations at the southern periphery of distributions and those in the high Arctic, could become reduced in size or further isolated as a result of climate warming. Smaller populations may experience higher inbreeding, increasing the possibility that highly deleterious recessive alleles are expressed (Hedrick & Kalinowski 2000). Isolation has profound effects on genetic variability and ultimately on the ability of a species to withstand environmental or biotic challenges. Wright's (1931, 1938) effective population size ($N_e$) is a fundamental parameter in many population models that can be used to monitor populations that have experienced decreases (Johnson *et al.* 2010). However, low effective population size alone is not necessarily predictive of population decline due to inbreeding. Many Arctic plants are regularly and predominantly self-pollinating, leading to very small effective population sizes and, in diploid species, high levels of homozygosity. Because the majority of truly Arctic plants are polyploids and combine divergent genomes inherited from various diploid progenitor species, they can retain extremely high levels of heterozygosity in spite of inbreeding ('fixed heterozygosity'). For example, a 16-ploid selfing plant, the cushioned draba *Draba corymbosa*, combines the genomes of eight original diploid progenitor species, with a single plant theoretically harboring 16 different alleles per locus. Six alleles have been identified at one locus to date (Brochmann & Steen 1999, Brochmann *et al.* 2004). Polyploidy in Arctic plants may serve as an escape from losses of genetic and ecological variation caused by inbreeding and genetic drift (Brochmann & Elven 1992), a finding with important consequences for conservation. Because a single plant can carry most of a population's gene pool (in the form of fixed heterozygosity), the optimal conservation strategy for many Arctic plants is to conserve many small populations rather than a few large populations (Brochmann & Steen 1999).

### 17.3.2. Peripheral populations

Although peripheral populations may have reduced levels of variability, these populations often harbor unique alleles that comprise a significant portion of the genetic variability maintained by individual species. Hence, peripheral or isolated populations become key factors in the long-term persistence of individual species. Novel genetic variability in peripheral populations may increase the adaptive potential necessary for species to respond to novel challenges (Box 17.7). At the northern distributional margins, conserving evolutionary processes in peripheral populations on the edge of species distribution may be important to northward range shifts (Lessica & Allendorf 1995, Hampe & Petit 2005, Gibson *et al.* 2009). The circumpolar plant, drooping saxifrage, contains genetically variable Arctic populations (Gabrielsen & Brochmann 1998, Kjølner *et al.* 2006) and isolated, genetically depauperate populations in southern mountains (e.g. the Alps). However, southern peripheral populations in the Ural Mountains were genetically enriched via hybridization with a diploid ancestor, bract saxifrage *S. sibirica* (Kapralov *et al.* 2006).

### 17.3.3. Isolation and endemism

The Arctic includes a spectacular set of islands and archipelagos that support a number of species, some of which are restricted (endemic) to particular islands. Island endemics are particularly vulnerable to climate warming and other anthropogenic disturbances such as the introduction of invasive alien species (Vitousek *et al.* 1995), but our understanding of most Arctic archipelagos is limited (Box 17.8 and 17.9). If specimens are available, molecular genetic analyses allow us to readily identify endemic organisms and monitor changes to insular faunas and

## Box 17.7. Peripheral populations can evolve rapidly

Rapid evolution can occur when a peripheral population becomes isolated with no gene flow and evolves rapidly to a novel adaptive optimum, as hypothesized for polar bears and brown bears *Ursus arctos* and corroborated by fossil and genetic evidence. Studies of fossils indicated polar bears diverged from the more widely distributed brown bear. Kurtén (1964) suggested polar bears became isolated on Siberian coastal enclaves during the mid-to-late Pleistocene (100,000-70,000 years ago) and became increasingly specialized as carnivores hunting solely on sea ice. Genetic studies confirm the close relationship between brown and polar bear, and further demonstrate that brown bears occupying Admiralty, Chichagof and Baranof (ABC) islands of southeast Alaska's Alexander Archipelago share a mitochondrial DNA lineage more closely related polar bears than to other brown bears (Talbot & Shields 1996). This mtDNA lineage may have been more widely distributed, possibly becoming isolated on refugia during the Wisconsinan glaciation, and remaining restricted recently.

Lindqvist *et al.* (2010) and Miller *et al.* (2012) conducted ancient DNA analyses on the lower jawbone of a polar bear excavated in-situ at Poolepynten, on Svalbard. Long-term stratigraphic studies of the Poolepynten site, including dating of both sediments and the jawbone, suggested the ancient polar bear lived between 110,000 to 130,000 years ago, the oldest polar bear fossil known. Using high-throughput 'next-generation' sequencing technology, these researchers generated a complete, multifold-coverage of the mitochondrial genome (Lindqvist *et al.* 2010), followed by shallow genomic sequencing (Miller *et al.*, 2012) of this specimen, to compare to deeply sequenced mitochondrial and nuclear genomes of extant polar and brown bears. Analyses included the enigmatic ABC brown bears that are characterized by mitochondrial DNA sequences as more similar to those of polar bears than other brown bears (Talbot & Shields 1996).

Comparative analyses of mitochondrial DNA genomes placed the ancient polar bear almost directly at the branching point between polar bears and the ABC brown bear lineage, consistent with the divergence of polar bears from within brown bears approximately 150,000 years ago, or with an ancient hybridization event. The mitochondrial data from the fossil polar bear demonstrated that polar bears survived the last interglacial warming period of ~ 130,000-110,000 years ago, and suggested that modern polar bear populations experienced a recent and rapid expansion throughout the Arctic since the Late Pleistocene, perhaps followed by a climate-related population bottleneck.

In contrast, comparative analyses of nuclear genomes of the same and additional brown and polar bears, and an American black bear, placed the divergence of polar and brown bear at approximately 4-5 million years ago, coinciding with the Miocene-Pliocene boundary, a period of environmental change that may have launched a radiation of bear species (Krause *et al.* 2008). Subsequent to this ancient split, the two species embarked on largely independent evolutionary trajectories. In addition to the mitochondrial genome, however, 5-10% of the nuclear genome of the enigmatic ABC brown bears is 'polar bear-like', suggesting the initial split was apparently followed by occasional admixture that left a clear polar bear imprint on the nuclear genomes of the ABC bears. Further, the nuclear genome-based analyses uncovered historical fluctuations in effective population size (the number of breeding bear individuals, *Ne*) that strongly indicate polar bear evolution tracked key climatic events since the Late Pleistocene. While considerably larger in the past, polar bear *Ne* declined during periods of long-term climate change. Lower genetic diversity observed in extant polar bears relative to brown bears is consistent with a prolonged and considerable population bottleneck in polar bear, coupled with recent expansions from small founder populations, as estimated from the mitogenomic data.

Despite ancient admixture and population fluctuations, the unique evolutionary pathway taken by polar bears since their divergence from brown bears is reflected in unique genomic signatures. Miller *et al.* (2012) identified potential regions of genes in polar bears that may relate to adaptation to the Arctic environment, including genes controlling fatty acid metabolism, hibernation, and pigmentation. Such studies in paleobiology have dramatic implications for conservation biology including predicting responses to anthropogenic climate change (Dietl & Flessa 2011).

floras which typically are highly susceptible to extinction (Diamond 1989, Olson 1989, Burkey 1995, Blackburn *et al.* 2004, Whittaker & Fernandez-Palacios 2007).

Molecular population genetics can also demonstrate other forms of cryptic isolation among populations. A molecular study detected that the marine Atlantic cod *Gadus morhua* were subjected to fisheries-induced evolution that caused a significant difference in fitness (relative survival rate) between cod adapted to shallow water and those adapted to deep water. The length and age at which the fish matured also decreased. These findings provide general lessons for population and conservation genetics, showing that anthropogenic changes in habitat can lead to intense selection even if the mortality is non-selective in the habitat in which it occurs. The study highlights the

### Box 17.8. Distinguishing endemics from exotics

Cook *et al.* (2010) analyzed variation in mitochondrial sequences and nuclear microsatellite loci across more than 200 Arctic ground squirrels *Spermophilus parryii* representing 17 populations in western Alaska (12 on islands of the North Pacific). Significant geographic structure suggests a combination of both long-term isolation and diversification of endemic populations, as well as recent human-mediated introductions that corroborate historic reports from early European explorers of Alaska. Managers now have a framework to prioritize the removal of non-native (introduced) populations which are impacting nesting birds, while leaving long-established endemic populations intact.

### Box 17.9 Insular populations can be heavily impacted

The concept of island endemics also applies to species on mountaintops ('sky islands') and aquatic organisms in lakes. For instance, semi-isolated populations of Atlantic cod *Gadus morhua* occur in three saline lakes on islands in the Canadian Arctic Archipelago (Hardie *et al.* 2006). These populations show much lower levels of genetic diversity, but greater levels of genetic differentiation from each other and from adjacent marine populations than is typical of marine Atlantic cod populations. Their isolation from one another and their relatively low population sizes and small geographic range are important considerations for future harvest and management strategies.

importance of applying evolutionary principles to detect and study isolated or insular populations (Arnason *et al.* 2009, Jakobsdottir *et al.* 2011).

Parasites also reveal complex histories for faunal assemblages distributed in archipelago systems, and more generally (Koehler *et al.* 2009, Hoberg *et al.* 2012a, 2012b) they can provide clear signals about the origins, distributions and history for host species (e.g. Brooks & Hoberg 2000). Unequivocal genetic signatures can be used to demonstrate (1) endemic populations of hosts, (2) persistence of parasite lineages and species in the absence of ancestral hosts, and thus historical evidence of wider ranges occupied by a host species, or (3) introduced populations. Further, such signatures reveal historical interactions between host lineages and species (e.g. ecological relicts, patterns of contact, sympatry, extirpation and extinction). All have implications for wildlife management and conservation. Genetic signatures for parasites reveal host history at fine temporal scales, and the interaction of historical and anthropogenic factors. For example, phylogeographic analyses demonstrate episodes of invasion for host parasite assemblages in martens *Martes* spp. and other mustelids and carnivores from Eurasia into North America (e.g. Zarlenga *et al.* 2006, Koehler *et al.* 2009). Intricate patterns of geographic colonization and development of mosaic faunas composed of endemic and introduced species reveal the disparate mechanisms that contribute to faunal structure in space and time (Hoberg 2010, Hoberg *et al.* 2012a).

Prior hypotheses related to complex Arctic systems were posed before modern molecular methods were available. New methods now allow us to test these hypotheses related to degree of isolation in ways not previously possible allowing a more robust picture of diversity, in addition to the biotic and abiotic drivers which structure the biosphere. Thus, molecular methods have altered our view of the world, particularly relative to temporal scale and landscape level processes that drive isolation and ultimately endemism.

### 17.3.4. Tracking the invasion of species

The contemporary northwards expansion of sub-Arctic as well as human induced invasive alien species into the Arctic could have profound effects on native flora and fauna through a variety of processes (e.g. competitive displacement, predator-prey interactions, hybridization and host-pathogen interactions; see also Lassuy & Lewis, Chapter 16). Rapid climate change could affect these interactions by expanding the 'climate envelopes' of more southerly-distributed species and/or by reducing the habitat suitability of native species (Stachowicz *et al.* 2002, Walther *et al.* 2002). The possibility that populations of Pacific salmon *Oncorhynchus* spp. that are found within the species' western Arctic distribution may be temperature-limited (Craig & Haldorson 1986) fuels concern that Arctic warming could cause north- and eastward range expansion, where they could negatively impact native anadromous and freshwater fishes (Reist *et al.* 2006; see also Christiansen & Reist, Chapter 6).

Contemporary host-pathogen assemblages across the Arctic represent complex mosaics that have been structured by historical episodes of biological invasion, primarily from Eurasia into North America over the Quaternary (e.g. Rausch 1994, Hoberg 2010, Hoberg *et al.* 2012a). Invasive processes are evident for pathogens of free-ranging ungulates, carnivores, rodents and a diverse array of parasites that are transmissible from animals to people (e.g. Kutz *et al.* 2004, 2009b). Secondarily, natural and human-facilitated invasion continues to structure this fauna. It is important to understand the implications of such invasions for geographic expansion under a regime of climate change and ecological perturbation (e.g. Hoberg *et al.* 2008, Laaksonen *et al.* 2010). Molecular genetics provides the framework and analytical tools to identify sources for invasions and introductions, the numbers and timing of events, genetic variability associated with source and founder populations, successful establishment and subsequent patterns of dissemination (e.g. Hoberg 2010).

### 17.3.5. Identifying emerging pathogens

Molecular and phylogeographic data are also instrumental in recognizing and documenting the introduction and emergence of pathogens and diseases in space and time. Molecular data allow the exploration of diversity in both a geographically extensive and site intensive manner that was not possible previously (e.g. Jenkins *et al.* 2005, Kutz *et al.* 2007). For example, our understanding of the diversity and distribution of tissue dwelling and pulmonary nematodes (protostrongylids) in ungulates (e.g. caribou, muskoxen and wild sheep) depended on laborious and often logistically difficult necropsy of mammalian hosts for recovery and definitive identification of adult parasites; larval stages of parasites could not be reliably identified. The development of species-specific markers for molecular identification has dramatically changed the process for survey and inventory, and now substantial numbers of potential host animals can be surveyed across broad geographic ranges simultaneously to provide a rapid picture of the distribution of pathogens and disease (Hoberg *et al.* 2008). Necropsy is no longer required, and assessments of diversity can be obtained by sampling and sequencing individual larval nematodes which can be simply and reliably recovered from fresh fecal samples. These methods facilitate rapid diagnostics and concurrently provide the basis for phylogeographic analyses to explore historical and contemporary processes as determinents of faunal structure. Molecular markers are increasingly important in tracking environmental perturbation linked to climate change that rapidly alters the host and geographic ranges for an array of parasites in both free ranging vertebrates and humans (e.g. Polley & Thompson 2009).

### 17.3.6. Threatened and endangered species, ESUs and MUs

Effective conservation of the contemporary characteristics and future potential of biodiversity requires an understanding of major units within species. Traditionally, the recognition of such diversity has taken the form of subspecies, but since the 1980s other descriptors such as 'evolutionarily significant units' (ESUs; Ryder 1986) or 'designatable units' (DUs; Green 2005, COSEWIC 2010) have been emphasized.

Relatively little work has focused on identifying ESU/DUs within Arctic habitats, although such units are often resolved as part of other biogeographic or population genetic analyses. For instance, Brunner *et al.* (2001) used mtDNA to identify five phylogeographic lineages within Arctic char *Salvelinus alpinus* across its Holarctic range. In some cases, these lineages were associated with distinct subspecific designations, but in other cases not. Holder & Montgomerie (2004) used genetic data to identify up to six ESUs in the rock ptarmigan *Lagopus mutus*. Because these lineages are thought to have arisen via isolation and subsequent dispersal from distinct glacial refugia, their genetic characteristics mark historical events that are part of each taxon's biotic heritage. Such historical groupings often form one of the key criteria for identifying ESU/DUs in a conservation context (e.g. Fraser & Bernatchez 2001, COSEWIC 2012). Given the commonality with which cryptic phylogeographical variation is resolved within sub-Arctic taxa (Bickford *et al.* 2007), a similar level of effort directed across Arctic landscapes would probably reveal considerable variation that would contribute to ESU/DU identification in Arctic taxa.

Genetic data have contributed more commonly to the resolution of shallower (in terms of inferred times of divergence) population structure and 'management units' (MUs; e.g. Moritz 1994), particularly in fishes and some terrestrial and marine mammals (e.g. Paetkau *et al.* 1995, 1999, Brown-Gladden *et al.* 1997, Harris & Taylor 2010). Other management-related applications of conservation genetic methods are only beginning in Arctic contexts. For instance, landscape genetics is a fast growing research activity that attempts to understand how underlying landscape features structure populations genetically (Manel *et al.* 2003). One application of landscape genetics is to enable predictions about how changes to landscapes may impact demographic and genetic connectivity. The importance of sea ice to life history attributes of many Arctic animals, for example, is reflected in its role in driving the evolution of population structure (e.g. Geffen *et al.* 2007).

## 17.4. ADVANCES IN TECHNOLOGY AND ANALYTICAL METHODS

### 17.4.1. New technology

One of the roles of conservation genetics is to understand the adaptive potential of species exposed to climate change and anthropogenic challenges. Genomics approaches allow the mapping of associations between adaptive genome regions and environmental gradients in space and time. Recent advances in genomics will revolutionize genetic analysis of natural populations. Previously, population genetics was confined to dozens of microsatellite markers or gene variants. New genomic and transcriptomic techniques produce much larger amounts of data that are well suited to solve problems in conservation genetics regarding the basis of inbreeding depression and adaption. These techniques include marker-based genotyping, reduced-representative sequencing (Altschuler *et al.* 2000) and whole genome/transcriptome sequencing (Fig. 17.2). Single nucleotide polymorphisms (SNPs) are by far the most common source of genetic variation and valuable as markers for genetic map construction, modern molecular breeding programs and quantitative genetic studies. SNPs are readily mined from genomic DNA or cDNA sequence obtained from individuals having two or more distinct genotypes. 'Next-generation' DNA sequencing technologies that utilize new chemistries and massively parallel approaches have enabled DNA sequences to be acquired at high depths of coverage faster and for less cost than traditional sequencing. For example, researchers can now address previously intractable questions in ecology and evolution with the aid of next-generation sequencing of ancient DNA preserved in permafrost sediments (Sønstebø *et al.* 2010). Restriction site associated DNA sequencing (RAD-Seq) is a powerful new method for sequencing and detection of SNPs across genomes of many individuals (Allendorf *et al*. 2010, Baxter *et al*. 2011). This approach has broad potential for genotype-phenotype association mapping, phylogeography and population genetics of non-model species with no genome sequences available. Population genomic approaches allows us to identify genes involved in adaptive traits without prior information about which traits are important in the species in question (Allendorf *et al.* 2010, Stapley *et al.* 2010, Ogden 2011).

A promising aspect of applying genomic tools to conservation is to identify signatures of selection in space and time, to provide insights into local adaption and adaptive responses to changes in environment (Oleksyk *et al.* 2010). Adaptive loci have been identified that show extremely high genetic divergence between populations of marine fish, while structural loci show no evidence of divergence (Waples 1998, Nielsen *et al.* 2009). Identification of individual loci with major adaptive effects raises the possibility of rescuing specific genetic variants. Genome scans will prove useful in assessing genetic diversity, estimating functional genetic variation and fitness, and monitoring and managing inbreeding depression to restore populations. For species reintroductions, genomics also provides insight into appropriate source populations (see reviews by Primmer 2009, Allendorf *et al.* 2010, Avise 2010, Ouborg *et al.* 2010). The quest to characterize genetic diversity in the Arctic should also be approached through application of metagenomics, where multiple taxa are combined in a single sequencing assay (deLong 2009) or environmental DNA (eDNA) screening of soils or aquatic environments (Jerde *et al.* 2011). The microbial community in the Arctic largely remains unexplored and might serve as a key factor in monitoring efforts (see Lovejoy, Chapter 11).

### 17.4.2. New theory and analytical approaches

Advances in bioinformatic theory and analytical approaches (Knowles 2009), along with new software and increased computing power, have all substantially changed our ability to make inferences about the biology of wild organisms based on the increased accessibility of genomic data. Coalescent theory, for example, is an extension of classical population genetics that builds on

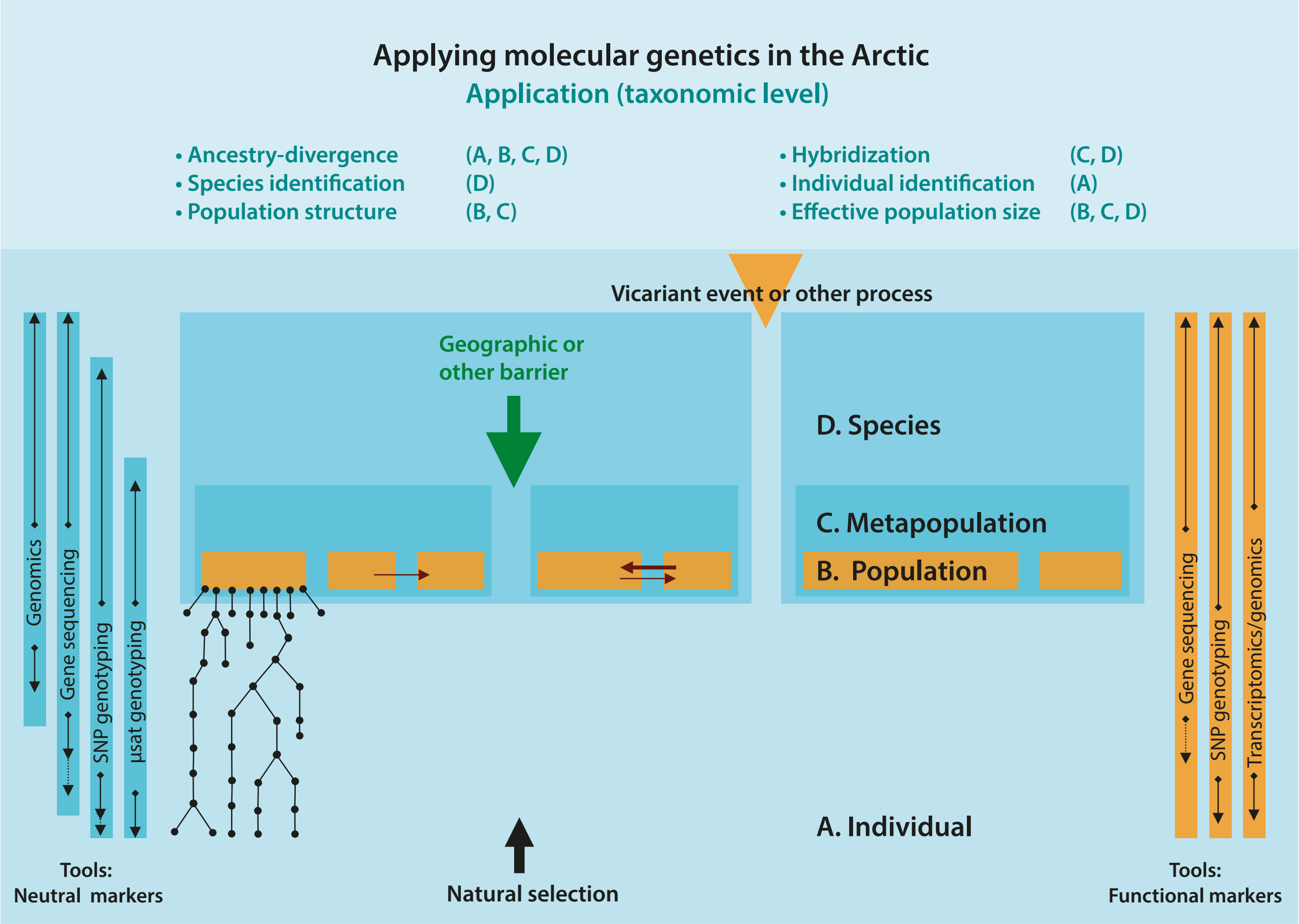


**Figure 17.2.** Molecular genetics can be used to study functional genes that are important in responding to environmental change or to identify individuals, and then determine relationships between individuals, populations (represented here by orange boxes), metapopulations (turquoise boxes) or species (blue boxes). We explore how species have responded to change in the past (such as vicariant events that split larger groups into smaller groups), so that we can forecast how species will respond to changes in the future.

the Fisher-Wright model (Kingman 1982, Wakely 2008). This approach has provided insight into topics as diverse as human migration into the Americas (Hey 2002), disease persistence and emergence (Rosenberg & Nordborg 2002) and beluga whale population structure (O'Corry-Crowe *et al.* 1997). Approximate Bayesian Computation is another powerful analytical approach recently developed to estimate historical parameters from genetic variation and compare quantitatively alternative demographic scenarios (Beaumont 2010).

## 17.5. RECOMMENDATIONS AND CONSERVATION MEASURES

Within the past 25 years, molecular genetics has radically shifted our perspective on biodiversity on the planet, with innovations continuing to increase our ability to rapidly characterize and investigate the processes responsible for life. However, a number of issues continue to hamper our ability to fully exploit new technology.

### 17.5.1. Call for immediate development of freely available, specimen-based archives

Arctic physical scientists have ambitiously developed a geographically extensive monitoring infrastructure to acquire vast quantities of data across terrestrial, oceanic and atmospheric systems related to climate change. Parallel resources necessary to develop infrastructure for monitoring biological systems in the Arctic continue to lag, limiting the integration of aspects of biological and physical processes. Perhaps the greatest limitation to effective use of genetic approaches to monitoring Arctic faunal and floral response to changing climate is the lack of biological specimens and, concurrently, the lack of cohesive protocols for acquiring and sharing synoptic data and samples from wild populations. The development and implementation of a comprehensive strategy to build archival resources (Fig. 17.1) that represent key faunal and floral populations across the Arctic should be a high priority. Collaborations among rural communities, local, regional, national and indigenous managers, subsistence hunters and trappers, field biologists and museum archivists to form networks to acquire biological information would significantly stimulate efforts across biological disciplines. Especially critical is the need to build much more robust archival collections for specimens and tissues that document and form the basis for monitoring changes in the complex biota that includes both free-living and parasitic organisms. Non-invasive methods of recovering DNA have improved tremendously and are often the most appropriate for studies of endangered species. Unfortunately, there are no coordinated or sustained efforts to archive and share such samples among investigators, so their value has been limited. In contrast, specimens in natural history museums remain the highest quality source of spatially and temporally extensive samples available for Arctic geneticists and managers. Because specimens are often used by multiple and diverse research projects, they automatically integrate and tie together distinct disciplinary approaches. Continued development and expanded financial support of these permanent collections is essential to future efforts to monitor Arctic biodiversity.

#### 17.5.1.1. Build European, Asian and North American tissue archives

One example of a collection that was established to archive and provide the materials necessary to a broad spectrum of investigators is the University of Alaska Museum of the North's Genomic Resources Facility. This cryogenic collection contains tissue samples from > 85,000 voucher specimens of mammals, birds, fishes, plants and insects. In Norway, a DNA bank focused on circumpolar vascular plants has been established at the Natural History Museum, University of Oslo, currently containing close to 100,000 tissue samples and frozen DNA extracts. Several other museums also hold large Arctic tissue collections. The Alaska Marine Mammal Tissue Archive Program is now housed at the US National Marine Mammal Tissue Bank archives and provides protocols for the long-term storage of tissues from marine mammals. The Tissue Bank uses a series of biomonitoring sites to collect tissues on specific indicator species (e.g. northern fur seal *Callorhinus ursinus*), animals from mass strandings and mortality events.

### 17.5.2. Expand biodiversity informatics

Explosive growth of information about both biotic and abiotic components of the environment has created a need to develop interconnectivity between large on-line databases so that we can rapidly and accurately assess changing conditions. Examples of such efforts are the Global Biodiversity Information Foundation (www.gbif.org) and VertNet (www.vertnet.org); efforts that facilitate the mobilization, access, discovery and use of information about organisms over time and across the planet. Permanent archival collections, as the foundation for informatics, represent critical historical baselines and self-correcting records for the distribution and structure of biodiversity.

#### 17.5.2.1. Connect GenBank, EMBL and DDJB to Archives

GenBank (www.ncbi.nlm.nih.gov), along with the European Molecular Biology Laboratory Nucleotide Sequence Database (EMBL) and the DNA Data Bank of Japan (DDJB), are the largest repositories for the vast amount of genetic information on wildlife populations in the Arctic. GenBank for example, began in 1979 and now contains publicly-available nucleotide sequences for more than 300,000 organisms. The amount of information in GenBank doubles about every 30 months with 95 billion nucleotide bases from more than 92 million individual sequences represented in 2008 (Benson *et al.* 2009). However, only a fraction of the genetic information in GenBank is from wild Arctic populations and less is associated with a specific geographic locality (i.e. georeferenced); however, this situation is changing. Without the georeferenced tag that museum specimens directly provide, genetic data have limited applicability to questions related to changing environmental conditions. With regard to genetic analyses of Arctic species, there remains an urgent need to implement a 'gold standard' for future development of genetic databases, because replication and repeatability are essential precepts of good science. In the case of GenBank and related databases, the gold standard would be to ensure that genetic sequences for Arctic species are backed by voucher specimens that are permanently archived in museums and thus available for future expansion and proofing of genomic databases (Federhen *et al.* 2009).

#### 17.5.2.2. Connect GenBank (Genomics) to GIS applications

Genetic and ecological niche models (Peterson 2001) can be combined to infer the historic distribution of a species to provide insight into the genetic structure of contemporary populations (Knowles *et al.* 2007), including Arctic species (Hope *et al.* 2010, 2011). Ecological niche models use georeferenced, voucher specimens to determine the environmental parameters that govern species distributions. These models then provide hypotheses that can be tested using genetic approaches, including the prediction of future response of wild populations to changing environments. Only a small subsection of genetic databases represent georeferenced specimens, so a sustained effort to increase the quality and applicability of these databases is needed.

#### 17.5.2.3. Stimulate emerging pathogen investigations through integrated inventories

Comprehensive survey and inventory for vertebrates, invertebrates, plants and associated pathogens using newly developed molecular-based methods allow for geographically extensive and site intensive explorations of diversity (e.g. Hoberg *et al.* 2003, Cook *et al.* 2005, Jenkins *et al.* 2005, Kutz *et al.* 2007, Hoberg *et al.* 2008). These surveys establish comparative baselines against which environmental change may be assessed. Surveys are further enhanced by linkage to integrated archival collections and informatics systems for both free-living organisms and an array of pathogens. Such integrated frameworks for survey and inventory are requisite to rapidly identify patterns of changing distribution and emergence of diseases associated with pathogens (e.g. Brooks & Hoberg 2006, Hoberg 2010, Hoberg *et al*. 2012a). There is an urgent need to increase survey efforts in the Arctic.

#### 17.5.2.4. Develop educational interfaces and portals for Arctic databases

The urgency of making large online databases more accessible cannot be overemphasized. These databases include those associated with genomic data (via GenBank), natural history collections (e.g. ARCTOS, arctosdb.wordpress.com) or long-term environmental monitoring efforts (e.g. Longterm Ecological Research). The data should be available to policy makers and central to educational initiatives in high schools and undergraduate university classes to engage the next generation more immediately in hands-on training efforts. Because the Arctic is geographically remote to most humans, portals that provide interpretation of the science as well as ready availability of data to teachers and the general public are essential to building a constituency who will appreciate and respond to the changes currently underway at high latitudes. The value of the vast environmental data held and managed by scientific programs, such as those in natural history collections, will continue to rise in the future. Online databases can form the basis for an interactive platform to address questions about the patterns of biodiversity and the impact of environmental change on varying temporal and spatial scales, but only if there is a clearer focus on these endeavors.

### 17.5.3. Identify, survey and monitor genes that influence fitness

We are just beginning to integrate ecological genetics with genome-scale studies to explore how variation at the level of the DNA molecule determines phenotypes of Arctic organisms (Höglund 2009). We need to incorporate our knowledge of evolutionary and ecological processes of endangered populations in the Arctic, so that a molecular genetics approach forms the basis for effective conservation planning and action. For example, studies have shown that the loss of genetic diversity both in neutral (mtDNA) and functional genes (the major histocompatibility complex, a gene family involved in immune response) has been observed in Arctic fox from the Komandorski Islands, particularly in the endangered subspecies *V. l. semenovi* from Mednyi Island (Dzikia *et al.* 2007).

### 17.5.4. Monitor response to climate change (neutral and functional variation)

Assessment of historical and contemporary connectivity among populations provides a starting point for elucidating this basic response to changing conditions. An Arctic-wide, multispecies monitoring and archival program across trophic levels could use sentinel or focal (Hodkinson, Chapter 7) species across the taxonomic spectrum to assess changes in both neutral and function molecular markers (Weider *et al.* 2010). These species should have widely different ecological characteristics and may respond differentially to climate warming.

Adaptive genetic variation among populations provides insight into the evolutionary potential of populations (Palsbøll *et al.* 2006, Schwartz *et al.* 2007), helps set the stage for conservation strategies (Hansen 2010) and can provide input to the definition of ESUs (Waples 1991). Assessment of functional genetic divergence (Box 17.10) or local adaptation, however, has proved elusive. Important gene expression differences exist in Atlantic salmon

## Box 17.10. Characterizing functional genes

Unfortunately, the importance of certain functional genes is not always clear-cut, requiring species-specific analyses. The melanocortin-1 receptor gene (MC1R) is responsible for melanic differences in at least two Arctic species (Mundy *et al.* 2004), the lesser snow goose *Chen c. caerulescens* and the parasitic jaeger *Stercorarius parasiticus*, where this derived trait is apparently under selection (Mundy 2005). In the parasitic jaeger of the Shetland Islands, UK, males with melanic morphs breed earlier in the season than males with pale morphs, but pale morph males may breed at an earlier age. Lesser snow geese show an approximate east-west cline in their Nearctic breeding distribution in frequency of pale or dark morphs, with blue morphs most common in the east. Although studies of fitness components failed to uncover any adaptive advantage associated with either morph, geese show strong mating preference based on the color of their parents, leading to assortative mating (Cooke *et al.* 1976, 1995). Single non-synonymous changes are perfectly associated with the presence of melanism in both the goose and jaeger, although different substitutions are involved (Mundy *et al.* 2004). The relationship between polymorphism at MC1R in other northern avian species, however, is not straightforward; Hull *et al.* (2010) failed to uncover a relationship between polymorphism in the MC1R gene between dark and light morphs of temperate and boreal red-tailed hawks *Buteo jamaicensis* in northern North America.

*Salmo salar* that are associated with distinctive ecological conditions, suggesting an important potential role for transcriptomes analyses in defining units for conservation (Tymchuk *et al.* 2010). Like next-generation genomics technologies, burgeoning next-generation transcriptomic technologies will revolutionize our understanding of gene expression in natural populations.

### 17.5.5. Management and forensic applications

#### 17.5.5.1. Ensure rigorous identification

Rapid identification of organisms is important to a number of management goals. DNA barcoding is gaining wide attention as it uses standardized sequences that can be obtained relatively cheaply as a molecular diagnostic tool for species-level identification. Importantly, this effort has extended molecular approaches into educational efforts and to a number of new applications including forensic identification. These and other markers commonly used in population genetics and phylogeographic studies of Arctic species can be used to address specific conservation and management goals, and include the use of (1) polymorphic genetic markers such as microsatellites in 'genetic tagging' and other non-invasive efforts to estimate population size and life-history parameters such as survival and mating strategies (Schwartz *et al.* 2007), (2) molecular techniques to determine the sex in species with little sexual dimorphism (Griffiths *et al.* 1998), and (3) genetic markers to determine the species and individuals involved in human-animal conflict to help identify specific animals involved in attacks and absolve those that are not (Farley *et al.* in press).

#### 17.5.5.2. Provide framework for assisted colonization or genetic restoration

Climate change is likely to amplify the negative effects of human exploitation and mismanagement in many cases. For populations on the brink of extinction, a detailed map of genetic structure is crucial for conservation efforts including a blueprint for rescue or restoration (Hedrick 2005) in the face of changing climate and increasing anthropogenic impacts in the Arctic. Because natural selection can rapidly accelerate the rate of introgression of certain regions of the genome, the source of the introduced individuals must be carefully chosen (Fitzpatrick *et al.* 2010). Assisted colonization is reintroducing species to locations where they do not now occur (Hoegh-Guldberg *et al.* 2008, but see Tallmon *et al.* 2004); such also may involve the unintended translocation and introduction of parasites with their hosts (e.g. Hoberg 2010, Hoberg *et al.* 2012).

Petit *et al.* (1997) noted that conservation priorities should consider genetic uniqueness as well as diversity. They suggested that a measure of 'allelic richness' provides an unbiased estimate of diversity and uniqueness. Taylor *et al.* (2011) applied this technique to rank populations of rainbow trout *Oncorhynchus mykiss* in terms of total genetic diversity (a combination of genetic divergence between populations and genetic diversity within populations). These genetic measures of diversity were combined with measures of morphological diversity (as a proxy measure of adaptive variation) to rank populations in terms of conservation priority. Similar approaches have been developed to rank species in terms of phylogenetic distinctiveness (Redding & Mooers 2006) and geographic areas in terms of species richness or biogeographic endemism (Myers *et al.* 2000), yet they have not been applied within the context of Arctic conservation.

## 17.6. CONCLUSIONS

In this review we have touched on several topics for which non-commercial genetic approaches are providing key insights into changing conditions in wildlife and plant communities in the Arctic. We have not addressed concerns about genetic prospecting and commercialization of genetic resources in the Arctic. Instead, our overview of not-for-profit genetic approaches in the Arctic emphasizes that an understanding of the influence of deeper (evolutionary) time in structuring diversity is essential to predicting the future response and persistence of the incomparable fauna and flora of the northern high latitudes of our planet. In many ways, new technology and analyses available to investigate Arctic biota have led to unprecedented insight. Future assessments will be limited primarily by our ability to provide representative samples from remote Arctic environments. This situation emphasizes the growing need to work collaboratively with rural Arctic communities as we aim to assess changing conditions.

Climate warming is substantially changing the distribution and population dynamics of marine, aquatic and terrestrial organisms in the Arctic. Population responses include adapting to new conditions, tracking climate shifts into new ranges that may lead to new zones of contact between species, or even the possibility of extinction. To forecast the impact of climate-induced perturbations, an essential first step is to develop an understanding of how high latitude species and ecosystems were structured by past episodes of dynamic environmental change. Today, molecular genetic approaches are used in a wide range of studies and provide comprehensive assessments of how species interact with their environments. Important insights have been gained related to the conservation status of high latitude species of concern so that these wildlife populations can be sustained. A number of factors influence the contemporary patterns of genetic diversity in Arctic organisms including the geological history of the region, the evolutionary and biogeographic past of individual species, modes of reproduction, contemporary community composition and shifting environmental conditions including those influenced by humans (Brochmann *et al.* 2003, 2004, Hewitt 2004, Lister 2004, Brochmann & Brysting 2008, O'Corry-Crow 2008, Derry *et al.* 2009). Because Arctic environments are remote and difficult to access, limited information is available about most of these essential factors for most species. Overcoming this lack of knowledge will require a coordinated investment to build infrastructure to enable us to apply the powerful insights provided by molecular genetic analyses as we integrate data across species and complex species assemblages as one of the pillars of future research and monitoring efforts.

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Resources from marine mammals have been pivotal to Inuit and other Arctic cultures for millennia. Meat and blubber were and are used for food for humans and dogs, blubber for light and heating as well, and skin and bones for clothing and tools. Seal meat remains a most appreciated food item. Photo: Carsten Egevang/ARC-PIC.com

*Chapter 18*

# Provisioning and Cultural Services

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## Contents

> » I was born in the tundra, without any doctors. I have lived all my life in the tundra, naturally it is my home. When we live in tundra we live in close interaction with Nature. For example a small bush is only a small bush to some people, but to me it tells many things. I can read from it what kind of a bird has been here… If I need to find something, for example if we have lost some reindeer, I can ask the fire by feeding it. And the fire starts to answer, it turns to a certain direction. And if I travel to this direction I will find the reindeer. Nature feeds me. It helps me. I can speak with the grass, bushes and water – I can speak with all things. I am connected to all things. I can be connected with the fire… It feeds me. This is a life for me. It is inborn. Our Elders did not pray, they just talked with nature. I can do the same. I just talk with the fire in the tundra. Tomorrow I will be lucky, Nature has heard me. I just talked with it.
>
> Dmitrii Nikolayevich Begunov in Mustonen (2009).

## SUMMARY

Ecosystems provide a range of services and values to humans. In this chapter, two types of services from Arctic ecosystems, provisioning and cultural services, are considered. Provisioning services deliver food and other materials that humans use directly. Cultural services support ways of life, enjoyment and other less tangible aspects of human life. There is overlap, of course, in that many provisioning services also entail cultural well-being. Other services, including supporting services that make possible other ecosystem functions, and regulating services, that keep ecosystems in balance, are not considered here. They are important, but relatively little information is available for the Arctic on these topics.

Provisioning services sustain Arctic residents through food, employment, identity and in other ways. Reindeer herding provides livelihoods across northern Eurasia and in a few locations in North America. It also provides meat and other products for local and distant markets. Commercial fisheries in Arctic and sub-Arctic waters generate the most money of any provisioning services in the Arctic, and are responsible for over 10% of the world's fish catch and 5.3% of its crustacean catch by weight. Commercial and subsistence hunting, gathering and small-scale fishing are traditional activities that have sustained Arctic peoples for millennia. They continue today and retain high cultural importance, although they are responsible for a smaller portion of the diet than in times past. Recreational and sport hunting is becoming more popular, and constitutes another way by which Arctic peoples and visitors can make use of Arctic wildlife.

Cultural services, beyond those associated with provisioning services, reach people in the Arctic and around the world. Tourism is increasingly popular in the Arctic, especially on cruise ships. Tourism brings opportunities for income, as well as the potential for largely localized social and environmental disturbance. It can also create advocates for Arctic conservation among those who have experienced the region and its biodiversity first-hand. There are also many non-market values associated with the simple existence of the Arctic and its ecosystems, which many people appreciate from afar without any direct experience in the region. In a world with fewer undisturbed places, intact ecosystems such as those in the Arctic are likely to become increasingly scarce and thus increasing valuable.

Most provisioning and cultural services are healthy at present. Reindeer herding is a possible exception, though it is also highly variable making it difficult to detect or predict trends. Sport hunting and tourism are increasingly popular, which may also produce more conflicts with other uses or users. Non-market values are likely to increase, but this is partly the result of increasing scarcity of undisturbed ecosystems. Further research is needed to evaluate such trends over longer periods and in more detail, and to attempt to quantify in monetary or other terms the values that accrue to human society from maintaining healthy, functioning ecosystems and associated services in the Arctic.

## 18.1. INTRODUCTION

The idea of 'ecosystem services' developed from the long-standing recognition that humans depend on the natural world directly and indirectly (Daily 1997). The term is an effort to identify and measure "the benefits that people receive from nature" (Cambridge Conservation Initiative and BirdLife International 2011). While the value of the direct use of living resources was reasonably well established, relatively little attention had been given to the value of less visible services such as flood control by wetlands, pollination by insects and the simple existence of wild places and species (e.g. TEEB 2010). For the most part, these functions were taken for granted, recognized only when they disappeared e.g. when a flood caused damage or a species went extinct. The possibility that some of these services might diminish or disappear provided a spur for better methods of recognizing their value while they were still working so that they might be conserved, or at least weighed in the balance against the consequences of human activity.

The Millennium Ecosystem Assessment (MEA 2005) placed ecosystem services in four categories: supporting services, provisioning services, cultural services, and regulating services. There is some overlap in that many services can provide benefits in more than one category e.g. hunting caribou *Rangifer tarandus*, herding reindeer or catching fish can provide both nourishment and cultural values. Intact wetlands that regulate water flow can also preserve species and habitats. Nonetheless, the categories help emphasize the range of services, direct and indirect, that healthy ecosystems provide. The MEA approach is not the only way to consider ecosystems and their services. Box 18.1 describes indigenous ways of considering the benefits that humans receive from their environment.

This chapter surveys four provisioning and two cultural services in the Arctic. Supporting and regulating services are important, but less well documented in the Arctic (see Box 18.2). The chapter is neither exhaustive nor definitive. Instead, a range of services have been selected, providing an exploratory look at how Arctic ecosystems benefit people. Where possible, quantification of services has been attempted. In many instances, circumpolar data are lacking, so that qualitative assessment is necessary for some or all of the region. The prospects for improved data and more detailed evaluation of ecosystem services are taken up in the Discussion (Section 18.4).

Reindeer herding; commercial fisheries; commercial and subsistence hunting, gathering, and small-scale fishing; and recreational and sport hunting and fishing are the provisioning services addressed here. These are the main sources of food produced in the Arctic. In tundra

## Box 18.1. Indigenous views about the concept of ecosystem services

*Tero and Kaisu Mustonen*

The notion of 'ecosystem services' is problematic in the context of indigenous cultures of the Arctic. Embedded in the scientific concept are notions that by measuring certain characteristics of ecosystems, we can assess the value of those places. These values, often expressed in financial terms, are then compared for example in discussions of conservation, natural resources extraction, transportation or other uses when making decisions on appropriate uses of an area. Arctic peoples, however, traditionally view themselves as part of a system that is structured by a web of mutual relationships and obligations, not one defined by a one-way flow with humans as the ultimate beneficiaries (Mustonen 2009). If this is true, then perhaps we should not impose comparative valuations on these places, implying that trade-offs in terms of potential land uses have no moral content. Or at least making final decisions on land use should not be based solely on measurement-based information.

Linking indigenous knowledge with scientific knowledge in different assessments in the Arctic is developing (Alexander *et al.* 2011). However, the difficulties of conveying the millennia-old relationships that the indigenous peoples have with their homelands should be recognized. Recent studies from remote Chukchi subsistence communities from northeastern Siberia indicate that the indigenous sense of place is multidimensional and hard to document or capture using scientific quantitative terminologies or paradigms (Mustonen 2009). Care should be taken when applying scientific values or measurements to places which may be very different in character.

## Box 18.2. The delineation of the Arctic

*Henry Huntington*

The Arctic Biodiversity Assessment uses a biological definition of the Arctic (see Section 2 in Meltofte *et al.*, Introduction). While entirely appropriate, such a definition does not always match the regions for which statistics and other measures are collected. This is particularly true for human activities, where data are typically collected according to political and administrative boundaries, many of which span two or more biomes. The challenge can be seen in as apparently simple a question as the human population of the Arctic. Various estimates have used various boundaries, resulting in a wide range of figures.

When considering ecosystem services, the problem is similar. While it is possible in principle to separate, for example, the hunting that occurs in the Arctic as defined by the ABA from that occurring outside, in practice this can be very difficult. Some communities are on or near the treeline, taking fish and animals from both forest and tundra. Community-level data are often available, but rarely are the specific hunting locations catalogued by biome.

Furthermore, one important goal of the ABA is to establish a baseline from which comparisons can be made in the future. The use of regularly reported statistics will make such comparisons easier, avoiding both the tedious tasks of disaggregating data and the risk of inconsistency in doing so that might cause inaccurate results and interpretations.

For these reasons, this chapter uses the most reliable, regularly reported figures available, even if those figures are not strictly limited to the Arctic region as defined elsewhere in the ABA. We have, however, endeavored to make clear when the figures reported herein include areas outside the ABA's Arctic.

regions, which are the main focal area of this chapter, there is little or no agriculture, and by definition no timber industry. Some activities south of the tree line are addressed in order to provide a more complete picture for migratory species and geographically extensive practices such as reindeer herding, and to include those indigenous peoples who participate in the activities of the Arctic Council.

Cultural services through inclusion of tourism and existence values recognize that provisioning services also entail cultural dimensions. Tourism and existence values are related services, based largely on the interest that people around the world have in experiencing the Arctic or simply knowing that Arctic places and species exist.

Two additional points are worth noting which help to place the ideas of ecosystem services in context. First, many Arctic communities and regions benefit from various forms of economic support, including transfer payments, government subsidies and other services such as mail service provided at rates below market costs, all of which help make it possible to live in remote Arctic regions with some degree of modern goods and conveniences (e.g. Glomsrød & Aslaksen 2006). Without such support local ecosystems are incapable of supporting the current population of Arctic regions at their current standard of living.

One strong piece of evidence for this conclusion leads to the second point. When the Soviet Union ended, taking various government support programs with it, the population of the Russian Arctic declined sharply (e.g. Huntington *et al.* 1998), causing an overall decline in the total Arctic population. The loss of economic support in the Russian Arctic led to an increase in use of some local species for foods. Thus, the level of use of Arctic provisioning services cannot be separated from demographic and economic trends. Assessing the full implications of these connections, however, is beyond the scope of this chapter.

The chapter concludes with discussion of the services provided by Arctic ecosystems, potential directions for future evaluation of ecosystem services, and recommendations for data collection and analysis to improve future efforts.

# 18.2. PROVISIONING SERVICES

## 18.2.1. Reindeer herding

### 18.2.1.1. Introduction

Domesticated reindeer populations are an important component of many terrestrial Arctic ecosystems and are an extremely valuable part of the cultural identity of many northern indigenous peoples, especially in Russia, Norway, Sweden and Finland. Reindeer and caribou are the same species; ‘caribou’ is used to refer to wild reindeer in North America. By either name, the animal is a keystone species, closely connected to human culture and socio-economic change. (The main sources for this section are Jernsletten & Klokov 2002, Ulvevadet & Klokov 2004 and Klokov 2007.)

### 18.2.1.2. Status and trends

The total number of domesticated reindeer in the circumpolar North is more than 2.2 million. The majority are found in Russia (about 1.5 million), Norway (240,000), Sweden (200,000) and Finland (200,000). The reindeer population in North America is relatively small, with about 10,000 in Alaska, USA, about 3,000 to 4,000 in the Northwest Territories, Canada, and about 2,000 to 3,000 in Greenland (Fig. 18.1).

In Russia, the main reindeer herding regions are the Yamal-Nenets Automomous Okrug in Western Siberia, the Sakha Republic (Yakutia) and the Chukotskiy Autonomous Okrug in the Far East. The reindeer population in Russia has experienced dramatic changes during recent decades. These changes were largely due to federal policies that affected all sectors of the economy. Different adaptive strategies of herding communities resulted in various (sometimes even opposite) trends of reindeer numbers at the regional level (see Fig. 18.2). The increase in reindeer husbandry in the Yamal and Gudan Peninsulas was the most striking in contrast to the general decrease of reindeer populations in other regions (Klokov 2011).

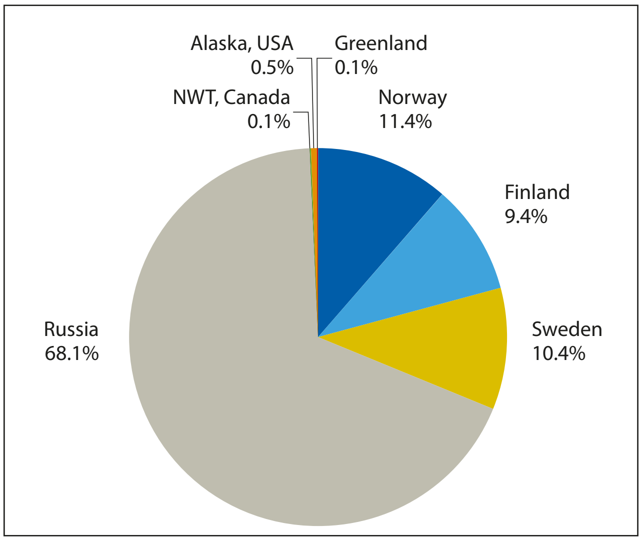


**Figure 18.1.** Distribution (per cent) of domesticated reindeer in countries of the circumpolar North (www.reindeerportal.org).

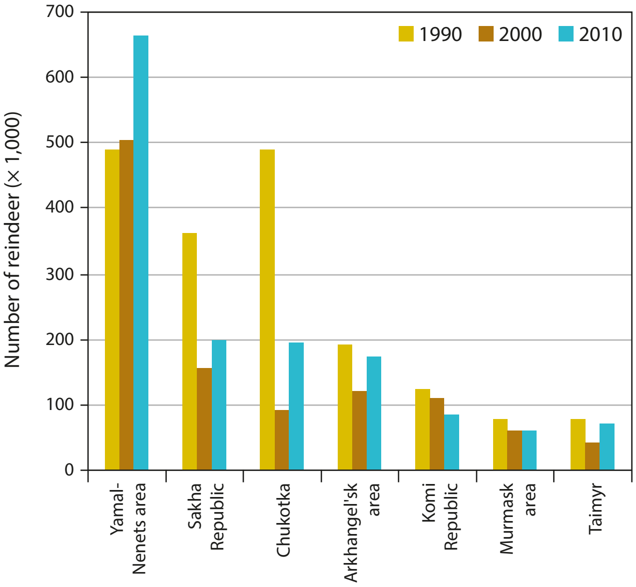


**Figure 18.2.** Numbers (× 1,000) of reindeer in the main reindeer husbandry areas of Russia, 1990, 2000 and 2010.

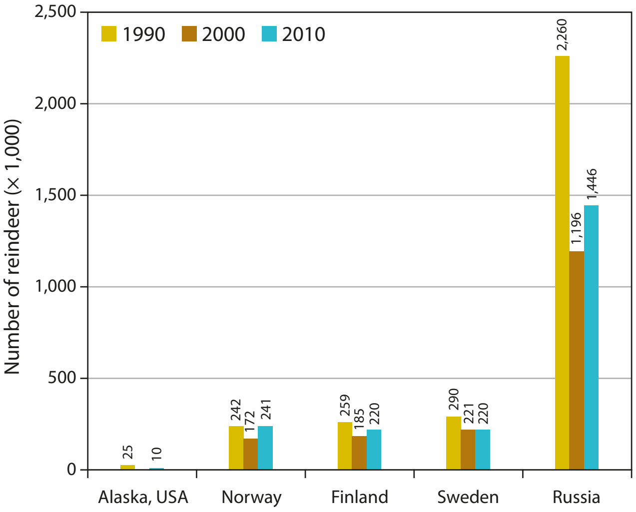


**Figure 18.3.** Reindeer populations (x 1,000) in selected Arctic countries, 1990, 2000 and 2007 (www.reindeerportal.com).

By contrast, reindeer populations in Scandinavian countries have remained relatively stable during recent decades. The number of reindeer in Norway, Sweden and Finland increased from the late 1970s with a peak between 1989 and 1991. After 1991 the trend has been a slow reduction or modest variation with no trend (see Fig. 18.3).

The practice of reindeer husbandry in North America is restricted to a small number of areas, including the Mackenzie Delta region of the western Canadian Arctic and St. Paul Island, Nunivak Island and the Seward Peninsula of Alaska. The populations are mostly declining (Christie & Finstad 2009).

Reindeer herding was introduced to Alaska in 1892 by Saami herders. Initially, Alaska experienced rapid growth in the reindeer population. By about 1930, it had approximately 600,000 reindeer, half of which were located on the Seward Peninsula. The decline of the reindeer population began in 1933, and by 1950 only 25,000 reindeer remained. Currently there are about 10,000 domesticated reindeer in Alaska, mostly in Seward Peninsula (Christie & Finstad 2009).

#### 18.2.1.3. Regional diversity

From a cultural point of view there are four types of reindeer husbandry in the circumpolar North:
Saami: in the Nordic countries and partly in the Kola Peninsula in Russia (about 700,000 reindeer),
Nenets-Komi-Izhem: in the tundra from the White Sea to the Yenisei River (about 1,000,000 reindeer),
Evenk (Tungus)-Sakha (Yakut): in the tundra of Yakutia and in the northern Siberian taiga (250,000 reindeer),
Chukchi-Koriak: in the tundra of the Russian Far East (about 250,000 reindeer).

The types differ in methods of pasture use and herd control, means of using animals for transport (different types of harnesses, using reindeer for transport), milking (or not), use (or not) of dogs for reindeer pasturing, construction of fences, sheds and other means of traditional economy, traditional clothing, shoes, equipment and construction of nomad dwellings.

The reindeer-herding situation in Nordic countries is complex and multi-faceted. At least four different herding systems exist there currently. The Saami mostly use a method of free pasturing, meaning that the reindeer are not tended year round. They often construct fences to keep reindeer away from roads, farms, other herds, and other sources of risk. In contrast to the Russian Arctic, many roads transect reindeer pastures in Fennoscandia. Herders often use cars, airplanes and helicopters to travel to their cabins and sometimes use cars to bring their reindeer from one pasture to another. The Saami-controlled free-ranging pastoralism has been discontinued due to the policies of the nation-states in the region, even though aspects of the older system survive in the Swedish-Norwegian borderlands.

Some distinctive features of the Nenets' reindeer husbandry include continuous control over a herd during the whole day, herd management with the help of dogs and reindeer teams, use of sledges throughout the year, and the lack of saddle- and pack-reindeer. Long meridian migrations up to 500 km from winter to summer pastures are typical. Herds are large (2,000-4,000 animals typically) and include a relatively high percentage of castrated bulls and unproductive females. These animals are necessary for transportation of loads using different kinds of sledges during migration and constitute the economic base of nomadic life.

Evenk (Tungus) taiga reindeer husbandry in Siberia is distinctive in several respects. The herds are small in number and the animals are used mostly for transport (sledge-, saddle- or pack-reindeer). Reindeer are kept inside fences or in free pasturing. Herders use different fodder and create smoke fires to protect animals against mosquitoes. Their reindeer are more domesticated than the reindeer of the tundra and are not afraid of people. During recent decades, the number of reindeer in the northern Siberian taiga has decreased to a few thousand animals. In Northern Siberia following the market crashes of the 1990s, reindeer herding went through several crises, and number of animals dropped. However in some regions such as in Lower Kolyma herds of up to 17,000 animals have been established in recent years in indigenous communities (Mustonen 2009).

In Canada, the Canadian government initiated the Reindeer Project in the 1920s to encourage reindeer husbandry, and by the mid-1930s reindeer had been brought from Alaska to the Mackenzie Delta. Saami families from Norway were brought to train local Inuvialuit in herding practices. Now, Inuvialuit and Saami descendents of the Reindeer Project herd approximately 3,000-4,000 reindeer near Inuvik, where they are locally owned and managed by the Kunnek Resource Development Corporation (World Reindeer Husbandry 2011).

#### 18.2.1.3. Management

Reindeer husbandry systems in Norway, Sweden and Finland are based on similar administrative principles, which include the use of subsidies to support herding. Ministries responsible for agriculture in each country are responsible for national policy concerning reindeer husbandry, with specific tasks delegated to Saami organizations on the principles of partnership. In Norway, the Norwegian Reindeer Husbandry Administration is directly under the Norwegian Ministry of Agriculture. The Reindeer Husbandry Agreement is negotiated every second year between the Norwegian Reindeer Herders Association and the Norwegian Ministry of Agriculture. In Sweden, the Saami Parliament (*Sametinget*) handles questions that concern the Saami people, including issues concerning reindeer husbandry together with the Swedish Agricultural Board (*Jordbruksvärket*) in Jönkøping, and by the County Administrative Boards (*Länsstyrelsen*) in Norrbotten, Västerbotten and Jämtland (Ulvevadet & Klokov 2004).

In Finland, however, reindeer herding is open to all citizens, not just Saami, and is organized by the *paliskunta* system (*paliskuntain yhdistys*) in which a cooperative of reindeer herdsmen administer a defined herding area, replacing the traditional Saami system which is no longer practiced in Finland. The Association of Reindeer Herding Co-operatives is a branch of the Ministry of Agriculture and Forestry of Finland, and is funded by the government. This Association is both an administrative body and advocacy organization for all reindeer herding members. There is also another association of reindeer owners in Finland, the Saami Reindeer Herders Association of Finland (*Suoma Boazosámit*), whose goals are to monitor, secure and promote Saami reindeer herders' rights (Ulvevadet & Klokov 2004).

Norway is divided into grazing areas that are almost identical with the counties of Finnmark, Troms, Nordland, Nord-Trøndelag and Sør-Trøndelag/Hedmark. Each grazing area is divided into several districts. In total, there are 77 'reindeer pasture districts' consisting of both summer and winter pastures. One district can have one or many reindeer owners. Only Saami people may herd reindeer in these areas. Reindeer herding is also carried out in southern Norway in special 'concession areas' where Norwegians can also herd reindeer (World Reindeer Husbandry 2011). In total, there are almost 3,000 reindeer herders in Norway.

The reindeer pastures in Sweden are organized through the Saami villages (*Sameby*). The *Sameby* is both an economic association and a geographical area. Its members have the right to engage in reindeer husbandry in this area. There are 51 *Sameby* with about 500 reindeer owners. All reindeer owners are members of a *Sameby*. In addition, there are about 1,000 people of non-Saami descent who primarily keep reindeer in the concession Saami villages (World Reindeer Husbandry 2011).

In Finland, there are approximately 5,600 reindeer owners, the vast majority of whom are Finns of non-Saami descent. The reindeer pastures in Finland are organized by different districts. The northernmost part of the Finnish reindeer husbandry region is classified as the 'Saami reindeer herding area', where Saami reindeer husbandry is concentrated. Reindeer herding is administered through a reindeer cooperative system of 56 such cooperatives. These are economical units and at the same time geographical areas in the counties of Lapland and Oulu. All reindeer owners in Finland are, as in Sweden, members of a cooperative/district (World Reindeer Husbandry 2011).

In contrast to the Nordic countries, Russia does not have federal legislation regarding the reindeer economy, but there are seven regional laws that pertain specifically to reindeer husbandry. There is no special administrative body responsible for reindeer husbandry in Russia, which is managed mainly by departments of agriculture of the northern regions. Thus, reindeer herders in Russia do not have the opportunity to participate in decision making processes regarding reindeer husbandry and management at the federal and regional levels. A specific feature of reindeer husbandry in Russia is the central role of reindeer enterprises with public and state forms of ownership. The number of privately owned reindeer still remains low, except in the Yamal-Nenets area. Most reindeer enterprises consist of herders' brigades; a group of herders' families, usually related to each other, who jointly manage herds within a designated pasture area. The brigade was introduced as an organizing principle during the Soviet period, and today is generally considered the basic productive unit in reindeer husbandry.

In Alaska, the *Reindeer Act* of 1937 restricted ownership of reindeer to Alaska Natives. On the Seward Peninsula, reindeer are managed by 21 herders who are members of the Kawerak Reindeer Herders Association. Herders practice an extensive management style of herding. Reindeer in this region are relatively sedentary and do not make long migrations. Currently, the entire Seward and Baldwin Peninsulas are designated as reindeer pastures along with St. Lawrence Island and areas near Shaktoolik and Stebbins. Ownership of the land is legally held by several governmental agencies (e.g. the federal Bureau of Land Management and National Park Service, as well as the State of Alaska) and private owners (e.g. Alaska Native regional and village corporations), which issue grazing permits, with the average size of large ranges being about 400,000 hectares. The main challenge facing reindeer husbandry on the Seward Peninsula concerns the loss of reindeer due to migrating caribou (see below).

#### 18.2.1.4. Markets for reindeer products

The reindeer industry in Eurasia produces primarily meat and antlers. Most of the antlers are sold for traditional medicines and similar products in East Asian markets, with a smaller number of antlers and skins sold locally to tourists. In the Nordic countries, the supply of reindeer meat is lower than demand, and so there is minimal export of reindeer meat, although some Finnish and Swedish meat is sold in Norway.

There is growing attention towards product development in the reindeer industry in the Nordic countries. Consumers want easy access to the traditional products of reindeer meat. Reindeer meat is well received in the national markets and is perceived as healthy and clean food. The price of reindeer meat is much higher than for other comparable meat products.

The reindeer owner sells live reindeer to the nearest slaughtering house. The slaughtering houses are strictly regulated and are obliged to conform to European Union directives. The regulations are the same for big slaughtering houses as for private, small-scale production. There are some exceptions in Norway and Sweden, which involve slaughter for personal rather than for commercial use.

In most regions of the Russian Arctic, the economic situation is not favorable for reindeer husbandry. The price of reindeer meat is low. The domestic market has enormous potential but remains undeveloped. Reindeer herding remains an important subsistence activity for indigenous peoples.

The marketing of reindeer meat in Alaska is, at present, primarily for local consumption. In many villages of the region, reindeer has become the preferred meat. There is also a viable export market for antlers, primarily to Asia.

#### 18.2.1.5. Reindeer pasture

All available areas for reindeer pastures in Norway, Sweden and Finland are already in use. There are 140,600 km$^2$ of potential reindeer pastures in Norway (about 40% of the total area of the country), 160,000 km$^2$ (34%) in Sweden and 114,000 km$^2$ (33%) in Finland. To prevent overgrazing, formal regulations prohibit an increase in the number of animals in most reindeer herding areas. There is a general agreement that an excessive number of reindeer is not sustainable for the reindeer husbandry industry. For example, the Finnish Ministry of Agriculture and Forestry sets a maximum number of reindeer both for the entire reindeer herding area and for each herding co-operative, a decision which is revised every decade. The maximum number of reindeer owned by a herding co-operative member is also restricted to 300 per owner in the southern reindeer husbandry region and to 500 per owner in the northern part. The current maximum number of reindeer in inland areas has been set at just over 200,000. Such restrictions have prevented overgrazing (see Ims & Ehrich, Chapter 12), however, they also inadvertently made it more difficult for young people to obtain reindeer to start a career in reindeer husbandry, which has consequently increased the average age of reindeer owners in all Nordic countries.

One of the main threats to the reindeer industry is the loss of pasture. The primary reason for loss of pasture in Norway, Sweden and Finland is connected to infrastructure development such as the building of new roads, infrastructure, military activities, powerlines, pipelines, dams, leisure homes and related activities, in addition to conflicts with the forestry sector. These have all contributed to a decline in ‘wilderness’ areas, which are prime reindeer pastures. Since the early 1990s, more than 800 recreational cabins have been constructed annually in Norwegian reindeer herding areas (Lie *et al.* 2006), resulting in extensive recreational activity.

Global Methodology for Mapping Human Impacts on the Biosphere (GLOBIO) scenarios show that currently approximately one quarter of the grazing land in northern Norway is strongly disturbed by development, including 35% of the coastal area and the most productive calving grounds and summer ranges. If no changes are made in national or regional policies, this figure has been estimated to increase to as much as 78% by 2050 (International Centre for Reindeer Husbandry 2011).

The total area of reindeer pasture in Russia is about 3.3 million km$^2$, with a carrying capacity of about 2.4 million domesticated reindeer with potential for existing numbers of reindeer to increase by almost 1 million. However, about one fifth of the pasture area is situated in the taiga, a landscape not favorable for the management of large reindeer herds and thus many pastures are underused. In tundra areas, pasture resources are sufficient for further development of sustainable reindeer husbandry in most parts of the Russian North, except the Yamal-Nenets area, where some pastures are heavily grazed. This is of special concern to reindeer herders, since the Yamal-Nenets area is the region experiencing the highest concentration of oil and gas activity Russian Arctic (Klokov 2007).

#### 18.2.1.6. Challenges and threats

Predators are a major concern for reindeer husbandry. Wolves *Canis lupus* cause most losses in Russia. According to official statistics there are 50,000 wolves in Russia (2010), and about half of them are distributed in the reindeer husbandry areas. There are no systematic data on the number of domesticated reindeer killed by wolves throughout Russia. However, in Chukotka wolves killed 38,756 reindeer during the 1998-2002 period (Jernsletten & Klokov 2002).

In Scandinavia, wolverines *Gulo gulo*, brown bears *Ursus arctos*, lynx *Lynx lynx* and golden eagles *Aquila chrysaetos* are more important predators than wolves. In Finland in 2000, for example, wolves killed 270 reindeer, while bears killed 716, lynx 136 and wolverines 1682 (Jernsletten & Klokov 2002).

Beside predators, reindeer husbandry often conflicts with wild reindeer. The combination of reindeer husbandry and wild reindeer management is a difficult problem to solve. In Alaska, reindeer husbandry is facing a major threat from the growing Western Arctic Caribou Herd (about 440,000 animals), which is penetrating further and further into the reindeer herding areas of the Seward Peninsula. The huge herd also attracts predators, but the most serious threat is the ‘run-off’ problem. When domesticated reindeer and wild reindeer (caribou) encounter one another and the herds mix, the domesticated reindeer will follow the wild herd on its migration, and be lost to the herder.

In Russia, confrontations between domesticated and wild herds occur in the Taymyr Peninsula, where there are about half a million wild reindeer, and in northern Yakutia and central Chukotka (200,000 and 100,000 wild reindeer, respectively). The main problems include:

- domesticated reindeer running off to join wild reindeer;
- combined damage to pastures;
- transmission of infectious diseases such as anthrax from wild to domesticated herds and vice versa.

The first problem is the most serious. Losses of domesticated reindeer sharply increase when large herds of wild reindeer change their usual routes of migration (the reasons for such changes are unclear) and migrate through areas where reindeer herders are not prepared for these encounters (Klokov 2007).

#### 18.2.1.7. Future concerns

Reindeer herding for the future should be ecologically, culturally and economically sustainable (Jernsletten & Klokov 2002, Ulvevadet & Klokov 2004, International Centre for Reindeer Husbandry 2011).

In Nordic countries, the main obstacle for further development of reindeer husbandry is limited pasture area. A continuous loss of reindeer pastures will lead to a situation in which there will always be 'too many' reindeer and herders in an area complicating the regulations for management. The principal tool of official reindeer husbandry management has been regulating the number of reindeer and reindeer herders.

The reduction of grazing land could also reduce the ability of reindeer to cope with extreme winter conditions due to loss of summer ranges, resulting in less growth and weight gain in summer, in turn reducing herd production (e.g. slaughter weights, calf production), thereby causing a loss of herder's income and quality of life. The most important actions to prevent this situation are:

- define an actual percentage of grazing land to be protected within a given time-frame;
- develop an integrated network of protected areas in tandem with reindeer husbandry;
- declare critical migration routes and calving grounds off limits for development if reindeer herding is to remain viable at or near current levels (International Centre for Reindeer Husbandry 2011).

In Russia, the main problem is the lack of land rights and federal legislation to ensure the priority of indigenous peoples in reindeer herding. Although some of the pastures of Yamal Peninsula, the main reindeer husbandry region in Russia, are heavily grazed, there is enough pasture area in other regions to increase the number of domesticated reindeer in Russia to over two million animals and therefore further growth of reindeer population may be expected (Jernsletten & Klokov 2002).

In Russia, many reindeer herding families live under difficult socio-economic conditions. Their income could rise if value-added production were to increase (such as creating high quality venison products instead of raw reindeer meat, tanned hides and finished clothing items, and dried and soft antlers). However, with the market located geographically far from herding areas, a lack of infrastructure and complicated formal regulations, current conditions do not favor the establishment of family businesses.

A circumpolar problem is internal recruitment. There is a definite need to recruit herders from the younger generation to ensure continuity of reindeer husbandry traditions, knowledge and practices. The separation of herders' families due to schooling is an important problem that is common for Russia and the Nordic countries (Ulvevadet & Klokov 2004). A more flexible school system might prove positive for herders' families, if this can meet the children's need to be better prepared for reindeer husbandry without compromising their formal education.

Considerable effort needs to be directed towards reducing the vulnerability of reindeer husbandry. Sustainable reindeer husbandry founded on traditional knowledge and science forms a viable way forward in the circumpolar Arctic. New models of co-productions of knowledge are developed and reindeer herders are no longer seen as standing in the way of progress, but rather as partners in sustainable development and as caretakers of the region's cultural and biophysical diversity. More sustainable alternatives for herding would have to be developed as part of an integrated program involving both herders, their communities, the indigenous scientific community, resource managers, policymakers and industry (International Centre for Reindeer Husbandry 2011).

> » *Reindeer herding makes this world richer. One day the mining of gold and other minerals will come to an end here. Reindeer herding, on the other hand, will always be able to go on.*
>
> (Grigorii Andreevich Tynakergav in Bat'yanova 2008).

> » *Our local and regional authorities usually consider reindeer husbandry only from the point of view of its potential impact on the economy of this region. But reindeer husbandry should never be seen as simply some kind of branch of economic activity. It is a way of life for many people. In fact, it is life itself for this region as it has been for centuries.*
>
> (Yakov Kymet, Chukchi journalist, Anadyr, Chukotka Autonomous Okrug, summer 1999 in Bat'yanova 2008).

### 18.2.2. Commercial fisheries

#### 18.2.2.1. Introduction

Ice cover, cold water temperatures and low primary production prevent the development of fish stocks of commercial interest in the central Arctic Ocean, whereas in the seas surrounding the Arctic Ocean there are commercial fisheries of global importance (Hoel & Vilhjamsson 2005). These areas comprise the Bering Sea and the Aleutian Islands, the Northwest Atlantic between Canada and Greenland, the waters around Greenland and Iceland, the Norwegian Sea and the Barents Sea. Although fish stocks in these oceans wax and wane as fish stocks do everywhere, in a global perspective most of the major commercial fisheries in these areas are currently comparatively well managed. Fishing is important to the local and national economies in most of these regions (Hoel & Vilhjamsson 2005; see however Christiansen & Reist, Chapter 6 for further discussion).

**Figure 18.4.** Map of international waters (beyond the coastal states' EEZs) in the Arctic Ocean and marginal seas.

There are six coastal states to the Arctic Ocean, the sub-Arctic and cold temperate oceans: Russia, the US, Canada, Denmark/Greenland/Faroe Islands, Iceland and Norway. Except for four areas of high seas, northern oceans are under the jurisdiction of these countries (Fig. 18.4), and the management of fisheries is therefore their responsibility. The high seas areas are found in the Bering Sea, the Northwest Atlantic, the Norwegian Sea and the Barents Sea. There is also an area of high seas in the central Arctic Ocean.

### 18.2.2.2. Status and trends

Some of the world's largest commercial fisheries take place in the oceans surrounding the Arctic. The most prominent examples are: Alaska (walleye) pollock *Gadus chalcogramma* from the Bering Sea and Aleutian Islands areas (Total Allowable Catch (TAC) levels in 2011 and 2012 of approximately 1.2 million tonnes; NOAA 2011); North Atlantic cod *Gadus morhua* (TAC 2012 750,000 tonnes; Norwegian Fishery and Coast Departments 2011a), and Atlantic herring *Clupea harengus* (TAC 833,000 tonnes in 2012; Norwegian Fishery and Coast Departments 2011b). Most economically important fish stocks have substantial north-south migrations; Atlanto-Scandic herring, for instance have annual migrations spanning a vast area in the Northeast Atlantic. Other important species include redfish *Sebastes* spp., saithe *Pollachius virens*, Atlantic halibut *Hippoglossus hippoglossus*, various flounder and sole species, and haddock *Melanogrammus aeglefinus*. There are also important crab, shrimp and shellfish fisheries in these oceans.

The total average landings of these fisheries are globally significant. It is estimated that in the four last decades of the 20th century, the annual average landings in Arctic and sub-Arctic waters were about six million tonnes (Hoel & Vilhjamsson 2005). In comparison, the total for global marine capture fisheries in 2006 was 82 million tonnes (FAO 2009a). This latter figure includes substantial quantities of low-value species not used for direct human consumption. Commercial fisheries in the seas surrounding the Arctic therefore account for more than 10% of the global supply (Lindholt 2006).

These fisheries constitute a major economic activity in the high North of these countries, and in many regions they are critical to the economy of local communities (Hoel & Vilhjamsson 2005). The fisheries in the Bering Sea and the Aleutian Islands, for example, provided a value of two billion USD in 2008 (Plan Team 2009). Northern cod fisheries were worth some 10 billion NOK in 2013.

A distinctive feature of the commercial fisheries in the high north is that they are single-species fisheries. With relatively few species and large stocks, commercial fisheries usually target one fish species at a time. Due to the warming influence of the Atlantic current, commercial fisheries in the Northeast Atlantic occur up towards the Svalbard archipelago at 75° N. In the Northwest Atlantic, cold currents from the north keep fisheries at more southerly latitudes, while the commercial fisheries in the Bering Sea are limited to the area substantially south of the Bering Strait at 65° N.

Illegal, unregulated and unreported (IUU) fisheries have in the past been significant in the Arctic, in particular in the high seas areas. Following developments in the United Nations (UN) Convention on the Law of the Sea in the last decades (see Section 18.2.2.3) and a substantial improvement in international co-operation, as well as in domestic implementation, IUU fishing now appears to be on the decline in the oceans surrounding the Arctic Ocean. In the Barents Sea cod fisheries, for example, estimated unreported catches fell from 90,000 tonnes in 2002 to 15,000 tonnes in 2008, and have been close to zero since 2009 (ICES 2011).

### 18.2.2.3. Management

The international legal foundation for fisheries management is the 1982 *UN Convention on the Law of the Sea* (United Nations 1982). The Convention gives coastal states sovereign rights over the natural resources in an Exclusive Economic Zone (EEZ) of 200 nautical miles (370 km), a duty to conserve and the right to utilize fish stocks, and a duty to cooperate with other countries on the management of transboundary fish stocks. The global fisheries regime has been enhanced by the 1995 *UN Fish Stocks Agreement* (United Nations 1995), which provides for a precautionary approach in management, improved regional co-operation in the management of fisheries on the high seas, and stricter enforcement of regulations. The UN Food and Agriculture Organization (FAO) has adopted a number of binding as well as non-binding global instruments pertaining to various aspects of fisheries and their management. The most recent is the 2009 *Port State Agreement*, which aims to stop illegal fishing by closing ports to boats containing illegal catch (FAO 2009b).

This global framework applies also in the Arctic, and is implemented by all Arctic Countries (the USA, though not a party to the Law of the Sea Convention, nonetheless implements its provisions). A number of important fish stocks in the sub-Arctic are transboundary and shared by two or three countries. In such instances countries cooperate through bilateral agreements on fisheries management, as for example Norway and Russia do in the Barents Sea (Hønneland 2012). Where fish stocks also occur on the high seas, regional fisheries management organizations or arrangements (RFMOs/RFMAs) should be established. In the Northeast Atlantic, the Northeast Atlantic Fisheries Commission (NEAFC) has authority over the high seas areas, including areas beyond national jurisdiction in the European sector of the Arctic Ocean (NEAFC 2012).

Fisheries management essentially entails three functions, the implementation of which is critical to the success of resource management:

- the development of scientific understanding of the stock in question, so as to estimate stock size, assess impacts of the fishery and provide scientific advice on catch levels;
- the establishment of science based regulations, so as to limit the impact of the fishery on the resource and the ecosystem; and
- the enforcement of these regulations.

The ways in which these three functions are institutionalized varies greatly between countries, depending on political systems, whether fish stocks are owned by one state or are transboundary, and regulatory traditions in the coastal states. In the North Atlantic, the International Council for the Exploration of the Sea (ICES) plays a critical role in the provision of scientific advice. Based on the work of the marine science institutions in its member states, the coastal states in the North Atlantic, it provides an international review process and scientific advice on management to its members, the EU Commission, and the regional fisheries management organizations in the region. The corresponding organization in the North Pacific, the North Pacific Marine Science Organization (PICES), does not provide management advice for fisheries.

As to the regulation of fisheries, the TACs are set by the coastal states in the case of fish stocks found in the waters of one state (see Box 18.3). In the case of transboundary fish stocks TACs are set in various arrangements for international co-operation. The most important in the oceans surrounding the Arctic Ocean is the Norway-Russia bilateral fisheries commission, which sets quotas for Atlantic cod, haddock and capelin *Mallotus villosus* (Hoel 2008), as well as Greenland halibut *Reinhardtius hippoglossoides.* There are a substantial number of such arrangements among the coastal states in the region, as well as regional fisheries management organizations for the high seas areas: the Northeast Atlantic Fisheries Commission (NEAFC), the Northwest Atlantic Fisheries Organization, and an international agreement covering the so-called ‘donut hole’ in the Bering Sea.

Fisheries management is conducted by the coastal states through regulations limiting participation in fisheries, restricting quantities of catch and providing various restrictions on how, when and where a fishery can occur.

These management functions are institutionalized in the Arctic coastal states. While the effectiveness in implementation may vary over time and from country to country, each has developed the institutional structures associated with effective resource management. In particular, each has devised arrangements for rights-based management, providing for allocation of fishing rights among the participants in a fishery. In a recent, global study this was found to be a critical determinant of effective fisheries management (Costello *et al.* 2009).

## Box 18.3. Maximum Sustainable Yield in fisheries management

The 1982 Law of the Sea Convention establishes 'Maximum Sustainable Yield' as an objective for the management of living marine resources (Article 61.3). Since the adoption of that convention, the ecosystem approach and the precautionary approach have also become important concepts to fisheries managers.

The International Council for the Exploration of the Sea (ICES) describes MSY this way (ICES 2011):

> Maximum sustainable yield is a broad conceptual objective aimed at achieving the highest possible yield over the long term (an infinitely long period of time).

In practice, MSY depends on:
- the production of the unit, which describes the relation between productivity and the size of the unit (e.g. population biomass), which in turn depends on the growth rates, natural mortality rates and reproductive rates of the members of the production unit;
- interactions between members of the production unit and interactions with other production units (intra- and inter-specific interactions);
- environmental conditions (e.g. climate, environmental quality), which affect production and intra- and inter-specific interactions; and
- fishing practices and fishery selectivity that determine the size and age composition of the catch (both the landings and the discards). The models (mathematical and conceptual) used to estimate MSY and associated parameters typically assume that all of the factors not explicitly included in the models remain constant. Thus, MSY estimates are generally conditional on current conditions and assumptions.

The enforcement of such fisheries regulations is carried out by the coastal states in their *Exclusive Economic Zones (EEZ)* and by the state whose flag a vessel is carrying on the high seas. Generally, enforcement systems have been much strengthened over the last decade, with increased international collaboration and the introduction of satellite-based vessel monitoring.

As stated above, in global perspective, therefore, major Arctic commercial fisheries currently appear to be relatively well managed. While the status for most commercial stocks globally leaves a lot to be desired (FAO 2009a), the status of the major sub-Arctic fish stocks is good. This conclusion is based on reports in the case of the Barents Sea in the North Atlantic from the International Council for the Exploration of the Sea (ICES 2012a). For the Bering Sea and Aleutian Islands the report that identified the scientific groundwork for the North Pacific Fisheries Management Council states that "Overall, the status of the stocks continues to appear relatively favorable. No groundfish stocks are overfished" (Plan Team 2009). The impression of well-managed Arctic fisheries is also supported by the fact that several major fisheries (e.g. Alaska pollock and Norwegian spring-spawning herring) in the oceans surrounding the Arctic Ocean are certified by the Marine Stewardship Council (MSC), which provides an independent, science based assessment of fisheries.

There are, however, numerous examples of management failure also from these ocean regions surrounding the Arctic Ocean. In the late 1960s Norwegian spring-spawning herring was heavily overfished, necessitating a more than 20-year re-building period before the stock recovered. Today it is one of the world's largest fish stocks and sustains one of the world's largest fisheries. Another example of management failure is that of Northwest Atlantic cod, which collapsed in the early 1990s and has not since recovered. The most important cause of the collapse was probably a failure to reduce catch levels sufficiently. In the Barents Sea, for example, cod was severely overfished in the 1980s, leading to an extended rebuilding period. The development of fisheries in the longer term is associated with climatic conditions (ACIA 2005). A warm climate during the 1930s and 1940s led to a substantial cod fishery off Greenland. With the onset of a cooling climate in the 1960s this fishery disappeared (see Fig. 6.15 in Christiansen & Reist, Chapter 6).

A new challenge to management regimes are alien invasive species (see Lassuy & Lewis, Chapter 16). Red king crab *Paralithodes camtschaticus*, not a native species in the Northeast Atlantic, was introduced from the North Pacific into NW Russian waters in the 1960s. In recent years the stock has expanded vastly, providing for a substantial coastal fishery as well as causing changes in nearshore ecosystems.

#### 18.2.2.4. Future concerns

An important aspect of current fisheries management is the gradual movement towards ecosystem-based management (FAO 2003). While there is an important distinction to be made between Ecosystem Based Management (EBM) of oceans as opposed to management just of fisheries, ecosystem based management of a fishery essentially means that its management has to be considered in relation to its environment: how the environment affects the fish stock in question, and how the fishery affects the environment. EBM management is a process of developing new practices on the basis of existing ones, rather than devising entirely new approaches in a short time. Many countries are now in the process of developing and implementing such policies in this regard (Murawski 2007).

In the Arctic countries, fisheries management is gradually taking EBM into consideration. This has implications for all three management functions: the science underlying the management of a fish stock has to be expanded so as to include information on how environmental factors are likely to affect a fishery, as well as information on how the fishery will impact its environment. For bottom trawling, for instance, this means that its impact on benthic communities has to be considered. An example of how this is done in practice can be found in the scientific background material for the Bering Sea, which contains explicit ecosystem considerations (Witherell *et al.* 2000, Plan Team 2009). Countries are also becoming increasingly restrictive with regards to trawling in vulnerable marine ecosystems (VMEs). The Northeast Atlantic Fisheries Commission, for example, has introduced a series of measures to protect VMEs since 2004 onwards.

For the regulation of a fishery, an ecosystem based approach entails restrictions set on a fishery that are configured to take the effects of environmental factors e.g. changes in water temperatures into account. At the same time, the impacts of the fishery on the ecosystem have to be minimized, for example by placing restrictions on the type of gear that can be employed in a given area. In Norway, demersal fishing gear is not permitted in marine protected areas in efforts to protect cold water corals.

These developments in management approaches take place in the context of more ambitious schemes to develop EBM in the Arctic seas. This is a global process, and the Arctic countries are at the forefront of these developments (Hoel 2009). At the 2009 Arctic Council Ministerial meeting of the Arctic Council in April 2009, a set of “Observed Best Practices in Ecosystem-based Oceans Management in the Arctic Countries” was adopted. At the 2011 ministerial, an ecosystem management expert group was appointed, and delivered to the Arctic Council Ministerial held in May 2013 a set of recommendations as to how EBM can be implemented and supported within the Arctic.

It is expected that climate change will produce a more pronounced warming in the Arctic than the global average (ACIA 2005, Koç *et al.* 2009). One anticipated effect is that marine ecosystems, including fish, will shift northwards to adapt to changing oceanographic conditions (Vilhjamsson & Hoel 2005). It is, however, simplistic to assume that there will be a simple, linear response in fish stocks to increased temperatures. The effects of climate change on marine ecosystems are manifold and complex. Major changes in density and distribution of species can trigger significant changes in ecosystem structures, with positive or negative consequences for commercial fisheries (Loeng 2008). A critical aspect is how primary production in the ocean will be affected by climate change (Wassmann *et al.* 2011).

The reduction of sea ice in the central Arctic Ocean has brought speculation that substantial fisheries may develop there. In the USA, this has led the North Pacific Fisheries Management Council (NPFMC) to adopt a fisheries management plan for its Arctic Management Area in 2009, consisting of the US EEZ north of the Bering Strait (NPFMC 2009). Currently, there are virtually no commercial fisheries in the central Arctic Ocean. The US plan does not cover fisheries under State of Alaska waters, Pacific halibut *Hippoglossus stenolepis*, salmon *Oncorhyncus* spp. or recreational and indigenous fisheries. It does not permit any commercial fisheries at this stage, and provides for a future development of commercial fisheries when sufficient information is available.

## 18.2.3. Commercial and subsistence hunting, gathering and small-scale fishing

### 18.2.3.1. Introduction

Foods from wild animals, fish and plants provide nutritional and cultural sustenance for many Arctic peoples and residents. Commercial fishing (discussed above) is a profit-making enterprise. Much hunting and fishing in the Arctic is or is regulated as sport hunting and fishing (Section 18.2.4). A third category of consumptive use encompasses a range of activities and purposes, with the common characteristic that they are concerned primarily with the production of food for local consumption. In addition to nutritional benefits, such activities often have strong cultural significance, especially for indigenous peoples, and are often regulated separately from sport hunting and fishing (see Box 18.4 for an example concerning caribou). Traditional hunting, gathering and fishing for food often involve the use of large areas of land and sea. This section begins with a review of land use, then addresses the nutritional and cultural significance of wild food production, and concludes with data on harvest quantities, participation and trends.

### 18.2.3.2. Use of land and sea

Land use and occupancy studies initiated in Alaska in the 1960s (Arnold 1976) in the context of political action that culminated in the 1971 *Alaska Native Claims Settlement Act* illustrate the extent and intensity of land and natural resource use by Arctic indigenous peoples. By constructing map biographies of the seasonal land and resource use of each hunter or herder and collating and combining them community by community and region by region, a detailed picture emerges of how, when, where, why and how frequently and intensely the natural environment is used. These studies reveal extensive travel and a geographically vast use of the natural environment.

In the early to mid-1970s, 80-85% of Inuit hunters in Canada’s Northwest and Yukon Territories were interviewed, and map biographies were prepared for each, revealing use and occupancy of slightly less than four million km$^2$ of land and ocean (Freeman 1976). A similar study, entitled *Our Footprints are Everywhere* (Bryce-Bennett 1977), was conducted in Labrador at the same time.

The map biography methodology has been further refined and applied elsewhere in the circumpolar world. In the late 1990s, this methodology was used to study land use and occupancy of Saami residents in the Kola

Peninsula of Russia focusing on the community of Lovozero (Robinson & Kassam 1998). During 2000-2010, a major land use documentation study continued this work in Kola (Mustonen & Mustonen 2011), documenting Eastern Saami oral histories, land use and occupancy from the 1400s to 2010 with 64 maps. The Russian Indigenous Peoples Association, RAIPON, documented land use by the Nenets in the 2000s. In the near future the Evenk of Southern Sakha-Yakutia plan to release a similar land use and mapping atlas with toponymic knowledge – such initiatives represent the very first of their kind in the Russian context.

These studies support the efforts of Arctic indigenous peoples to acquire legally enforceable rights to use, manage and/or own land and natural resources in their traditional territories. At the same time, however, land use for hunting in northern Russia has decreased by half since the 1980s and by two-thirds since the 1950s (CAFF 2010).

### 18.2.3.3. Nutritional and cultural significance

Mixed economies that blend formal and informal economic activity are now the norm in the Arctic. Cash is needed to purchase snowmobiles, rifles and other paraphernalia required for hunting, herding and life on the land (see Ross & Usher 1986 for further discussion of mixed economies). Traditional food is shared among extended families, reinforcing social ties as well as ties to the land and sea (Nuttall 2005).

The diet of Arctic indigenous peoples has changed considerably in recent years through the introduction of non-local foods available from stores. Traditional foods typically account for less than half of energy intake (e.g. Hansen *et al.* 2008). In Greenland, for example, consumption of local foods ranged from 10% of the diet of women in Nuuk to one quarter of the diet in the hunting districts of Uummannaq and Qaanaaq. The same studies found that consumption of local foods also varied by the age of the person, from an average of 13% local food for those under 30 years of age to one quarter for those older than 50 (Hansen *et al.* 2008). Nonetheless, traditional foods can provide the majority of many vital nutrients (protein, vitamins, minerals) in some communities (e.g. Kuhnlein & Receveur 2007).

Another indicator is participation in local food production, which can illustrate the cultural significance of hunting, gathering and fishing. For example, a 2007 study in the Iñupiat community of Kivalina in Alaska (Magdanz *et al.* 2007) found that at least one household member in 95% of households surveyed had harvested wild food that year. Sharing among households remains important and widespread, so that levels of use are often higher than levels of participation in the actual harvest. In the Kivalina study, fish were the most widely used (98% of households), followed by marine and land mammals (by 93%). The extent of use in Kivalina is typical of most Alaska villages (ADF & G n.d.).

The annual replacement value of traditional food consumed by Inuit in Nunavut is approximately 40 million CAD (Statistics Canada 2001). Moreover, beef, lamb, cow milk, chicken eggs and other 'southern' foods are often expensive in Arctic communities, though where local foods are sold commercially, their prices may be high as well. The 2010 Arctic Social Indicators report (Larsen *et al.* 2010) prepared by the Arctic Council Sustainable Development Working Group (SDWG) proposed the consumption of country food as a key indicator for 'contact with nature', which is deemed a particularly important component of a healthy society in the Arctic (e.g. Wheeler *et al.* 2010).

Flora and fauna do far more than sustain Arctic indigenous peoples economically and nutritionally. As many researchers have concluded, the natural environment provides the everyday context and basis for social identity, cultural survival and spiritual life. Hunting, fishing, trapping, herding, gathering and the sharing and distribution of country food are the core of what Inuit refer to as *inummarit*, which Brody (1975) synthesizes and translates as 'being a real Inuk'. Nuttall (2005) outlines the importance of first catch celebrations by boys and resulting sharing of food as a key component of cultural validation and passing on of values, including respect for nature, from one generation to the next.

Brody (1983) also notes that for Arctic indigenous peoples many features in the landscape are sacred places, especially along migration routes, where animals reveal themselves to hunters in dreams, or where people encounter animal spirits while travelling. Oral histories of Arctic indigenous peoples are replete with myths and stories that elaborate the relationship between humans and nature. Inuit, Dene, Saami, Nenets and other Arctic indigenous peoples have rich and detailed vocabularies that describe how the natural world functions, and have named places and components of the landscape that to outsiders seem monotonous and featureless (see also Barry *et al.*, Chapter 20). Place names may well be mnemonic devices to record detailed understandings of the natural world. Indeed, Nuttall (2005) suggests that place names summarize and store information about animals, landscapes, community histories and mythological events. This raises fascinating and largely unexplored questions about linkages between biodiversity conservation, traditional knowledge and language (see Barry *et al.*, Chapter 20).

### 18.2.3.4. Status and trends

Documentation of the harvest and use of wild foods in the Arctic is inconsistent, with varied methods and indicators in use, and often large gaps between surveys. As a result, recent information, especially at regional and national scales, is not available, nor is it simple (or even possible in some cases) to compare harvest, participation, consumption, and other indicators around the Arctic. Instead, older information must be used, supplemented where possible with information on recent

## Box 18.4. Caribou

*Thomas Jung and Harvey Jessup*

The abundance and availability of species and populations has a direct impact on the consumptive use of biodiversity. Surveys of barren ground caribou herds across northern Canada and Alaska have shown significant declines in populations. This has led to harvest restrictions on all hunter types. Inuvialuit subsistence harvesters of the Bluenose and Bathurst Caribou Herds, faced with harvest limitations, have shifted their attention to the Porcupine Caribou Herd, a shared population between Alaska, Yukon and Northwest Territories hunted traditionally by Gwitch'in subsistence harvesters and by licensed hunters. Concerns over declining population trends and increasing pressure from non-traditional harvesters resulted in the imposition of controversial harvest restrictions on this key herd, one of the few Barren Ground caribou herds in North America with a major highway bisecting its winter range. In Canada, recreational hunters of porcupine caribou now have a bag limit of a single bull animal, down from a bag limit of two caribou of either sex. The number of outfitters serving recreational hunters is limited through the use of quotas. Subsistence harvesters, though not limited in numbers, are restricted to harvesting bulls only.

trends, and quantitative comparisons are elusive (e.g. Huntington *et al.* 1998). There is some evidence for declines in harvest levels, but the importance of this activity remains high (e.g. Wheeler *et al.* 2010). Data on seabird harvests are perhaps the most readily available, and are summarized in Box 18.5 in the following section.

In addition to quantitative information about harvest levels and participation, there is considerable qualitative information demonstrating that nearly all available local food resources are utilized at one time or another by Arctic communities (e.g. ADF & G n.d.). The list of species used for food is lengthy, reflecting the biodiversity of a given place. While only a few species comprise the majority of the diet for most communities (and those species vary by location), other species can provide fresh meat at particular times of the year, some variety in the diet, special flavors or nutrients, backup foods if the main species are unavailable, and the chance for more people to participate in harvests. Thus, the weight of foods harvested is only one indicator of cultural significance, and consideration of the variety of foods harvested is also important to understand the importance of biodiversity and healthy ecosystems to Arctic communities.

In Alaska, harvests in the 1990s in areas largely beyond the treeline in the Arctic, western and southwestern parts of the state averaged, respectively, 234 kg, 301 kg, and 169 kg of edible food per person per year (Wolfe 1998, 2000). In the Arctic area, marine mammals comprised the largest share, at just over 40% of the total harvest, followed by fish and terrestrial mammals (Wheeler *et al.* 2010). In the other areas, fish contributed over 60% of the total harvest. In all areas, birds, shellfish, plants and other foods made only modest contributions by weight. There are several indications that overall harvest levels are declining around Alaska, due to many factors, but the trend varies spatially and temporally, making it difficult to confirm any patterns in the limited data that exist.

In Canada, the 1989 harvest in the Northwest Territories (NWT, which at the time included what is now Nunavut) was about five million kg of fish and animals, or 232 kg per person (Weihs *et al.* 1993). More recent data from the current NWT focus on participation rather than harvest (Northwest Territories Bureau of Statistics 2009). About half of NWT residents participate in hunting, fishing or trapping. 40-60% of the residents of small communities obtain three quarters or more of their meat and fish from hunting and fishing in the NWT, a figure that has not changed in the past decade. In medium sized communities, however, consumption of local fish and meat appears to be declining. Participation in hunting, fishing and trapping has declined in the past decade or two, but appears to be stabilizing.

Local wild food production operates differently in Greenland than in Canada or Alaska. The government licenses professional hunters and fishermen, who sell their products in local markets known as *brædtet*, which have existed since the 18th century (Marquardt & Caulfield 1996). Professional hunters provide 80-90% of the locally produced meat that is consumed, with the rest coming from personal activity including sport hunting (Rasmussen 2005). The number of active professional hunters is decreasing, however, and the average age of hunters has increased sharply in recent decades. In 1987, half of the professional hunters were under 35 years of age, whereas today only a quarter of the hunters are that young. Another quarter of hunters are over 55 years old. Informal exchange of hunting and fishing products in small settlements remains important, but professional hunting in Greenland is experiencing an overall downward trend (Nordregio 2010).

In Arctic Russia, there is both commercial hunting and personal-use (or subsistence) hunting (CAFF 2010). These activities were increasing in the late Soviet period, due to population increases in the region as well as improved access and transportation, such as off-road vehicles, snowmobiles and motor boats. In the post-Soviet period, however, the population has dropped across much of the Russian Arctic, and higher prices have made access to hunting more difficult. As a result, most commercial hunting activity has declined. Hunting of migratory birds, for example, has declined by 30-60% in the Russian Arctic since the 1970s, which together with reduced hunting and improved winter feeding possibilities in Europe has resulted in sharply increasing W Palearctic goose populations (see Ganter & Gaston, Chapter 4). Subsistence hunting and fishing, however, have increased, especially around settlements, as wild foods have become increasingly important in local diets due to the lack of alternatives. Traditional marine mammal harvests have been resumed in Chukotka, for example. At the same time, some illegal hunting has increased as enforcement has declined. The future of hunting in the Russian Arctic is tied closely to economic conditions in the region and across the country, making projections difficult at best (CAFF 2010).

Most hunting and fishing in Iceland, Finland, Norway and Sweden is sport hunting and covered in Section 18.2.4. However in the Saami territories at the Norwegian-Finnish borderlands, the rivers Näätämö/Neiden and Teno/Déatnu are important cultural repositories of subsistence Saami fisheries. Along the Teno/Déatnu, spring-time drift netting for salmon *Salmo* spp. as well as the salmon dam fishery and netting are age-old practices that still contribute to community well-being and renewal of traditions. Along the Näätämö/Neiden both Skolt Saami and local Finns practice cultural fisheries. The Finnish settlers on the Norwegian side continue to harvest salmon with small seines designed for the fast flowing rapids of the river. The annual catch is approximately 1,000 kg, and the practice is derived from the Skolts who used to live in the community. Contemporary Skolts on the Finnish side maintain their net fishery and family-owned customary fishing spots along the Neiden river. The Skolt language is only spoken along the Neiden today and the place names, stories, legends and surviving traditional knowledge are crucially intertwined with the surviving net fishery. A co-management plan with both Finns and Saami is being developed to revitalize salmon hatching places and adapt to climate change along the Neiden (Mustonen 2012).

Commercial exploitation of marine mammals occurs in several Arctic countries. In Norway, minke whales *Balaenoptera acutorostrata* (Wikipedia 2012a) and harp seals *Pagophilus groenlandicus* are exploited, in Iceland minke whales and fin whales *Balaenoptera physalus* are hunted (Wikipedia 2012b), and in Canada harp seals are hunted in the Northwest Atlantic. In Russia, harbor seals *Phoca vitulina* are harvested in the White Sea (Wikipedia 2012c).

The hunting of marine mammals is, in the case of the large whales, regulated globally by the 1946 *International Convention on the Regulation of Whaling* (ICRW) (IWC 2012). In the North Atlantic, the North Atlantic Marine Mammal Commission (NAMMCO) is the regional management body (NAMMCO 2012). ICES provides scientific advice to member states on management (ICES 2012b).

#### 18.2.3.5. Future concerns

While recognizing the significance of traditional hunting and fishing practices to Arctic peoples, it is also important to note that such practices are not always synonymous with sustainability or conservation. The fact that most populations of Arctic species remain healthy is a positive sign of compatibility, but there are also examples of overharvest leading to population declines and local exterminations (e.g. Koch 1945, Krupnik 1993, Freese 2000). At the same time, there are examples of distortion of population trends or predictions to foster other political aims regarding Arctic peoples, so some accounts of overhunting must be treated with skepticism (e.g. Kulchyski & Tester 2007, Sandlos 2007). The political dimensions of indigenous rights, colonial legacies and historical contexts are important, but do not change the fact that harvests can pose risks to biodiversity, just as harvests benefit in the long term from sustaining biodiversity.

### 18.2.4. Recreational and sport hunting

#### 18.2.4.1. Introduction

Both residents and visitors enjoy and use the Arctic environment through the pursuit of recreational (sport) fishing and hunting, which play an increasing role not only in defining requirements as to the quality of the environmental goods and services but also in the organization and goals of wildlife management regimes (Reis & Higham 2009). Recreational and sport hunters and anglers derive considerable benefits from the biodiversity of the Arctic, and their continued enjoyment of the Arctic environment depends on healthy local fish and wildlife populations. The ability of the biodiversity of the Arctic to continue to provide harvest opportunities is, in part, dependent on implementation of effective wildlife management practices, policies and regimes.

In the most general sense, recreational and sport hunting can primarily be considered leisure activities, although many northern residents likely would view it as an intrinsic part of the social and cultural setting of everyday life. However, the terms ‘recreational’, ‘sport’, ‘pleasure’, ‘hobby’, ‘leisure’, ‘spare-time’, ‘trophy’ and ‘non-occupational’ hunting indicate that the hunting activities take place outside what is normally considered the sphere of commercial or subsistence production.

These activities are in some cases intrinsically linked to local traditions and cultures and in other cases to the tourism or food industries. Recreational hunting may be understood as dissimilar from commercial and subsistence hunting due to the different value put on hunting activities. Both subsistence and commercial hunting have an economic component, and in both systems there is a strong link to livelihoods. In some cases, these two modes of production interact and cannot be seen as separate (Lonner 1986). Recreational hunting approaches the activity more as *consumption* than *production*. It is thus understood as part of a lifestyle rather than a source of livelihood or even food production. Legislative institutions in the Arctic have related to these systems of production and consumption in a variety of ways and as a result have constructed multiple and often different categories of hunters – categories that in some cases may not reflect the way people perceive their activities.

Consumption in this context is understood as the use of biodiversity to satisfy needs or interests very often related to the enjoyment derived from *direct* interaction with the environment. This type of consumptive use of the environment and biodiversity brings quality of life to people (Vaske *et al.* 1986). As with production, consumption decisions and behavior by recreational hunters are driven by values, and any change in cultural values may both be limited by biodiversity status and trends, and itself have potentially significant positive or negative effects on biodiversity.

One of the most important potential benefits of recreational hunting is that residents and non-residents further value biodiversity and the environment. Value attributed to game populations and the environment that sustains them can result in initiatives to protect these populations and their habitat, which acts to conserve both the target species and associated species (Loveridge *et al.* 2006). If properly managed and monitored, the benefits may thus outweigh potential disadvantages such as conflicts with other users or provide reasons to combat overhunting and environmental degradation (Lent 1971, Freese & Trauger 2000).

### 18.2.4.2. Cultural dimensions

Recreational hunting often has an important cultural and social significance that should not be underestimated, but is difficult to quantify. For this category of hunters, the direct interaction with wildlife in its natural environment is attractive (for example reflected by appreciation for biological diversity and the quality of the natural setting), and recreational hunting can thus be characterized as driven by a multidimensional set of inter-related motives (Radder 2005, Loveridge *et al.* 2006). The opportunity to hunt is vitally important to many Arctic residents, and often linked to a person's sense of cultural identity, even though the opportunity may not always be used. Some recreational hunters maintain harvest rights, although actual harvesting does not necessarily take place (Sejersen 2003).

Many recreational hunters ascribe positive value to a continuous relationship between humans, the environment and wildlife. These positive values may differ immensely; some are moved by cultural ideas of 'wilderness' and 'authenticity' as something different from modern urban life (e.g. Martin & Tyler 1995), where nature is considered as a source for recreation, healing, personal growth, inspiration and transformation (Jackson 1986, Sande 2000, Daigle *et al.* 2002). For other recreational hunters these ideas are far from the way they consider their historical and contemporary relationship to the environment (Sejersen 2003).

In the Arctic, recreational and sport hunting is pursued by both resident and non-resident, indigenous and non-indigenous hunters. The Arctic Human Development Report (AHDR 2004) concludes that for the indigenous peoples and other residents of the Arctic in particular, "failure to stay close to nature results in a loss of roots and various forms of alienation from the natural world. Separation from productive contact with nature also gives rise to a detached view of the natural world in which humans are perceived as alien and unwanted intruders in a pristine wilderness."

However, the opportunities and privileges of recreational and sport hunters and the qualitative and quantitative impacts derived from and imposed on biodiversity are closely linked to the rights-regime present in each region (Orlove & Brush 1996, AHDR 2004).

### 18.2.4.3. Access to biodiversity

Interests of recreational hunters are considered in harvest management regimes and governance of harvest rights, which differ substantially between and within Arctic countries. As a main tool to lay the groundwork for sharing of the benefits derived from the use of biodiversity, management regimes differentiate hunters into categories which are ascribed different rights and obligations.

The activities of recreational hunters are managed and administered by including this user-group in a complex corpus of rights, which is at times contested as it reflects specific political priorities and cultural understandings of property, user, access and disposition rights (see examples in Scott & Webber 2001, Sejersen 2001, Andersson *et al.* 2007, Hull *et al.* 2007). Not only do these understandings differ among regions and cultures, but historical changes within the same region, as well as contemporary conflicts over the distribution of access and rights to different user-groups, are also commonplace.

In some regions, recreational hunting is demarcated clearly (e.g. Greenland) whereas in others regions the category of recreational hunters merges into broader categories of hunters (e.g. Alaska and Canada). Due to these policies, it is impossible to make a consistent analysis of the number of recreational hunters and the size of their harvest, as separate from subsistence and commercial harvest, at a circumpolar scale. In Canada, for example, it is not possible to make these comparisons even within the country, as the legal classifications and licensing requirements of hunters varies substantially between various Canadian provinces and territories.

In the Arctic, both small and big game are attractive to recreational hunters, but the popularity of particular

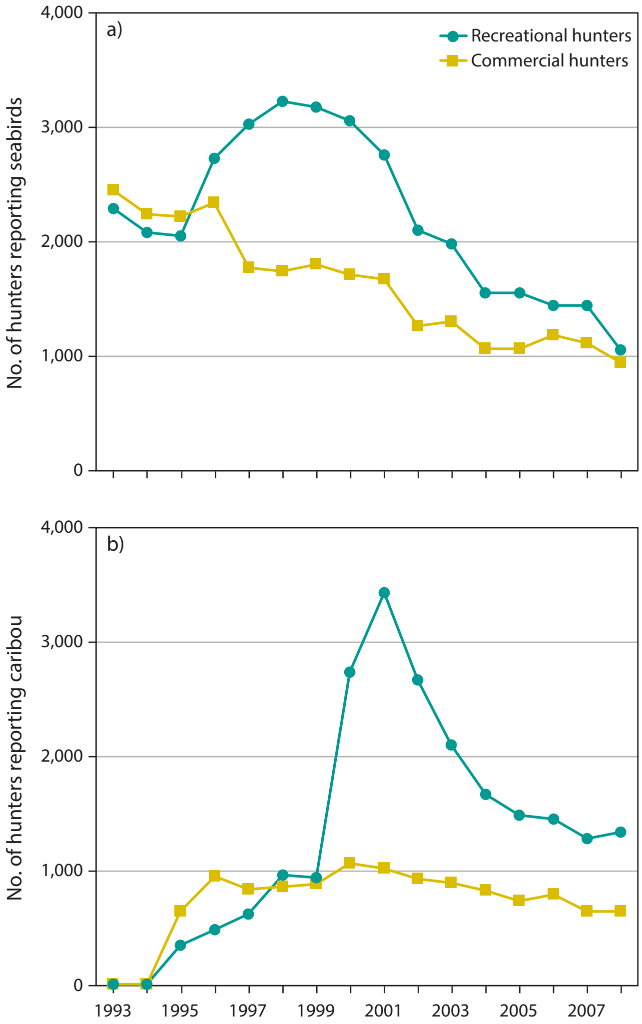


**Figure 18.5.** a) Numbers of commercial hunters (yellow) versus number of recreational hunters (green) who have reported harvest of seabirds since 1993 in Greenland; b) Numbers of Greenland hunters who have reported harvest of caribou since 1993 (Department for Hunting and Fishing, Greenland, unpubl. data). In 1993 and 1994 caribou hunting was closed due to small population sizes. From 1995 to 2000 there was a strict hunting quota, and recreational hunters were only allowed to hunt few caribou (Jensen & Christensen 2003). Due to increasing populations, the caribou quota has increased for recreational hunters since 2000, which can explain the peak in numbers of recreational caribou hunters. Note that there has been a strong decrease in numbers of recreational seabird hunters since 2000, at the same time that the caribou hunt increased. This may indicate that hunters often look for replacement resources. However, there is no evidence that there is a clear correlation between these observations. In 2002, new and stricter hunting regulations for seabirds were introduced (Merkel 2010b). This may partly explain the decrease of seabird hunters since 2002.

game species is relative to the presence of alternative game species, hunting regulations, availability and technology, to mention but a few drivers (Fig. 18.5).

Arctic species are in many cases migratory, and many populations are thus exposed to recreational hunting in more than one country, and in some cases outside the Arctic as well as within. In some instances, international management regimes are established (e.g. various migratory bird conventions and agreements) in order to coordinate and manage the harvest of migratory species across political boundaries (Huntington 1992). For instance, it is widely accepted nowadays that a ‘range-wide’ (flyway) approach is required for effective conservation of migratory Arctic breeding waterbirds. There are documented examples on how coordinated international conservation measures and protection from hunting on the wintering grounds has allowed Arctic breeding population of certain waterbird species to increase (Fox 2003, Hagemeijer *et al.* 2004, Ganter & Gaston, Chapter 4).

Seabirds in the Arctic are also migratory, and are among the principal game species in many places both within the Arctic (see Box 18.5) as well as outside. Therefore, management and assessments, including harvest of seabirds, has been a priority within CAFF where its Circumpolar Seabird Expert Group (CBird) has produced conservation strategies and action plans for selected seabird species (CAFF 1996, 1997, Gilchrist *et al.* 2008) as well as a series of circumpolar assessments of seabird harvests analyzing the current situation (Merkel 2010a; see also Ganter & Gaston, Chapter 4).

Aside from the legal access to biodiversity afforded and allocated by management regimes, the ability of biodiversity to support recreational hunting is also dependent on physical access to game populations. The increased availability, affordability and efficiency of different means of transportation improve access by hunters, allowing them to more reliably obtain desired ecosystem services. Today, a variety of means of transportation are used, including boat, snowmobile, dog sledge, all-terrain vehicle, car, helicopter and bush plane. Improved snowmobile technology has allowed hunters to travel more quickly to traditional hunting areas (Aporta & Higgs 2005). This has allowed an increasingly urban Arctic population to continue pursuits on the land, while maintaining a lifestyle that is increasingly sedentary and removed from daily interaction with the environment. Although improved technologies may sustain a level of interaction with the environment, this may also have negative impacts on biodiversity. Biodiversity that was previously inaccessible and *de facto* protected from harvest may now be susceptible to overharvest (Fig. 18.6; Due & Ingerslev 2000). For example, faster, more reliable snowmobiles have allowed hunters in parts of northern Canada and Russia to access larger numbers of wolves than in previous years, and this has been a cause of concern for biologists (Mitchell 2011). Similarly, in

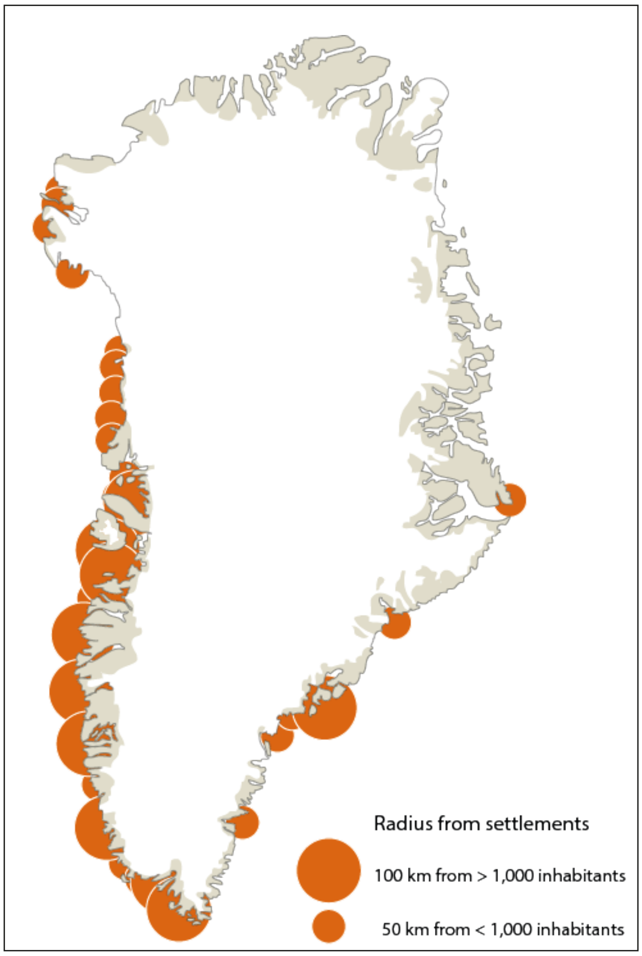


**Figure 18.6.** The regions of Greenland's coastal areas that can be reached on day trips by motorboat, shown by circles with a radius of 100 km from communities of more than 1,000 inhabitants and generally bigger boats and 50 km from settlements of less than 1,000 inhabitants with generally smaller boats. The figure illustrates that no locations in the populated west coast of Greenland are out of reach for hunters (Due & Ingerslev 2000).

northwestern Canada, more advanced snowmobiles have allowed people to access remote areas and overharvest some winter fish stocks (Reid *et al*. 2010).

### 18.2.4.4. Status and trends

There are several drivers that impact the relationship between recreational hunting and biodiversity. Changes in society and cultural perceptions may work as strong drivers in influencing the values, possibilities, behavior and activities of this group of hunters. Some of these drivers are global, while others are circumpolar or more regional.

Urbanization is a circumpolar driver. Arctic urban centers are growing rapidly fed by an influx of rural Arctic and southern migration into Arctic urban centers (Nielsen 2004). Other demographic changes, such as the age composition of the human population, may also play a role, if for example there were decreases in males of hunting age (Hull *et al*. 2007, Matilainen 2007).

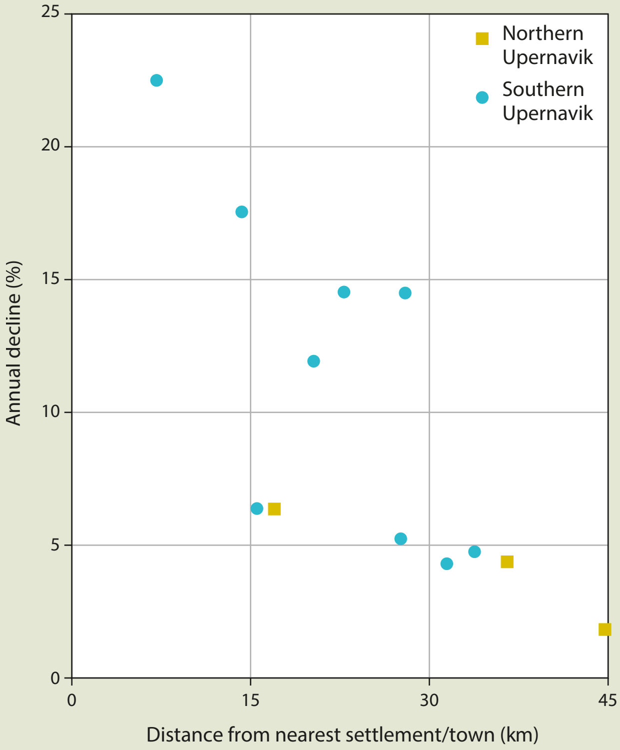
## Box 18.5. Seabirds

*Flemming Merkel and Tom Christensen*

Seabirds are among the principal game species in many places in the Arctic. However, human use of seabirds varies between the circumpolar nations, both in scale and in form, and harvest methods have changed over time to include more efficient tools, making seabirds more exposed to excessive harvest (Denlinger & Wohl 2001).

There is a tendency toward increasing seabird harvests for cultural or recreational reasons, rather than for basic subsistence or commercial purposes. In most countries, commercial hunting of seabirds is forbidden, but in the Faeroes, Iceland and Greenland it is legal to supplement other sources of income by domestic or local sale of seabirds (Merkel & Barry 2008).

The game species and the number of birds currently harvested, or believed to be harvested, vary enormously between the nations (see Box 18.5 Tab. 1). Over the past three decades, depending on the country, harvest levels have declined in most countries due to more restrictive hunting regulations, declining seabird populations, fewer or less active hunters, or a combination of these factors. In some countries, particularly the Faeroes, Iceland and Greenland, the decline in harvest has been drastic.



**Box 18.5 Figure 1.** Rate of population decline of bird colonies in the municipality of Upernavik in relation to distance to the nearest settlement or town. The shorter the distance, the greater the rate of decline (Evans & Kampp 1991).

Although the impact of harvest on seabird populations is often poorly documented in the Arctic as a result of limited information on both seabird numbers and harvest levels, there is no question that it has played a key role in the population dynamics of many species. There are examples of both overharvesting causing substantial decreases in breeding populations and rapid population recovery following major changes in harvest regulation (Merkel & Barry 2008; see Fig. 1.4 in Meltofte *et al.*, Chapter 1). There are also examples from the Faeroes and elsewhere about traditional practices that created sustainable harvests (e.g. Nørrevang 1978, 1986, Olsen & Nørrevang 2005), in addition to examples from Greenland and elsewhere over the years about rapid overhunting of eiders *Somateria* spp. and other seabirds (e.g. Koch 1945).

Seabirds are often sensitive to reductions in adult survival rates since they produce small clutch sizes and have delayed maturity (Furness & Monaghan 1987). Anthropogenic stressors including overharvest have in some parts of their range caused population declines (Gaston & Irons 2010). On a local scale, such declines can also negatively affect the harvest and thus reduce ecosystem services for future generations (Falk & Kampp 2001). One example is the thick-billed murre *Uria lomvia* colony in Sagdleq, close to the Greenlandic town Uummannaq, where large numbers of these birds formerly bred. Here, the population declined from at least 70,000 pairs in 1949 to zero in 1987. Many other murre colonies in Greenland have seen similar declines or extirpations, so that except for large intact colonies in the thinly populated Thule District in N Greenland, less than 20% of breeding population is currently left in the remaining Greenland colonies, compared with the beginning of the 20th century (Kampp 1994 and F. Merkel unpubl.). Perhaps in combination with large bycatches in salmon drift nets during the 1960s and 1970s (Tull *et al.* 1972, Falk 1998), local summer hunting close to the breeding colony has been identified as the main reason for this decline (Evans & Kampp 1991, Kampp 1994, Mosbech *et al.* 2009), an interpretation that is supported by a close correlation between proximity to settlements and rate of decline (Box 18.5 Fig. 1; see also Ganter & Gaston, Chapter 4).

By using this example, Falk and Kampp (2001) illustrated the way in which an unsustainable harvest of thick-billed murres can greatly reduce the goods and services to a local community for generations. They predicted that if the hunting was carried out sustainably and on the right segment of the population (young birds), the total harvest could have been up to 14 times higher over a 120 year period than the actual harvest. This corresponds to 1.3 million birds that could have been harvested instead of the approximately 70,000 pairs and their offspring that actually disappeared from the colony.

The thick-billed murre is still a very important seabird species harvested in Greenland. Today all seabird species are protected in the spring and during the breeding season. For some species such as common eider *Somateria mollissima*, reduced harvests have had a documented positive effect on population level (Merkel 2010b, Ganter & Gaston, Chapter 4), though for others, such as the thick-billed murre, it is unclear if existing regulations are sufficient to lead to population increases.

**Box 18.5 Table 1.** Seabird harvests around the Arctic (from Merkel 2010a). Pop. = population.

| Country/region | No. of species harvested | Most important species | Estimated annual seabird harvest | Estimated annual egg harvest | Overall trend in harvest | Reason for change |
|---|---|---|---|---|---|---|
| US/Alaska (sea ducks not included) | > 25 | Auklets, murres | 30,000 (2001-2005) | 145,000 (2001-2005) | Variable annually, no trend evident (1995-2005) | Survey methods may not be comparable |
| Canada | 8 | Murres, common eider | 260,000 (2002-2008) | Some | Decreasing (1980-2002) | Regulation and fewer hunters |
| Faroe Islands | 9 | Fulmar, puffin | 65,000-240,000 | 1,000-12,000 | Decreasing (1980-2006) | Regulation and decreasing pop. |
| Finland | 6 | Long-tailed duck, common eider | 31,000 (2000-2004) | Banned since 1962 | Decreasing (1995-2005) | Decreasing pop. and regulation |
| Greenland | 19 | Thick-billed murre, common eider | 153,000-220,000 (2002-2006) | 6,600 (2006) | Decreasing (1993-2006) | Regulation and fewer hunters |
| Iceland | 19 | Puffin, common murre, common eider (down, eggs) | 158,000-285,000 (2002-2007) | Many | Decreasing (1995-2007) | Decreasing pop. (except for common eider) |
| Norway/Svalbard | 5/4 | Gulls/ black guillemot | 4,000/150 (1995-2008) | Some | Stable (1995-2008) | - |
| Russia (west) | ~10 | Eiders, murres, gulls | ? | Some 1000s (<10,000) (illegal) | Increase in 1990s, now stable or decreasing | Changing law enforcement and social-economic situation |
| Russia (east) | ~20 | Eiders, alcids, gulls, terns, cormorants | Eiders (50-62,000), other seabirds (~100,000, mainly illegal) ~100.000 (mainly illegal) | ~100,000 (mainly illegal) | Decrease in early 1990s and gradual increase in 2000s | Changing law enforcement and social-economic situation |

## Box 18.6. Polar bear sport hunting in Canada: cross-scale effects on recreational hunting regimes

*Douglas Clark*

The history of polar bear sport hunting in Canada is an instructive example of how international-scale policy processes and legislation can profoundly shape local and regional recreational hunting regimes. Conservation efforts for polar bears in Canada are based on the 1973 *International Agreement on the Conservation of Polar Bears and Their Habitat*, and are implemented by provincial and territorial governments, along with indigenous co-management organizations. With the 1973 passage of the US *Marine Mammal Protection Act*, Canada became the sole destination for polar bear sport hunters worldwide. The 1973 International Agreement provides for signatory countries to permit the harvest of polar bears by local and aboriginal peoples exercising traditional rights. Within Canada's Northwest Territories and Nunavut, Inuit and Inuvialuit communities have often decided to allocate part of their existing polar bear quotas to visiting sport hunters. Those quotas are based on established scientific management principles, and international demand for polar bears parts is not a factor in setting them (Environment Canada 2010).

Significantly, no community in Nunavut allocates its entire quota for sport hunting; instead, the average is a little over 20% per community (Dowsley 2009, Foote & Wenzel 2009), from a total of approximately 600 animals hunted annually nationwide (Lunn *et al.* 2006). Guiding polar bear hunts provides a range of important cultural and economic benefits which have been thoroughly documented (e.g. Keith *et al*. 2005, Wenzel 2005, 2009, Freeman & Wenzel 2006, Foote & Wenzel 2007, Tyrrell 2009). The community benefits associated with these provides a strong incentive to abide by the quota system (Foote & Wenzel 2007). In the Northwest Territories, tags from a failed hunt are returned and not reassigned, so maximum quotas there are rarely reached.

Polar bear sport hunters are predominantly American, so when the US listed polar bears as a threatened species under the Endangered Species Act in 2008, preventing importation of polar bear hunt trophies, the clientele for polar bear hunts in Canada was substantially reduced (Slavik 2009). A proposal by the US to list polar bears to Appendix I of the *Convention on International Trade in Endangered Species*, which was narrowly defeated in 2010 and again in 2013, would have effectively eliminated the entire international clientele. There is considerable concern that these recent listing efforts are reducing the economic incentives for indigenous people to participate actively in polar bear co-management across the Canadian Arctic (Foote & Wenzel 2009, Nirlungayuk & Lee 2009). Paradoxically, such international designations may lead to more bears being killed when quotas are fully met in the absence of sport hunters, and – speculatively – even through deliberate violation of quotas by hunters who have had enough of outside control of traditional activities.

Land use and hunting patterns of those in more urban communities reflect different trends. For some users, *de facto* access is often restricted by a number of factors such as the lack of leisure time and the lack of hunting knowledge and skills (Rutanen *et al*. 2007). Economic factors such as decreasing disposable income, increasing fuel prices or the cost of hunting equipment (particularly snowmobiles, boats and all-terrain vehicles) have a strong negative influence on people's abilities to pursue recreational hunting, as transport has become expensive to distant hunting locations. Nonetheless, high cultural value is often placed upon hunting and outdoor lifestyles, whether linked to the subsistence system (Fienup-Riordan 2000) or to recreational hunting. In Greenland and much of northern Canada, about 80% of the population lives in an urban setting, and hunting and fishing are still continuously accentuated and developed because they are considered an integral part of living in the Arctic. In W Greenland, the number of motorboats has increased tremendously (Rask 1993, Nielsen 1998, Due & Ingerslev 2000), sustaining recreational activities both near the towns and also farther away as mobility has greatly increased. In general, access to biodiversity has improved considerably with improved transportation technology (Klein 1972, Bernes 1996, Due & Ingerslev 2000). This latter trend can be attributed to cash generating activities and more secure jobs in urban areas. These two different trends can be observed within the same urban areas due to the existence of socio-economic stratification.

Parallel to the process involving improved mobility, the number of private cabins is increasing in many regions (Bernes 1996). In 1998 in Nuuk, Greenland 150 cabins were registered. Three years later, in 2001 the number had increased by two thirds to 250 (Nuup Kommunea 2003). In order to control this interest in outdoor life, the municipality set aside special areas for recreational purposes. In Iceland, a similar tendency can be seen where the number of cabins tripled from 2,300 to 7,000 between 1973 and the beginning of the 1990s (Bernes 1996). The presence of cabins in the landscape improves the conditions of recreational hunters, but it may place high pressure on resources accessible close to urban centers and in cabin areas, where use often peaks during specific periods of time, such as weekends and holidays.

Interest in experiencing the Arctic by non-residents is increasing (Snyder & Stonehouse 2007; see Section 18.3.2). To the accomplished sport hunter, the Arctic may represent a unique opportunity to combine adventure, cultural experiences, and the harvesting of unique trophy species unavailable elsewhere, such as polar bear *Ursus maritimus* (see Box 18.6). It is anticipated that interest in sport hunting by non-residents will increase for species new to sport hunting, such as walrus *Odobenus rosmarus*, and some indigenous guides in Nunavut, Canada, are asking for increased quotas to meet the projected demand. Bans on importation of trophies into non-Arctic countries may however put limitations on the interests of non-resident recreational hunters (Foote & Wenzel 2009).

As outdoor life in general is considered culturally important, authorities in many regions are setting up programs and school curricula to stimulate these activities. In some regions (e.g. northern Scandinavia) it is estimated that the number of rural hunters will decrease in the near future due to the age structure of rural regions (Hull *et al*. 2007, Matilainen 2007) or due to immigration trends (Rutanen *et al*. 2007). In contrast, recreational hunting in Iceland is growing, even though hunting does not have a significant role in society. From 1995 to 2006, the number of hunting permits increased 68% from 11,574 to 19,470 (Sigursteinsdóttir *et al*. 2007).

In the US, the 2006 National Survey of Fishing, Hunting and Wildlife-Associated Recreation (US Fish and Wildlife Service 2008) indicated a decline in hunting participation by one quarter nationwide. These figures triggered a public concern that hunting was on its way out. However, an analysis by the Alaska Department of Fish and Game indicated that more than 174,000 residents or one quarter of the Alaska population went hunting between 2003 and 2007 (Woodford 2009). State records also indicate that between 56,000 and 66,000 resident individuals participated in big game hunting in the period 2001 to 2006. The Alaska Department of Fish and Game concluded that the number of hunters in Alaska is stable, but due to a population increase in the state, the percentage of the population that hunts is decreasing (Woodford 2009).

In Greenland, the number of commercial hunters has been stable (around 2,700) or slowly decreasing (Department for Hunting and Fishing, Greenland, unpubl.). As the population of Greenland is rising, the relative number of commercial hunters is indeed decreasing. However, the number of recreational hunters decreased by one third from 5,455 in 1993 to 3,609 in 2010 with an extreme peak of 9,686 in 2002. This peak can be explained by management decisions and the availability of attractive target species (in this case caribou) (Grønlands Statistik 2008). The fluctuations in numbers of recreational license-holders and in their harvests indicate that this category of hunters, is more open for recruitment than the category of commercial hunters, and that their harvest levels may change rapidly.

#### 18.2.4.5. Future concerns

Recreational hunting is an important activity in the Arctic for residents and non-residents with fluctuating intensity and extent. The pursuits of this category of hunters may have both positive and negative impacts on biodiversity. The temporal and spatial impacts of activities are driven by a multiplicity of factors such as demography, economy, cultural values and management priorities, and prognoses can be hard to formulate. The link between biodiversity trends and recreational hunting increases in complexity, as many of the target species are migratory and thus exposed to recreational hunting outside the Arctic as well.

## 18.3. CULTURAL SERVICES

### 18.3.1. Tourism

#### 18.3.1.1. Introduction

Arctic tourism began in the early 1800s. By the mid-19th century the North American Arctic, Greenland and the Scandinavian north especially had become venues for small-scale but growing tourism, mainly ship-borne, from the US and Europe. The industry has continued to grow and diversify being stimulated in more recent decades by the development of large-scale air transportation. Since the ending of the Cold War it has extended into hitherto forbidden areas of Siberia.

Tourists are attracted to the remoteness of the Arctic, the intrinsic beauty and grandeur of its mountains and glaciers, its wildlife, history of exploration and indigenous people. Each summer season now sees tourists outnumbering residents in most Arctic venues, and tourism has come to exert a substantial role in many polar economies, not least providing a source of income tied to healthy ecosystems.

A recent survey of polar tourism identified five overlapping but distinct market segments, "… each with its own distinguishing visitor experiences and economic dimensions, involving different tourists' motivations, expectations, on-site behaviour and resource uses" (Snyder 2007). These are:

1. the *mass market*, comprised of tourists primarily attracted to sightseeing in comfort;
2. the *sport fishing and hunting market*, with participants pursuing fish and game in a wilderness setting (this form of tourism is addressed above in Section 18.2.4);
3. the *nature market*, observing wildlife species in their natural habitats and in the solitude of natural areas;
4. the *adventure tourism market*, providing visitors with a sense of personal achievement from meeting challenges and potential perils; and
5. the *culture and heritage* market, in which tourists experience personal interactions with the lives and traditions of indigenous and local people, and with historic places and artifacts.

Each of these market sectors continues to grow and diversify (Snyder & Stonehouse 2007), energized by media campaigns that compete for business in what has become a multi-million dollar enterprise. For most of its history, Arctic tourism in most regions has largely been run by entrepreneurs based and operating from outside the Arctic. While Arctic residents have undoubtedly benefited to some degree, most of the profits have remained outside the Arctic. Recent trends have resulted in more equitable distribution of planning, financing and profits: Arctic peoples themselves are exerting more decisive and dominant roles, and insisting that their voices are heard and views respected.

Arctic tourism is a major international market, and its accurate portrayal requires recognition of its unique geographic scope and diversity. 'Arctic Tourism' usually begins at major cities that are often situated south of the Arctic. These cities serve as important gateway communities providing entry points for tourists travelling by means of vessels, commercial air transport, and a wide variety of backcountry guide services. All Arctic nations and many local governments have made substantial infrastructure investments in order to facilitate access to Arctic areas with the intention of capturing a large share of the market.

Mass tourism departs from these communities and then disperses through the Arctic by means of historically popular transits, shore excursion programs, and travel aboard land based transport modes such as trains and motor coaches. Individual travelers or small groups also use gateway communities to gain access to the Arctic and to serve as bases from which they pursue numerous attractions such as sport fishing, hunting, trekking, kayaking, charter boating, mountaineering and many other special interest activities.

Based on two centuries of experience, Arctic tourism is a very mature industry. Tourism products include recreation and cultural experiences in all seasons for all Arctic nations and indigenous peoples' lands. Recreational activities are constantly expanding due to the invention of new technologies and the improvement of cold weather clothing and equipment. The number of persons engaged in each tourism activity are recorded and evaluated by the several jurisdictions responsible for natural and cultural resource management; governments seeking to expand economic development; local governments endeavoring to establish a stronger economic base; and industry associations operating in the Arctic. Those sources provide information regarding the tourism experience, number of participants, duration and season use, receipts from licenses and fees, personal expenditures and employment. Given disparate motivations, the extent and rigor of tourism data varies considerably among the reporting organizations. Brief descriptions of four distinct Arctic tourism markets are presented here (sport hunting having been discussed in Section 18.2.4).

**Table 18.1.** Marine incidents involving cruise ships in Arctic and Antarctic waters (the same vessels often alternate polar region according to season) (aggregated from reports from national coast guards, admiralty courts and insurers, and www.cruisejunkie.com).

| Marine incidents | Total events | Events since 2000 | Percent since 2000 |
|---|---|---|---|
| Polar cruise ships sunk 1979-2007 | 8 | 5 | 63 |
| Polar cruise ships running aground 1972-2009 | 27 | 16 | 59 |
| Pollution and environmental violations 1992-2009 | 64 | 42 | 65 |
| Disabling by collisions, fires and propusion loss 1979-2009 | 34 | 28 | 82 |

### 18.3.1.2. Mass tourism

The largest and fastest growing segment of the Arctic tourism market is mass tourism. The steady advancement of new and improved transport technologies has enabled increasing numbers of people to experience the Arctic in comfort aboard ships, aircraft and trains. The modernization of each of these transport modes and intense competition among transportation companies now provides a cost and time effective way for hundreds of thousands of people to travel to diverse Arctic destinations. Since the end of World War II, the growing demand for tourism has been accompanied by Arctic governments' attempts to capture this very lucrative market. Economic development strategies to attract the tourism industry resulted in the expansion of existing ports and airports and the development of new facilities in previously inaccessible Arctic regions.

From the mid-1800s to the present, the vast majority of Arctic tourists have traveled aboard cruise ships. Currently, cruise ships transiting northern and Arctic waters carry hundreds of thousands of passengers to diverse, and, for a large period of human history, unimaginable destinations. Traditional destinations such as Norway's North Cape remain popular but are now supplemented by journeys to the North Pole aboard nuclear powered icebreakers or transits through the Northwest Passage and Northern Sea Route. The cruise ships now under construction will further expand both passenger capacity as well as the number of vessels serving the Arctic market.

The popularity of mass tourism, and cruise ship travel in particular, is clearly demonstrated by the growing number of passengers touring Arctic nations (though not necessarily to Arctic destinations within those nations or regions; separating Arctic statistics from broader ones can be difficult or impossible depending on the jurisdiction and how the statistics are compiled):

**Norway**: 370,000 cruise passengers visited Norway as a whole in 2007, double the number that arrived just seven years earlier in 2000. While the majority do not travel north of the Arctic Circle, travel there has also increased. For example, in 2007, Svalbard had 45 cruise calls, 17 more than the year before.

**Iceland**: Tourism is the nation's second largest industry, with annual growth of 9% since 1990. Modern air transport and cruise ships have enabled this remarkable rate of growth. Since 2000, the annual number of tourists visiting Iceland has exceeded the number of Icelanders living there.

**Canada**: Cruise ships to Arctic waters doubled in just one year from 11 in 2005 to 22 in 2006. Inuit-owned Cruise North Expeditions entered the market in 2008 with trips to Ellesmere Island.

**Russia**: The Northern Sea Route, White and Barents Seas now have cruise tourism. The Kamchatka and Kola Peninsulas offer commercial air and marine based sport fishing and wildlife tours.

**Alaska**: In 2007, the number of cruise visitors was 1,029,800. This is an increase of 7.3% from the previous year. The vast majority of this traffic, however, was outside the Arctic and sub-Arctic, with only a few cruises reaching the Bering Sea or Arctic Ocean. Some tourist traffic on flights to Arctic destinations such as Barrow, Kotzebue, Nome and Anaktuvuk Pass is most common in the summer months of June, July and August, usually consisting of at most a few dozen people a day (e.g. Huntington *et al.* 2007).

**Greenland**: The number of cruise ship tourists increased from 9,655 on 13 ships in 2003 to 28,891 on 39 ships in 2008 (Grønlands Statistik 2010).

Major factors contributing to the growth of mass tourism include commercial airport development; decisions by Arctic communities that tourism is a desirable economic activity; and how a warming climate is dramatically reducing the amount and extent of sea ice, historically the most significant barrier to Arctic travel. The construction and expansion of commercial air facilities to accommodate larger aircraft allows entry by a greater number of tourists. The recognition by Arctic governments that tourism requires support to provide jobs and revenues will assure its long-term presence.

The growing popularity of Arctic mass tourism now represents a significant challenge to environmental resource managers and agencies responsible for providing emergency services. The number of tourists now greatly exceeds the host populations and infrastructure capacities of Arctic communities. When large numbers of tourists travel across either wilderness land expanses or polar seas, there are insufficient resources to either monitor their environmental impacts or provide assurance of a timely response to their emergencies (AMSA 2009). The adequacy of an emergency response is further reduced by the vagaries of severe weather conditions and the paucity of reliable communication networks. The reality of this danger is obvious when reviewing the rapidly growing number of marine incidents occurring in Arctic seas (see Tab. 18.1 and Fig. 14.6 in Michel, Chapter 14).

#### 18.3.1.3. Nature tourism

The Arctic's unique, resident wildlife species and seasonal congregation of migratory species represent prominent tourist attractions (Snyder & Stonehouse 2007). The opportunity to view these animals within a wilderness setting substantially adds to the nature tourism experience. Large populations of marine and terrestrial wildlife populations provide a diversity of attractions that fuels a market of wildlife photographers, wildlife enthusiasts and birders seeking to add to their life lists. Most recently, tourists are travelling to the Arctic to view animals at risk from climate change such as polar bears and ringed seals *Pusa hispida*.

The Arctic also attracts nature tourists seeking a collection of essentially intangible qualities such as solitude, enormous vistas, and environmentally wild and pristine regions. These people value experiences that include clean air, quiet settings, and the spontaneity of seeing wild animals. Both the marine and land environments of the Arctic can provide those unique settings and experiences. These experiences are delivered by means of specialized tour companies. Their method of transport may be ship, all-terrain vehicle or plane, but their scale is small and their passengers generally share similar values. These tourism activities are often characterized as 'expeditions' that allow tourists to explore the Arctic with knowledgeable guides and lecturers.

Currently, the nature tourism market is increasing with people wishing to personally view the Arctic's rapid climatic changes. There are also tours dedicated to sharing the experiences of diminishing ice and wildlife species threatened by a warming environment.

The management of nature tours is greatly dependent on the service provider and the qualifications of their personnel. In most cases, tour providers offer responsibly delivered experiences that respect both the quality of the Arctic environment and the safety of the visitor. Governments enforce a variety of maritime regulations and guide licensing requirements. These are supplemented by international laws and regulations pertaining to many aspects of the tour operation including vessel management, endangered species protection and protection against environmental pollution. Despite these safeguards, the hazards of Arctic weather, ice infested seas and multiple intrusions of tourists at wildlife viewing sites can pose risks to the environment and to the tourists themselves. On the other hand, nature tourists are probably the most knowledgeable and concerned not to cause harm. Furthermore, they often become some of the best advocates for nature conservation in the Arctic, having experienced it firsthand.

A common belief appears to be that nature tourism can play an important role in strategies for both sustainable development and environmental conservation in the Arctic. Yet studies on land have shown local degradation of low and high Arctic vegetation and soils from hiking and camping by as few as 100 tourists annually, with somewhat higher thresholds evident in sub-Arctic regions (Forbes *et al.* 2004). In contrast to evidence from other research, strategies for dispersing traffic that were intended to reduce impacts were proven to actually increase visible degradation (Forbes *et al.* 2004). Whoever operates future nature tours in the Arctic, the onus will be on the governing bodies to mandate appropriate guidelines, and the tour leaders and guides to carefully educate and monitor their groups before allowing tourists to explore potentially sensitive areas. In some cases, prohibiting access altogether may be merited when the risks of damage (e.g. species introductions, wildlife or habitat disturbance) are simply too great.

#### 18.3.1.4. Adventure tourism

The Arctic's adventure tourism market is constrained only by the imagination of its participants. The adventurers are individualists seeking to experience the exhilaration of personal accomplishment. Their exploits may include ocean transits of unchartered coasts by sea kayak or private yacht, mountain ascents by new routes or during new seasons, or trekking vast Arctic expanses on ski or snowshoe. In all instances they are usually unaccompanied by local guides.

Most of the Arctic landmass may be characterized as sparsely inhabited wilderness, and the majority of its polar seas lack accurate hydrographic data and reliable charts. These conditions represent the attraction of the unknown to the adventurer and significant management challenges to Arctic jurisdictions. Limited monitoring and enforcement resources constrain effective environmental protection of both terrestrial and marine environments. Jurisdictional ability to provide timely responses to adventurer emergencies is extremely difficult.

The growth of the adventure tourism market has been remarkable in terms of both numbers and diversity of activities. New recreation equipment technologies and the popularity of extreme sports have contributed to this growth. Improved transport technologies, reduced sea ice, allowable jurisdictional entry, and promotion of year round tourism are all contributing to the growth of adventure tourism in the Arctic.

Currently, the best sources of adventure tourism information are the numerous specialized recreation publications and organizations that cater to the adventure enthusiast. Adventurers such as mountaineers, kayakers, rafters, skiers, mountain bikers and wilderness backpackers share exploits, test equipment and propose new challenges in publications dedicated to their pursuits. Clubs provide a social venue for sharing similar information, and equipment manufacturers sustain these sports by technological innovations. Growing perceptions that the Arctic is increasingly accessible will, most probably, increase demand for this type of tourism.

#### 18.3.1.5. Culture and heritage tourism

Indigenous peoples throughout the circumpolar north possess a rich diversity of cultures and traditional practices that are popular tourist attractions. Cultural values, subsistence practices, art forms, and lifestyles adapted to polar seas and lands are unique characteristics that indigenous peoples can potentially share with tourists. As indigenous peoples have progressively attained self-rule, the decisions to share their heritage and cultural practices have increasingly been made by their own governing institutions. This decisive role is at once a vital function and a challenge. The realization of these inherent conflicts offers considerable insight into the current circumstances that characterize Arctic cultural tourism.

The attainment of self-governance is accompanied by the need to achieve economic self-sufficiency which will provide jobs and revenues needed to support local communities and infrastructure. Subsistence economies do not provide sufficient jobs and money needed to care for entire indigenous populations living in modern societies. One method for meeting that need and participating in a global market economic system is to encourage tourism. All Arctic governments strongly promote cultural tourism as a means of securing jobs, income and sales revenue, and preserving cultural traditions and languages.

The strong promotion of tourism by Greenland's government provides a striking illustration of the benefits and the stresses associated with the pursuit of this type of economic development. In the year 2003, a total of 13 cruise ships made 164 port calls. By 2008 the number had tripled with a total of 39 cruise ships making 375 port calls. The number of cruise ship passengers who arrived in 2008 was 24,999 persons in addition to the crew and staff that accompanied them. This amounted to over 44% of the total population of Greenland. Given this numerical perspective, there are real challenges associated with the preservation of cultural values and the capacities of local infrastructure.

The promotion of cultural tourism is accompanied by stresses caused by insufficient infrastructure and emergency response services and intrusive behavior by some tourists. Consequently, the achievement of a successful Arctic cultural tourism program requires the difficult balancing of local values, capacities and natural resources with the economic necessities of jobs and incomes. Furthermore, balancing local activities such as hunting with visitors' interests such as viewing undisturbed and approachable wildlife can be difficult.

#### 18.3.1.6. Future concerns

Compared with some earlier forms of exploitation e.g. commercial whaling, mineral extraction and military exploitation, tourism has so far proved largely benign toward the sensitive environment in which it takes place. Environmental impacts due to tourism are typically modest; environmental damage due to tourism is hard to identify, except perhaps in truly wilderness areas where the very presence of people can be regarded as an intrusion. Tour operators, equally as responsible for management as government agencies, have every reason to keep tour operations as ecologically friendly as possible. Thus far they appear to have largely succeeded.

The downside is that polar tourism is expanding faster than the development of the infrastructure required to exert any reasonable control over the effects of tourism. Tourism in wilderness areas is difficult and expensive to manage effectively, due in part to poor revenues, and in large part to the relative scarcity, in under-populated areas, of qualified guides, rangers and others to maintain safety standards and environmental quality. Regional and national desires to attract tourist revenue may also override local concerns (e.g. Mustonen & Mustonen 2011). Such is the case with the internationally owned salmon tourist camps in Kola Peninsula, where local Saami and Komi are prevented from accessing traditional salmon fisheries.

Mass tourism to popular areas are the most manageable activities: massed tourists bring sizeable revenues that can pay for the infrastructure required in guiding, ranging, policing, monitoring and providing the safety factors on which continuing tourism depends. However, the recent advent of cruise liners creates special problems for maritime agencies. Big ships operating in Greenland waters, for example, cannot expect the coastguard services and safeguards provided by wealthier and more populous countries.

Sport fishing and hunting, along with culture and heritage tourism, are usually well organized and controlled, again in recognized locations where revenues accrue and management is relatively easy. More difficult to manage are the visits to vast tracts of wilderness attractive to nature-lovers and adventurers, areas wider and more remote than any form of governance can adequately supervise or manage.

Arctic tourism is flourishing, bringing pleasure to millions of tourists and benefits to many communities. All Arctic governments need to welcome tourism with caution, and to manage its progress with wisdom and care.

### 18.3.2. Non-market values

Cultural services are not limited to hands-on experiences with Arctic biodiversity. Many people benefit from the fact that Arctic biodiversity exists, and enjoy the fact of sharing a world with iconic polar bears and charismatic Inuit and Saami, or appreciate the fact that such biodiversity will remain available to their descendants to enjoy, to use or to make new discoveries. Such values are typically expressed in terms of what they mean to people, but there is also a case for biodiversity having value for its own sake, regardless of human subjectivity. While the characteristics of such values may be described, placing a monetary or other quantitative value on them is less exact practice, though still worth attempting, as discussed below.

#### 18.3.2.1. Definitions and significance

Existence value: People, organizations and institutions worldwide can find value in the biodiversity of the Arctic. A vast array of printed and electronic media highlighting Arctic wildlife, and adventure contribute to awareness and knowledge about the Arctic. Many people can value Arctic ecosystems and species just by knowing that they exist and are healthy, even if those people never visit the Arctic or receive direct benefits from Arctic ecosystem processes or services.

Option value: In addition, people may value Arctic ecosystems for a possible future benefit they may directly derive from them. For example, people may wish to have the option to visit the Arctic in the future. Or perhaps an Arctic plant may prove at some future time to have pharmaceutical or other commercial values.

Bequest value: People may value the biodiversity of Arctic ecosystems because they wish to ensure that future generations benefit from these places or processes. For example, they want to know that their grandchildren and great grandchildren will have the opportunity to see a polar bear, visit the Arctic coastal plain, or benefit from knowing that migratory birds such as the Arctic tern *Sternea paradisaea* or the sandhill crane *Grus canadensis* have intact and productive breeding grounds.

Cultural value: This is different than the perceptions of existence value held by economists and most resource managers. Indigenous residents in the Arctic have a holistic view of themselves and humans as part of, rather than separate from, the larger ecosystem that includes plants, animals, landforms, water and weather (Cajete 2000, Kovach 2009). The cultural and individual identity of Arctic peoples, is intimately linked to their surroundings. In this value system, Arctic biodiversity is directly linked to cultural identity and survival, especially through linguistic diversity and survival. While indigenous values of Arctic biodiversity include direct use values for food, clothing, shelter, subsistence harvest, ceremonies and the like, they also include the existence value of biodiversity, which is linked to adaptive capacity and cultural survival (Berkes 1999, Krupnik & Jolly 2002).

Intrinsic value: Philosophers have defined intrinsic value in nature as a value in and of itself regardless of any human benefit which can be derived from it. This is an important concept in environmental ethics and is recognized by The Convention on Biological Diversity (CBD) and the US National Research Council (Callicott 1986, NRC 2004, CBD 2012).

### 18.3.2.2. Measurement and indicators

Ecosystem service values are measured by economists through several means including revealed-preference, stated-preference and replacement costs. These involve methods such as hedonic pricing, travel cost and hypothetical scenarios known as the contingent valuation method (CVM). CVM is the most common economic method for estimating existence values. Responses are collected on per individual or per household basis for willingness to pay for a good or service, or willingness to accept payment for the destruction of a good or service (Walsh *et al.* 1984, Freeman 1993, Hanley & Spash 1993). Other methods involving deliberation and decision matrices have been proposed to capture ecosystem values (Wilson & Howarth 2002).

Key issues to consider in the economic valuation of ecosystem services include connections between ecological and economic context, geographic scope and spatial and temporal scale. It is important to consider whether the valuation estimates marginal (i.e. per unit) value or average value as well as the implicit assumptions and uncertainties (NRC 2004). When estimating value over time, economists use what is known as a discount rate to account for the difference in value in the present versus value in the future. If a high discount rate is used, then the future value will be less than if a low discount rate is used. Thus, selection of the discount rate can influence the outcome of ecosystem valuation. In addition, as noted above, since there is a high degree of interdependency within and between ecosystems, the geographic scope, spatial and temporal scale of analysis will impact the valuation outcome. Finally, economic valuation often assumes that substitute goods or services will be available. However, on a global and regional scale, substitutes for ecosystem goods and services often do not exist (Daily *et al.* 2000).

Based on synthesis of existing research at the time, Colt (2001) estimated net economic value of existence values of Alaska ecosystems to range from 309 million USD to 9,652 million USD. These include two Alaska-specific studies that found annual willingness to pay of 3 USD per US household to prevent an oil spill such as that which occurred in Prince William Sound by the *Exxon Valdez* tanker and 25-50 USD annual willingness to pay per US household to preserve wildlife habitat in sub-Arctic Bristol Bay (1997 USD equivalent). While largely or entirely south of the Arctic, the results of these studies are representative of reported existence values for ecosystem services in northern latitudes.

Costanza *et al.* (1997) estimated the total value of all ecosystem services in the biosphere to approximately equal or exceed global gross national product (mean 33 trillion USD). Colt (2001) applied Costanza's methodology and arrived at a rough estimate of the value of Alaska's ecosystem services to be 1.2-1.6 billion USD annually (1998 dollars). The interdependence of provisioning, regulating and cultural ecosystem services may also require simultaneous consideration of a constellation of values in resource management and conservation practice, whereby measurement of existence values are just one part of the overall valuation of ecosystem services (Heal *et al.* 2001).

Other indicators of Arctic existence values could be membership in, volunteering for, and financial contributions to conservation organizations that support Arctic protection. These include international organizations such as The Nature Conservancy and World Wide Fund for Nature as well as specific national or regional organizations in each country. In addition, the funds that these organizations spend in public education campaigns about Arctic biodiversity and protection can be an indicator of existence, option and bequest values.

Both formal legal protection, such as the *Endangered Species Act* in the US, and public campaigns for species protection can be seen as indicators of existence value of Arctic biodiversity (see Huntington *et al.*, Chapter 19).

The value of intact, functioning ecosystems (i.e. not just distinct endangered species) is reflected in national and international management practices and priorities, for example those based in ecosystem management and adaptive management (Norton & Steinemann 2001).

Because Arctic indigenous peoples rely directly on functioning and healthy Arctic ecosystems for cultural identity as well as for food and other goods and services, the existence value of Arctic biodiversity from the indigenous perspective described above has also been framed as a human-rights issue. Thus, the number and extent of law suits, or statements to the United Nations and Arctic Council by indigenous groups regarding the rights of Arctic native peoples, may also be an indicator of existence value (McLean *et al.* 2009, Trainor *et al.* 2009).

### 18.3.2.3. Future concerns

Based on economic and other indicators of existence value of Arctic biodiversity, it is reasonable to project that existence value will remain constant or increase over time. Economic measures of existence value are a function of population (individuals or households) and stated willingness to pay, which in turn is a function of ability to pay. Based on analysis of all Arctic countries from 2000-2005, Mäenpää (2008) reported that the population of the Arctic increased overall in that period, but with considerable variation by country including some with Arctic population declines. In this period, the USA, Canada and Iceland showed overall population growth, including in Arctic areas of ~5-7%. These same countries also had three of the top four highest reported per capita Gross Regional Product and the highest household disposable income in 2005 in both Arctic and non-Arctic regions (the fourth is Norway, which experienced a decline in its Arctic population in the 2000-2005 study period). In this same time period, Arctic countries experienced overall economic growth in both Arctic and non-Arctic regions from ~1% (Denmark) to ~8% (Russia) (Mäenpää 2008). With a longer-term view, the Arctic Human Development Report (AHDR 2004) reported an overall population increase in Arctic countries between 1940 and 2000. For countries experiencing population decline during a given reporting period, that decline was less than 1% with the exception of Russia which experienced 2% per year population decline between 1989 and 2002 (Bogoyavlenskiy & Siggner 2004).

Overall, given anticipated increases in population and economic conditions, it is reasonable to anticipate that economic measures of the existence value of Arctic biodiversity will increase over the next one to two decades.

Colt (2001) projects increasing economic existence values in Alaska:

> "Looking ahead between 50 and 100 years, it is clear that Alaska's functioning, protected ecosystems will become increasingly valuable global assets in a crowded industrialized world. Direct use values are likely to decline in relative importance while existence values are likely to increase significantly. It is likely that world population, average per capita income and average education levels will all double within the next 25 to 50 years, leading to an eight-fold increase in the key factors that drive up existence value. In addition, the continuing degradation of other ecosystems in other places will further increase the relative scarcity and hence the value of Alaska's ecosystems. And the increasing pressure to manage global environmental change will put an increasing premium on scientific knowledge gained from large-scale ecosystems that are not human-dominated. Alaska is one of the few places likely to retain such large areas of undisturbed lands and waters."

As climate change impacts the Arctic, and valued ecosystems and species become increasingly scarce, the non-market values of Arctic ecosystems can be expected to rise. The Arctic is experiencing, and likely will continue to experience, rapid warming that results in dramatic ecological changes such as reductions in sea ice extent and thickness, sudden and gradual drying of lakes, decreases in surface water availability, increased risk of wildfire, warming permafrost, northward shifts in species distributions and overall increasing annual temperatures that allow for the introduction of exotic species and for changes in pests, insects and disease (ACIA 2005, Markon *et al.* 2012, Ims & Ehrich, Chapter 12, Wrona & Reist, Chapter 13, Michel, Chapter 14, Lassuy & Lewis, Chapter 16). Given these existing and expected future changes, it is reasonable to anticipate increasing stress on habitats and thus increasing listings of threatened and endangered species. These stresses may lead to scarcity and thus increased value of ecosystem properties and services. It is also theoretically possible that ecosystem changes due to climate change may lead to new species and new conditions that have added non-market values. However, the exact nature of these new values cannot be determined at this time.

Although dependent on administrative priorities, there is a growing trend away from single-resource management and towards ecosystem-based management, indicating increasing priorities for system approaches and growing values over time for ecosystem function, health and biodiversity (Chapin *et al.* 2009). Finally, indigenous groups are gaining momentum in organizing and asserting their values and rights for Arctic ecosystems. These trends may help to stabilize those aspects of the Arctic ecosystems that are valued outside of the market and may also lead to greater awareness of non-market values and more people ascribing non-market value to Arctic ecosystems.

## 18.4. DISCUSSION AND CONCLUSIONS

Arctic ecosystems provide a wide range of services locally and globally. The specific services described in the preceding sections, while not exhaustive, are important examples. Without Arctic ecosystems, the world would be a poorer place economically, ecologically and culturally. To some extent, the value of ecosystem services in the Arctic can be calculated or estimated in monetary terms. Commercial fishing, for example, is a profit-making enterprise, and the value of fish landed and of ancillary activities in fishing communities is an often-reported figure, used among other purposes to advocate for various management approaches or decisions. The value of cultural reliance on local foods, on the other hand, is typically considered in qualitative terms, with reference to an inherent worth that cannot be reduced to a monetary figure. That said, economists routinely derive at least an implied value of things such as the life of an individual human being, based for example on the extent to which society is willing to accept greater risks in the name of efficiency. While few would wish to see a price tag put on their lives or the lives of their loved ones, it is also clear that society will not expend limitless resources to protect or save people from harm. Similarly, though the idea that a species may have a finite value to human society might not be the most welcome, it is also clear that reducing to zero the level of human impact on the environment is not feasible without a return to prehistoric ways of life (TEEB 2010).

This chapter has introduced a range of ecosystem services together with the quantitative and qualitative metrics and descriptions that can be used to show the status of those services at the present time. This effort establishes a baseline against which change can be recognized and measured, with the caution that a snapshot of conditions in the early 21st century provides relatively little context for the state of the environment and society at that moment. Further research and analysis on trends in ecosystem services would help provide more detail for understanding future gains and losses. For example, a service that has been declining but becomes stable may show promise, whereas a service that has been increasing but becomes stable may indicate an area of concern. Trade-offs among services must also be taken into account, recognizing that an increase in one service may come at the expense of another. Additional research is needed to better quantify individual services, and also to provide a basis for comparison across ecosystem services and in contrast to other components of the Arctic system such as mineral resources and their extraction. Estimating the monetary value of all services offers one way to develop a common metric, but should be approached with caution and a recognition that the value of some services may be difficult to capture in their entirety.

One challenge faced in this review of ecosystem services is the availability of data to support an assessment. Some data, such as commercial fisheries harvests, is routinely reported and generally available. Nonetheless, there remains the possibility of unreported harvests or intentionally erroneous reports. Data for other services, such as traditional hunting or existence values, may be available only for certain regions or species, leaving the potential for under-reporting of the aggregate value to human society. Furthermore, there is overlap among services. Traditional hunting, for example, provides food, clothing and other material benefits to Arctic peoples. It also provides a sense of identity and a basis for culture, including language perpetuation and thus linguistic diversity (see Barry *et al.*, Chapter 20). The abundance of books, magazine articles and other materials on Arctic peoples attests to the value placed on them and their way of life by people around the world. Thus the act of hunting a caribou or a seal is potentially far greater than the sum of the nutrients and energy the animal provides to those fortunate enough to eat it.

### 18.4.1. Data availability

An assessment of ecosystem services, as with any other such undertaking, can only be as good as the data upon which it relies. Data availability for the services described in this chapter is variable by service, region and time. While some services can be estimated based on limited data, a comparison over time is difficult if data collection methods or practices change. A systematic approach to data collection is desirable, as has been noted in other assessments of aspects of the Arctic environment (e.g. Baffrey & Huntington 2010 and the Circumpolar Biodiversity Monitoring Program). What data can be realistically gathered is another question. The evaluation of ecosystem services is unlikely to be sufficient justification for an extensive data gathering effort. On the other hand, such an evaluation can be a worthwhile and valuable additional outcome to a broad monitoring effort. Commercial fisheries catches are required by law to be reported, providing a reliable and continuous data stream. Traditional hunting and fishing, however, is reported sporadically, depending on region, making even a snapshot of harvest levels difficult to obtain on a wide scale. Existence values are perhaps the most elusive to document on a regular basis, but can nonetheless be gauged in part by simple indicators such as membership or contribution levels in organizations that promote healthy Arctic ecosystems, or by media coverage of Arctic issues as a reflection of widespread interest outside the region.

Further analysis and discussion of data needs is required, ideally as part of a wider discussion of data gathering.

### 18.4.2. Provisioning and cultural services in perspective

Provisioning and cultural services capture at least a portion of the value of Arctic ecosystems and ecosystem services to people. But the Arctic provides other services and values, such as the worth of mineral and petroleum resources that are extracted and exported to other parts of the world. While a simple comparison of costs cannot and should not be the sole basis for deciding whether a development project should be undertaken, monetary gains and profits are nonetheless regularly considered against environmental impacts. McDonald *et al.* (2006), in a survey of Arctic economies, found that the value of mineral and petroleum extraction dwarfed fisheries, forestry and agriculture in northern Canada, Alaska and Russia in 2002. In Greenland, Iceland and the Faroe Islands, however, fisheries made a far larger contribution to gross domestic product than did mining and petroleum activities. This is not to say that there is a simple trade-off between renewable and non-renewable resource exploitation, but merely to point out that a simple measure of the value of a single ecosystem service (commercial fisheries) allows an equally simple comparison with extractive industries to place the commercial value of ecosystem services in a wider context of national or regional economies. A wider evaluation of ecosystem services may help avoid the pitfall of comparing a limited indicator (commercial fisheries, but not all other ecosystem services) with a more comprehensive indicator (the value of a purely economic activity such as petroleum extraction). Even if extractive values are greater than those provided by an intact ecosystem, it is important to protect ecosystem functions and services as much as possible when engaging in activities that threaten them.

### 18.4.3. Arctic provisioning and cultural services in a global context

Arctic and surrounding seas produce more than 10% of global marine fisheries catches by weight and 5.3% of global crustacean catches (Lindholt 2006). As other regions are overfished, the percentage of catches from the Arctic may increase, even as global catches are declining. Pinning down global percentages for many other services is likely to be more difficult, but one attempt to quantify in economic terms the loss of climate regulation services from a melting cryosphere put the cost of global climate services lost in 2010 at 61-371 billion USD (Euskirchen *et al.* 2010; see also Huntington, Chapter 19). The value of cumulative services likely to be lost from 2010 to 2050 was placed at 2.4-24 trillion USD. This estimate does not explicitly include Arctic ecosystem services beyond climate regulation, though the valuation of impacts does aggregate loss of global ecosystem services. As ecosystems elsewhere in the world are subject to increasing pressure and degradation, the value of intact Arctic ecosystems, viable populations of large predators, and other components of the Arctic are likely to become correspondingly more prominent. Existence values, tourism and other such services will thus increase as well.

### 18.4.4. Other services to consider in future

The Millennium Ecosystem Assessment (2005) identifies a number of services and sub-categories under the provisioning, regulating and cultural headings. As Tab. 18.2 shows, many potential ecosystem services have not been addressed in this chapter. Some, such as crop production, do not typically occur north of the treeline, and thus are outside the strict definition of the Arctic used in this report. Others, such as fresh water, have not received a great deal of attention in the Arctic, in some cases because they may not be perceived as services in short supply or under threat. Nonetheless, future assessments of Arctic ecosystem services should examine this list, among others, to determine which services might usefully be added, if sufficient information is available.

### 18.4.5. Trends

Six ecosystem services are evaluated in this chapter, and rough trends are indicated in Tab. 18.3. Assessing trends is difficult because there can be great regional disparities, conflicting trends depending on the time scale in question, and simply because an ‘increase’ may not be a good thing. For example, increasing existence values for the Arctic may in part reflect loss of intact ecosystems, landscapes and species in the rest of the world. Increasing commercial fisheries catches may indicate increased productivity, or poor management. A better measure

| MEA category | MEA service | MEA sub-category | Covered in this chapter |
|---|---|---|---|
| Provisioning Services | Food | Crops | No |
| | | Livestock | Reindeer herding |
| | | Capture fisheries | Commercial fisheries |
| | | Aquaculture | No |
| | | Wild foods | Commercial and subsistence hunting, gathering and small-scale fishing |
| | Fiber | Timber | No |
| | | Cotton, hemp, silk | No |
| | | Wood fuel | No |
| | Genetic resources | | No |
| | Biochemicals, natural medicines, pharmaceuticals | | No |
| | Fresh water | | No |
| Cultural Services | Spiritual and religious values | | (see Barry *et al.*, Chapter 20) |
| | Aesthetic values | | Existence values |
| | Recreation and ecotourism | | Tourism; recreational and sport hunting |

**Table 18.2.** Provisioning and cultural services identified in the Millennium Ecosystem Assessment (2005), compared with the six services examined in this chapter. Note that two other MEA categories (supporting services, regulating services) are not addressed in this chapter.

| Service | Trend | Notes |
|---|---|---|
| Reindeer herding | ? | Reindeer herding is highly variable |
| Commercial fisheries | ? | Some fisheries have seen increased catches, others have seen decreases; fisheries management appears robust overall in the Arctic |
| Commercial and subsistence hunting, gathering and small-scale fishing | ? | Traditional activities are decreasing in some areas, increasing in others, often in response to population and other demographic trends |
| Recreational and sport hunting and fishing | Increasing | The Arctic is an increasingly popular destination |
| Tourism | Increasing | The Arctic is an increasingly popular destination |
| Existence values | Increasing | Areas perceived as ‘unspoiled’ are decreasing worldwide, raising the value of those left, such as much of the Arctic |

**Table 18.3.** Trends in the six ecosystem services examined in this chapter. Note that an increasing trend is not necessary a good thing overall, as increased use of Arctic resources may lead to increased conflicts among user groups, or increasing existence values may be the result of decreased wilderness areas or wild species, creating higher value for what remains.

might be the extent of effective fisheries management regimes, rather than catch levels. Here, too, further work would be useful to identify key indices and assess trends individually and in aggregate to determine how best to characterize the state of Arctic ecosystems and the services they provide to human beings.

### 18.4.6. Conclusions

Ecosystem services in the Arctic are important economically, environmentally and culturally. These services benefit Arctic residents directly, providing food and material benefits as well as supporting indigenous cultures, including language. The Arctic ecosystem also serves the rest of the world, as a destination for tourism in various forms, simply by existing, and by providing a large amount of food from commercial fisheries and reindeer husbandry. Recognition of the importance of these services, and an assessment of how they are changing, is vital to design effective Arctic conservation strategies.

At the same time, ecosystem services must be viewed in a wider context. First, the services are not necessarily compatible. For example, the allocation of hunting or fishing rights may pit one user group against another, resulting in a debate about the relative values of different types of use. At the same time, the Arctic and its resources have value for humans in other ways, such as extractive industries like mining and oil and gas. While extraction is not necessarily incompatible with a healthy ecosystem, there are usually impacts of one form or another, and the value of extraction is weighed – implicitly or explicitly – against the value of the ecosystem services that may be lost. Such comparisons may be inherently uneven, in that they compare a direct value (e.g. barrels of oil extracted) with values that are often indirect and difficult to quantify (e.g. the existence value of a polar bear). Furthermore, indirect services are often diffuse, and thus most measures may be partial rather than comprehensive. Nonetheless, an articulation of the values of ecosystem services is necessary to understand what is at stake from environmental degradation, and to understand the benefits of conservation of the Arctic environment.

This assessment of ecosystem services should be seen as preliminary, providing what we hope is a useful baseline for future comparisons, but also recognized as incomplete in that many services, such as the provision of freshwater, have not been addressed, and the full value of some services has probably been underestimated because their full dimensions have not yet been encompassed. Further studies of ecosystem services, their delineation and their valuation are necessary to provide a more complete picture of the many ways that human societies benefit from the Arctic ecosystem. Arctic biodiversity is a world heritage, its significance extending around the globe in ways we are only beginning to see.

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## LIST OF ACRONYMS

| | |
|---|---|
| AHDR | Arctic Human Development Report |
| CAFF | Conservation of Arctic Flora and Fauna |
| EBM | Ecosystem-based management |
| EEZ | Exclusive economic zone |
| FAO | Food and Agriculture Organization |
| ICES | International Council for the Exploration of the Sea |
| IUU | Illegal, unreported, and unregulated (fisheries) |
| MSY | Maximum sustainable yield |
| NEAFC | Northeast Atlantic Fisheries Commission |
| NPFMC | North Pacific Fisheries Management Council |
| PICES | North Pacific Marine Science Organization |
| RFMO/RFMA | Regional fisheries management organization/agreement |
| SDWG | Sustainable Development Working Group |
| TAC | Total allowable catch |
| UN | United Nations |
| USD | U.S. dollars |
| VME | Vulnerable marine ecosystem |

Species protection has focused on preventing overharvest, which has historically been the largest threat to Arctic biodiversity. Seabirds are an example of biodiversity that is susceptible to such overharvest, and this has caused population declines in some parts of their range. In these areas, careful regulation of harvest is necessary as part of a conservation and restoration strategy. Kippaku, NW Greenland. Photo: Knud Falk.

*Chapter 19*

# Disturbance, Feedbacks and Conservation

**Lead Author**

Henry P. Huntington

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## Contents

> **We were told not to hunt animals for the sense of killing. Because you are not able to use that animal for eternity. I believe we were also taught that there is a certain purpose here in this particular time for us to utilize these marine mammals. That was what I heard the elderly people say from the older generation, like Pelaasi and others, used to say. They were saying: the 'plan' has been already made. The 'master plan' is that our purpose is to hunt marine mammals, but that we should not take that for granted. This is why conservation is so important in our culture.**
>
> George Noongwook in Oozeva *et al.* 2004.

## SUMMARY

Humans disturb the environment in various ways, notably from industrial development and other activities in formerly pristine areas. Components of the earth system affect one another in a web of feedbacks, including between ecosystems and climate. Conservation is the human attempt to avoid or minimize negative impacts of human activity on species and habitats. This chapter examines all three topics.

Disturbance here refers to the disruption of normal ecological functions or distributions at the landscape level. While many types of human activity can affect local environments, industrial development is most likely to affect larger areas, followed by spatially extensive practices such as reindeer herding that can lead to heavy grazing and trampling. Around the Arctic, human activity is increasing, with more roads and other infrastructure, leading to a greater overall impact, especially in areas with oil and gas or other valuable commodities.

Feedbacks occur in many forms at many scales. Here, we look at the primarily positive feedbacks from Arctic warming to global climate, which are likely to lead to still greater warming. For example, the loss of ice and snow leaves a darker surface, so that more sunlight is absorbed, leading to greater warming and so on. Changes in the Arctic's role in the carbon cycle, through release of carbon dioxide and methane and possible increased uptake of carbon dioxide through increased vegetation growth, will affect global climate. Forcing through positive feedbacks is likely to outweigh the impacts of negative feedbacks within the Arctic.

Three measures of conservation are addressed next. Habitat protection is usually measured in terms of protected areas, which are generally strong on land in the Arctic but nearly absent in the marine environment. Species protection includes those species listed in various categories at risk of extinction, and unfortunately these lists appear to be growing in the Arctic as elsewhere in the world. Effective conservation also requires the participation of the people who are likely to either create threats or be affected by management measures. A growing number of programs seek to include Arctic residents in gathering, analyzing and making use of observational data, which often cannot be obtained in other ways.

## 19.1. INTRODUCTION

Humans interact with Arctic ecosystems in many ways. This chapter examines three types of interactions: disturbance, feedbacks and conservation. Disturbance is the effect that human activity has on the natural environment. Taken broadly, nearly everything humans do creates some form of disturbance, since the natural world is altered by our presence and our activities. Some of this interaction is the normal result of people living as part of the ecosystem, and thus does not constitute a threat. For the purposes of this assessment, disturbance refers more narrowly to the disruption of normal ecological functions or distributions at the landscape level, posing a threat to biodiversity. While many types of human activity can affect local environments, industrial development is most likely to affect larger areas, followed by spatially extensive practices such as reindeer *Rangifer tarandus* herding that can lead to heavy grazing and trampling of vegetation.

Feedbacks are in one sense a part of the natural world, constraining the natural cycles of weather, climate and biology. Feedbacks large and small are thus present throughout the world. While negative feedbacks tend to push a system back to its original state, positive feedbacks lead to ever greater or faster change. Melting snow, ice and permafrost in the Arctic are one such positive feedback, and are described herein. This feedback is already important at the global scale, and likely to become even more significant in the near future as sea ice retreats in summer, snow cover becomes less extensive in space and time, and permafrost degrades and thaws, all of which will lead to greater warming and thus further change.

On a more optimistic note, conservation efforts are humankind's attempt to reduce its negative impacts on the environment. Habitat protection recognizes that biodiversity requires intact ecosystems for natural processes to continue. Species protection focuses directly on populations that are at risk, aiming at its simplest to avoid extinction from human causes. Environmental monitoring is essential to determine what is at risk and whether conservation efforts are succeeding. In the Arctic, sparse populations and remote areas create a special need for the involvement of local residents in community-based initiatives. These three conservation measures are addressed here.

This chapter is neither exhaustive nor definitive on the topics of disturbance, feedbacks and conservation. It aims instead at describing key aspects of human-ecosystem interactions, focusing on matters of special significance in the Arctic, with the expectation that these areas of focus will be relevant markers for future consideration of trends in Arctic ecosystems and their relationship to humans and to the world as a whole.

## 19.2. DISTURBANCE

### 19.2.1. Human footprint in the Arctic

Widespread concern regarding the prospect of large-scale resource development in the Arctic was first expressed 40 years ago (e.g. Bliss 1970a, 1970b, Bellamy *et al.* 1971). Human activities and associated disturbance regimes are much more extensive within the tundra biome than in the past. Sizable portions of the region are faced with widespread threats ranging from onshore and offshore oil and gas development to long-distance transport of contaminants, from mining to tourism. Direct effects on certain Arctic ecosystems with a significant human presence, such as the hydrocarbon fields of northern Russia, are likely to be even more imperative than climate change in the next few decades. These effects include direct and indirect impacts associated with, for example, resource exploitation and altered grazing regimes due to changing patterns of reindeer husbandry. Evidence shows that even small scale, low intensity disturbances can accumulate spatially from local to regional scales.

Besides habitat disturbance, human activities may cause disturbance in the form of displacement (scaring) of wildlife from preferred habitat. This is not dealt with here, but see Meltofte *et al.* (Chapter 1), Reid *et al.* (Chapter 3) and Ganter & Gaston (Chapter 4).

### 19.2.2. Direct impacts

In general, the direct mechanical disturbance of Arctic terrain, including vegetation, soil and the underlying permafrost layer, can lead to erosion where slope and/or ice-rich permafrost are present (Forbes *et al.* 2001). Unchecked, severe erosion can progress to eventually degrade entire landscapes. Among the aforementioned three components, vegetation has special importance, not only as the basic link to the upper trophic levels of an ecosystem, but also in terms of its controls over permafrost and ground-ice maintenance in tundra substrates. In addition, the regeneration of an ecosystem after disturbance is dependent upon revegetation, which is the essential first step of ecosystem recovery. Vegetation cover, therefore, is one of the best criteria to assess overall ecosystem status in the wake of previous environmental degradation. Restoration efforts are generally lacking in tundra ecosystems because of the constraints imposed by climate, although assisted revegetation efforts can succeed under certain circumstances when viable seeds or vegetative cuttings are properly cultivated and subsidies of nutrients and water are sufficient. Such efforts can be expensive, however, and most disturbed terrain is left to revegetate naturally, except where control of aeolian erosion is essential (Forbes & McKendrick 2002). Regeneration is slower in the high Arctic compared with the low Arctic and proceeds more quickly on moist-wet terrain, unless there has been subsidence from thawing permafrost. Some of the scars from oil exploration on Alaska's North Slope in the 1950s are still visible today (Forbes *et al.* 2001).

Anthropogenic impacts are complex in that various human activities can influence ecosystems simultaneously and cumulatively, and can have both immediate catastrophic and long-term effects. In practice it can be difficult to distinguish between direct and indirect impacts, and scientists may use different methods for classifying disturbances (Crawford 1997, Gilders & Cronin 2000, Nellemann *et al.* 2001, National Research Council 2003). For example, Russian scientists distinguish three main classes of disturbed areas: *ochagovyi* (local), *lineinyi* (linear) and *fonovyi* (spatial) (Khitun & Rebristaya 2002). The most striking example of the first type includes sites surrounding petroleum bore-holes (drill sites). Recent data from Arctic Russia indicate that each drilling denudes vegetation over an area of about 120-200 m in diameter, with moderate impacts beyond that distance (Forbes *et al.* 2009). Transport corridors appearing in connection with road and pipeline construction constitute linear disturbances. Large territories affected by air pollution are examples of spatial disturbances. Especially in the older gas and oil fields, the amount of terrain disturbed on Russian territories exceeds by an order of magnitude that from North American (Tab. 19.1). The track record in Russia has improved in recent years, particularly in the case of post-Soviet joint ventures, such as the Ardalin Oil Field first developed in 1993-94 by ConocoPhillips' Polar Lights Co. in the Timan-Pechora basin (Rasmussen & Koroleva 2003, Stammler & Forbes 2006).

> » *Freedom…this modern situation cannot be compared to the case when I was young. You cannot compare these times, and it did not change naturally, instead it is like a revolution has taken place. Once the highway was made here [in 1957], it changed every aspect of our system here… I think of this so that I have already witnessed several revolutions so far, even though I am not older than I am.*
>
> (North Saami hunter and Elder Aslak Ola Aikio, Utsjoki, Finland, regarding the arrival of roads, in Mustonen 2012).

**Table 19.1.** Comparison of land areas impacted by oil and gas exploitation in northern Alaska and NW Siberia, respectively (Walker 1996, Khitun 1997, Gilders & Cronin 2000, Khitun & Rebristaya 2002, VNIPIGazdovycha 2005, Forbes *et al.* 2009).

| Northwest Siberia | Area (km$^2$) | Area (km$^2$) | Alaska |
|---|---:|---:|---|
| Yamal-Gydan region | 235,000 | 230,000 | Arctic Coastal Plain |
| Yamal Peninsula | 112,000 | 71,000 | Canning to Colville River |
| Total area disturbed (Yamal-Gydan)[a] | 6,000-7,000 | 785 | Total area disturbed (Trans-Alaska Pipeline System)[b] |
| Bovanenkovo Gas Field (BGF)[c] | 2,052 | 991 | Prudhoe Bay Oil Field (PBOF)[c] |
| Bovanenkovo Gas Field[d] | 200 | 16.9 | Prudhoe Bay Oil Field[d] |
| Severely disturbed terrain (BGF) | 277-287 | 8.8 | Severely disturbed terrain (PBOF) |
| Indirect impact zone (BGF) | 448 | na | Indirect impact zone (PBOF) |
| To be disturbed in the near future[e] | 500 | na | To be disturbed in the near future |

a) Estimate from 1994. b) Includes territory south of the Brooks Range. c) Above-ground facilities. d) Below-ground lease area.
e) Includes territory between BGF and Kharasavey.

The point at which small disturbances create large impacts can be hard to identify, but for indigenous peoples it may begin with a sense of breaking the 'whole' that constitutes their environment and the role of humans therein.

One of the most widespread types of direct impact is damage to tundra from off-road vehicle traffic (Forbes *et al.* 2001, Kumpula *et al.* 2011). In vehicle tracks, plant and soil nutrient cycling regimes can become significantly different than in undisturbed areas, with increases and decreases variable among species, growth forms and soil types. Although the actual ruts may be small to begin with, the shift from scale-of-impact to scale-of-response can be several orders of magnitude, as in the case of drained wetlands. Even shallow ruts from as little as a single-pass vehicle track are capable of effectively diverting runoff from spring snowmelt away from wet and mesic sedge fens that depend upon this source of moisture. Such desiccation of wet tundra has resulted in the local extinction of aquatic sedges *Carex* spp., sphagnum mosses *Sphagnum* spp. and other hydric bryophytes, as well as an increase in surface albedo (Forbes 1997). Similarly, as little as a single passage of a vehicle in summer is sufficient to significantly reduce the abundance of soil arthropods (Kevan *et al.* 1995). In areas with substantial ground-ice, thermokarst activity can expand appreciably. In northern Alaska, some disturbances on silty sediments covered at least twice the original area of impact after 30 years, but most off-road traffic has been effectively banned since the mid-1970s (Forbes *et al.* 2001). A similar ban has been in place in the hydrocarbon fields of Arctic Russia since the late 1980s, but has proven far less effective (Khitun & Rebristaya 2002, Kumpula *et al.* 2011).

> » *We often learn of plans for industrial development only by accident; for example we have learned about the shelf oil-field development project from the American side, and we began to write about it. The authorities often hold back ecological information from us that is important for the society. That's why we often support something without being aware of the ecological consequences.*
>
> (Tatiana Yuryevna Achyrgina in Novikova 2008).

### 19.2.3. Indirect and cumulative impacts

In addition to direct disturbances of the ground surface, other, less visible impacts can accumulate over time. These may occur independently of each other, or may be exacerbated through synergy among various proximal effects. These indirect or cumulative impacts are well-documented, especially in the hydrocarbon fields of North America and Russia. Whereas in the early years of development they were often unforeseen, scientists are now better able to predict them (e.g. Gilders & Cronin 2000, Forbes *et al.* 2001, Kumpula *et al.* 2011).

Given the large amount of hydrocarbon extraction activities that have taken place over several decades on both the North Slope of Alaska and the Yamal-Nenets Autonomous Okrug (YNAO), it is worthwhile to compare the extent of impacts in these two regions (Tab. 19.1). In most cases, the extent of indirect impacts exceeds the physical footprint of an Arctic oil or gas field complex, although efforts at mitigation have continued to improve (Forbes *et al.* 2009). For example, construction of the entire 1,288 km Trans-Alaska Pipeline directly disturbed 785 km$^2$ of land (Walker 1996). It is claimed that if Alaska's Prudhoe Bay Oil Field were developed today using current technology and consolidation of facilities, gravel would cover at least 80% less area, and the oil field's direct footprint would be less than half its current size (Gilders & Cronin 2000, National Research Council 2003). In the case of the YNAO and the Nenets Autonomous Okrug (NAO), where migratory Nenets and their large reindeer herds move back and forth across actively exploited fields, it is important to note that it is not only a matter of how much territory is affected, but what kind of territory and which migrations routes are affected by the losses. Furthermore, research based on extensive participant observation and interviews with nomads has revealed that each territory has its own particular meaning and importance for users, so that one territory is not equivalent to another (Forbes *et al.* 2009, Kumpula *et al.* 2011).

By 1994, disturbed terrain comprised an estimated 6,000-7,000 km$^2$ of the YNAO. Most of the damage to date has been in the southern portion of the region (Khitun & Rebristaya 2002). The impact in the northern tundra zone is still in the early stages, but includes intensive terrestrial and aquatic impacts in and around the Bovanenkovo Gas Field on the territory of the Yarsalinski sovkhoz. At that time, the gas field encompassed more than 200 km$^2$, of which half was severely disturbed and which affected narrow migratory corridors. As of 2005, the visibly affected area around Bovanenkovo, including both direct and indirect impacts, had encompassed about 450 km$^2$ (Forbes *et al.* 2009). This has increased in the last several years as the gas field expands to the northeast so the affected area was 836 km$^2$ as of summer 2011 (Kumpula *et al.* 2012). Oil development in the Arctic regions of the NAO is some years behind that of the YNAO but is catching up quickly.

Several other indirect (and direct) impacts in both terrestrial and aquatic habitats stem from roads and railways. One example is the construction of a transport corridor on Yamal Peninsula between Bovanenkovo and the port of Kharasavey to the northwest (Fig. 19.1). According to nomadic Nenets reindeer herders, the building of about 130 bridges initially degraded key rivers and lakes so that the supply of fish for daily subsistence, especially critical for reindeer herders during summer migration, was less reliable for several years (Forbes *et al.* 2009). However, in 2011 the same herders reported that fish had begun to return in significant numbers (Kumpula *et al.* 2012). In the absence of strict regulatory oversight, poaching can be a chronic problem whenever access to formerly remote regions becomes possible for the general population. Thus, the ongoing influx of workers in both the NAO and YNAO is certain to increase fishing pressure and accelerate this process since enforcement of existing regulations remains lax relative to North America (Forbes *et al*. 2009). Throughout the Arctic, gravel roads and sand quarries are subject to wind erosion and can spread sand and dust up to one kilometer from the source (Forbes 1995, Myers-Smith *et al*. 2006). Road dust is alkaline and is capable of rapidly smothering bryophytes, lichens and mushrooms on the surface. Dust significantly increases the pH of soils and surface waters, and alters the nutrient contents of abundant vascular plants and mosses in as few as four years. During the same time period, blowing sand can bury all mosses and lichens, and many vascular plants, up to a distance of 250 m from the source (Forbes 1995).

### 19.2.4. Other indirect or cumulative impacts

Additional types of impacts result from oil leaks and spills. Massive oil spills, such as the Exxon Valdez or the Deepwater Horizon, have not yet occurred in truly Arctic waters. However, the multifaceted concerns surrounding offshore development continue to grow quickly as the economic viability of fields in the Beaufort, Barents and Kara Seas increases annually, where difficulties in cleaning up after a spill would likely be exacerbated by cold temperatures and ice in part of the year (Margesin & Schinner 1999). The scope of actual and potential development, and the environmental risks involved,

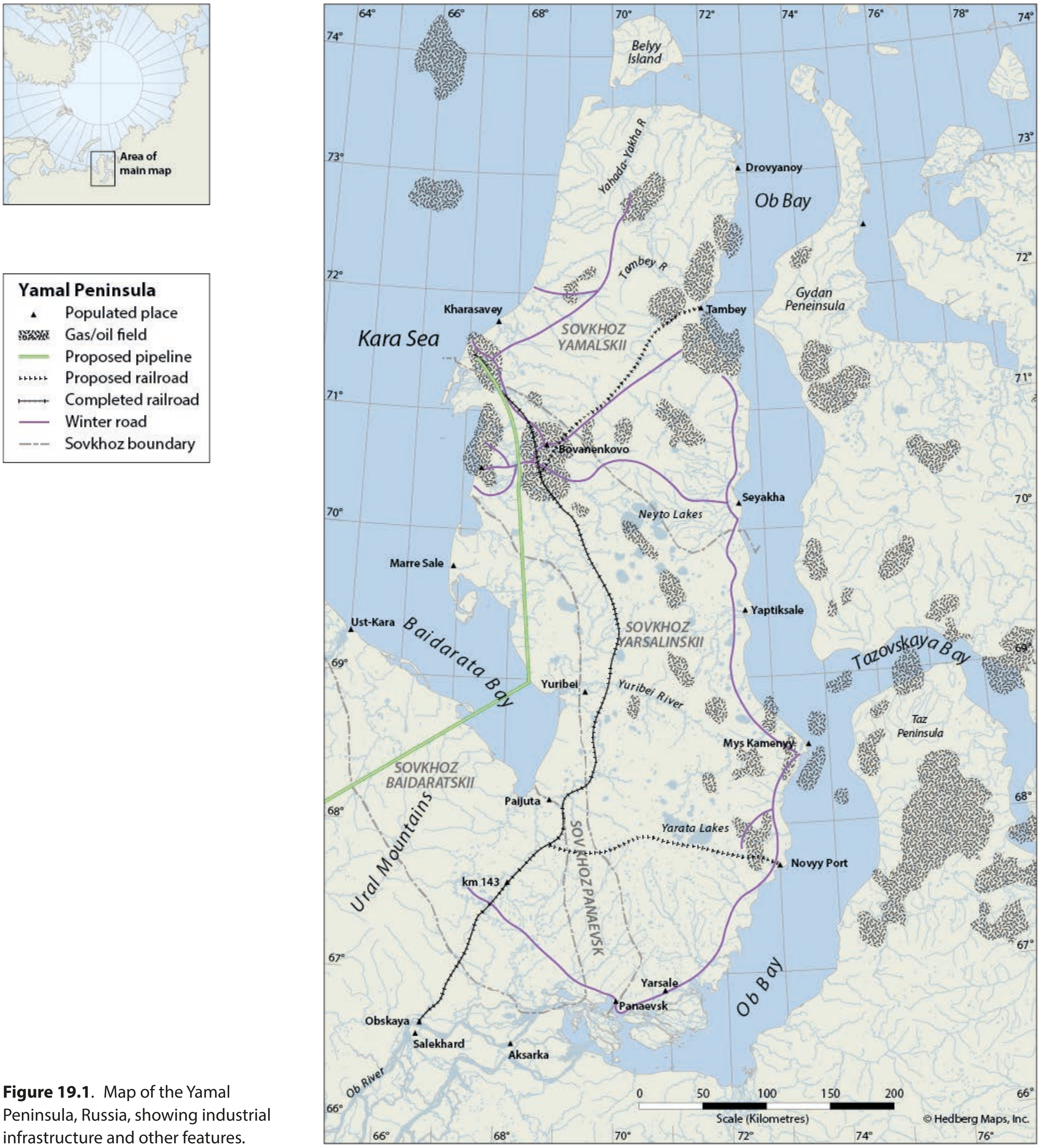

**Figure 19.1.** Map of the Yamal Peninsula, Russia, showing industrial infrastructure and other features.

has been detailed in two landmark reports by AMAP (1998, 2007). Onshore, one of the largest spills in history occurred near Usinsk, Komi Republic, in 1994, resulting in a release of oil into tributaries of the Pechora River estimated to be eight times greater than the Exxon Valdez spill (Crawford 1997). Experts argue that since cleanup of such accidents can be difficult or impossible, as well as astronomically expensive, the best solution is a sustained, all-out effort at prevention (Jernelöv 2010). However, the spotlight on British Petroleum's (BP) practices in recent years in Alaska and the Gulf of Mexico has detailed the extent to which certain companies clearly prefer to channel resources into production and profits rather than field safety and longevity (Graham & Reilly 2011, Goldenberg 2011, New York Times 2011a, 2011b). Other important issues are airborne pollution from the flaring of excess gas within active fields and, in the Murmansk and Norilsk regions, from smelters. Evidence from both North America and Eurasian high latitudes indicates that pollutants, including heavy metals, accumulate in terrestrial and aquatic systems downwind and can persist for decades (AMAP 1998). As in the case of drained wetlands cited earlier (Forbes *et al.* 2001), the shift from scale-of-impact to scale-of-response can be several orders of magnitude when pollutants spread outward from point sources and either settle on the surface or are entrained in atmospheric air currents for longer periods and carried out to sea, contributing to Arctic haze (AMAP 1998, 2007).

> » *The economic development of Chukotka has influenced the life of Eskimos because the environment has deteriorated and land rehabilitation is not being realized. Atmospheric pollution leaves its mark. Living in the permafrost zone means that filtration occurs very slowly, all the pollutants remain on top of the ground, the reindeers then eat it, and finally people eat their meat. The same thing happens to the sea. Nobody cleans oil spills, especially in cold waters. The pollutants do not disappear without a trace. Once we brought a whale and the meat was polluted with spilled oil.*
>
> (Raisa Mikhaylovna Zotova in Novikova 2008).

### 19.2.5. Herbivore responses to disturbance

Herbivory is important as a force to contend with, both as a form of disturbance in itself and as a potential limiting factor during succession (Forbes & McKendrick 2002) and under a warming climate (Post & Pedersen 2008, Olofsson *et al.* 2009). This is particularly the case in the relatively lush lowland and coastal tundra ecosystems with high herbivore densities where extensive hydrocarbon extraction is now active (e.g. Prudhoe Bay, Alaska; NAO, Russia) and expected to spread to (e.g. Naval Petroleum Reserve-Alaska and Arctic National Wildlife Refuge, Alaska; YNAO, Russia). Equally important is the displacement of populations of large herbivores (Cameron *et al.* 2005). The responses of caribou/reindeer to disturbance can be complex and highly variable depending upon sex, age and season, among other factors (Cameron *et al.* 2005, Haskell *et al.* 2006). In the case of new infrastructure, such as roads or power lines, animals (and particularly pregnant females) may initially avoid these. To date, the evidence that animals can adapt to the presence of infrastructure and associated disturbance within or across years is inconsistent (Haskell *et al.* 2006, Vistnes & Nellemann 2008).

Grazing by vertebrate herbivores can have profound effects on dynamic processes in Arctic ecosystems, particularly in successional communities. In addition to favoring graminoids and weedy mosses at the expense of lichens and certain selected dwarf shrubs, grazing is an ecologically important limiting factor in the regeneration of many vascular plant species (Forbes & Kumpula 2009). Numerous Arctic researchers have noted that herbivores ranging in size from lemmings to caribou/reindeer are attracted to the plants growing on experimental fertilization plots and that they can affect the structure, cover/abundance and successional trajectory of the affected communities. Caribou, for example, may use sites with high forage nitrogen concentrations more intensely as a strategy of maximizing nutrient intake, leading to a positive feedback loop over the long-term (Forbes & McKendrick 2002). The same pattern has been observed in the boreal zone, where selective grazing of vegetation plots has been reported for periods of up to five years after a one-time addition of NPK fertilizer (John & Turkington 1997). This has serious implications for areas where assisted revegetation is attempted because, although plants are selected primarily to prevent erosion, many of the chosen species also provide important food for wildlife. Since it is standard practice to apply organic matter and/or chemical fertilizers to subsidize the initial stages of growth, managers trying to restore the original vegetation cover need to be wary about the access of herbivores to sites either naturally recovering from disturbance or actively revegetated. On the other hand, if the aim is simply to encourage the growth of forage for herbivores then regardless of the species composition, free access to fertilized sites is encouraged because of the positive feedbacks likely to encourage biomass accumulation (Forbes & McKendrick 2002).

With regard to climate change, the prevailing assumption until recently has been that the dominance of woody shrubs will increase under ongoing and future warming. At least in systems with low erect shrubs (e.g. dwarf birch *Betula nana*, willow *Salix* spp.), large herbivores like reindeer and muskoxen may be able to check increases in shrub biomass/height (Post & Pedersen 2008, Olofsson *et al.* 2009, Ims & Ehrich, Chapter 12). However, in cases where high erect shrubs are already above the browse line (c. 1.5-1.8 m), herbivory does not limit shrub growth (Forbes *et al.* 2010, Macias-Fauria *et al.* 2012).

### 19.2.6. Future prospects

During the next few decades, hotspots to observe for extensive terrestrial ecosystem disturbances include the major oil and gas bearing regions, such as the Alaskan

North Slope, the Mackenzie River delta in Canada and the Timan-Pechora and W Siberian basins of NW Russia. Cumulative impacts from piecemeal tourism and residential development are of concern to rural communities in northernmost Fennoscandia, where new cabins, power lines and expanding ski areas and road networks threaten to further fragment territories used for forage and migration by reindeer and other forms of wildlife (Vistnes & Nellemann 2008). Another emerging topic being watched closely in Fennoscandia is that of the rapidly-expanding mining industry. Similarly, the development of wind power in northern and high elevation areas in Fennoscandia is being closely watched. The empirical literature is still quite limited, but a recent national review in Sweden identified groups of terrestrial mammals potentially affected by existing and planned developments (Helldin *et al.* 2012). Interestingly, the authors conclude that one of the presumed knock-on effects of wind power is very similar to the aforementioned piecemeal developments. Namely, that the expanding road system to access turbines will enhance access for recreation, hunting and leisure traffic, likely resulting in impacts on populations of wild and domestic reindeer, moose and large carnivores (Helldin *et al.* 2012). For the time being, however, the data remain inconclusive.

## 19.3. FEEDBACKS TO ECOSYSTEMS AND CLIMATE

Changes in climate affect the structure and function of ecosystems. The biosphere and the atmosphere are a fully coupled system, therefore changes in the structure and function of terrestrial ecosystems may, in turn, feedback to the climate. In order to project Arctic (and global) climate variability into the future with certainty, these feedback loops must be understood. In this section, we focus on: (1) the influence of climate on Arctic ecosystems and (2) the regional and global feedbacks to climate by these ecosystems. We examine a number of these climatically sensitive processes and feedbacks, including carbon and methane cycling, permafrost dynamics, soil conditions, air pollutants, snow and ice cover dynamics, vegetation shifts, fire regimes and lake area. Cryosphere phenomena such as snow cover extend far beyond the Arctic, but we have not attempted to separate the Arctic component of feedbacks such as the snow-albedo effect. It is simpler, and more consistent with current research and modeling, to use the full winter snow cover for the northern hemisphere. Similar considerations have been used for other feedbacks.

### 19.3.1. Greenhouse gases: carbon dioxide and methane

The Arctic plays an important role in the global carbon budget, making significant contributions to the global fluxes of carbon dioxide and methane between ecosystems and the atmosphere. Increasing concentrations of atmospheric greenhouse gases are key driving factors in warming trends in the Arctic. Both carbon dioxide ($CO_2$) and methane ($CH_4$) are increasing in the atmosphere, and are estimated to have caused a c. 1.66 $W/m^2$ and c. 0.48 $W/m^2$ increase in radiative forcing globally since 1750, respectively (Forster *et al.* 2007). Methane is present in the atmosphere in much smaller concentrations compared with carbon dioxide, but is relatively more potent with a high potential for global warming. Over a 100-year time scale, methane is 25 times more effective per molecule than $CO_2$ at absorbing long-wave radiation, despite its shorter lifetime in the atmosphere. Since terrestrial ecosystems fix $CO_2$ through photosynthesis and release it through respiration, any change that impacts these processes will feedback to climate.

These fluxes of carbon are particularly important since, in their efforts to regulate carbon emissions, governments rely on estimates of carbon losses and gains related to climate change. Notably, the 'social cost of carbon', the estimated price of damages caused by each ton of $CO_2$ released into the atmosphere, varies by country. Consequently, any mechanism that results in increased $CO_2$ sequestration in Arctic ecosystems, such as increased vegetation growth, would have a positive impact on climate mitigation. Likewise, any mechanism that causes decreases in $CO_2$ sequestration, including the potential loss of carbon from Arctic ecosystems caused by increased development and human disturbance, would have a negative impact on climate mitigation. While the monetary value of carbon sequestration potential in the tropics is now part of the UN-led climate negotiations (through the instrument Reducing Emissions from Deforestation and Forest Degradation (REDD)), this issue is not recognized in the case of Arctic ecosystems.

While Arctic terrestrial ecosystems are currently estimated to be a sink of atmospheric $CO_2$, the strength of this sink in a warmer Arctic is forecast to deteriorate and may switch to acting as a source in the future (Canadell & Raupach 2009, McGuire *et al.* 2009). This is due to a variety of factors, including increases in the decomposition of soil organic matter under a warming climate, permafrost degradation and acclimation of the plants to increased atmospheric $CO_2$. Consequently, this means that while Arctic terrestrial ecosystems currently exert a decelerating (i.e. negative) feedback to raising atmospheric greenhouse gas concentrations, in the future they are projected to wield a less decelerating, or even accelerating (i.e. positive) feedback to climate warming, although this depends on the effect of increased vegetation growth, as mentioned below. As the amounts of carbon stored in Arctic soils that are vulnerable to the effects of warming are vast, the potential of Arctic terrestrial ecosystems to accelerate climate warming is significant. In terms of methane, the Arctic is currently a source of atmospheric methane, due in large part to methane emissions from lakes and wetlands. It is thought that methane emissions will continue or increase in the warmer Arctic of the future, providing a positive feedback to climate warming (McGuire *et al.* 2009).

### 19.3.2. Permafrost degradation and changes to soil conditions

Predicting the response of permafrost thaw to climate warming is complicated by the wide variety of factors that influence soil temperature, including air temperature, snow depth, topographic effects on insolation, soil texture, organic layer depth, surface water and runoff, groundwater movement and soil moisture. Studies have documented increases in permafrost degradation across the Arctic (Jorgenson *et al.* 2001, Zhang *et al.* 2005), and with ongoing warming these trends are expected to continue (Lawrence *et al.* 2008). Permafrost is a strong heat sink that reduces surface temperature and heat flux to the atmosphere, and consequently, the thawing of permafrost releases heat, causing a positive climate feedback. Moreover, recent estimates suggest that the top three meters of permafrost soils contain more than twice the amount of carbon as the atmosphere (Tarnocai *et al.* 2009). This carbon has been accumulating over long periods of time as a result of cold and waterlogged permafrost soil conditions. Degradation of permafrost – from deepening of the annually developing thawed layer to its complete disappearance near the ground surface – fundamentally enhances the conditions for soil microorganisms to decompose old soil carbon. As a result, greenhouse gas releases from thawing permafrost may act as a more sustained and much larger positive climate feedback than previously thought (Schuur *et al.* 2008). An important landscape aspect controlling both magnitude and direction of climate feedbacks following permafrost thaw is the resulting soil wetness near the surface. An increase in wetness will promote anaerobic conditions and increased methane emissions while slowing overall decomposition and $CO_2$ release. In contrast, dryer conditions can promote greater decomposition and release of $CO_2$ and decrease methane emissions. On an ecosystem scale, climate feedbacks associated with carbon and methane releases related to permafrost degradation are likely substantial during this century – in the range of those projected to be released by global deforestation scenarios (Zhuang *et al.* 2006).

### 19.3.3. Air pollutants

While greenhouse gases are the dominant driving factor in warming trends and climate feedbacks in the Arctic and globally, Arctic air pollutants, including aerosols, are also important (Key & Stohl 2007). The aerosols are usually introduced to the Arctic from Eurasia in the form of sulfates and black carbon (soot). Boreal forest fires and tundra fires (Hu *et al.* 2010) act as significant aerosol pollution sources in the circumpolar Arctic and may become more prevalent in the future. The pollution influences the Arctic climate through changes in surface radiative forcing, i.e. heat being absorbed at, or near, the Earth's surface. Some of these particles of pollution absorb sunlight, acting as a positive feedback to warming, while others reflect sunlight, acting as a negative feedback to warming. For example, deposition of black carbon on snow reduces surface albedo, and acts as a positive feedback to warming, while sulfates scatter incoming solar radiation, resulting in a cooling effect. Globally, the radiative forcing of aerosols is a negative feedback to warming (Myhre 2009), but the net radiative forcing of these pollutants in the Arctic is still uncertain and a topic of study. However, recent work suggests that decreasing concentrations of sulfate aerosols and increasing concentrations of black carbon have substantially contributed to rapid Arctic warming during the past three decades (Shindell & Faluvegi 2009).

### 19.3.4. Snow and ice

Snow and ice albedo feedback loops in the Arctic are strong: as snow or ice melts, a dark surface is exposed, less solar energy is reflected back to space, and more energy is absorbed and transferred to the atmosphere, causing a positive feedback loop that reinforces warming. Across the Arctic, and between 1970 and 2000, a decrease in duration of approximately 2.5 days per year of the snow season translate to a 2.5 $W/m^2$ decade warming during this same period (Euskirchen *et al.* 2007). Changes in ice cover also represent a strong positive feedback to warming. The extent of sea ice has declined since the beginning of the record in 1953, with the lowest value recorded in 2012 (Stroeve *et al.* 2007, Perovich *et al.* 2012; see Fig. 1.5 in Meltofte *et al.*, Chapter 1), and a strong thinning of multiyear ice and an increase in the area of melt ponds. All of these factors exacerbate the ice-albedo positive feedback loop to warming (Light *et al.* 2008, Pedersen *et al.* 2009). The additional or amplified warming caused by the loss of sea ice is not constrained to the Arctic Ocean, but also influences adjacent land areas, especially during autumn and winter, and may lead to hastened degradation of certain types of permafrost (Lawrence *et al.* 2008; see also Section 19.3.2). There is also a negative feedback following the loss of sea ice due to an increase in evapo-transpiration, causing an increase in summer clouds, which then increases net radiation, and decreases heating to the atmosphere (Chapin *et al.* 2005). However, this negative feedback is expected to be relatively weak, and will likely not counteract the strong ice-albedo feedback loop (Chapin *et al.* 2005).

### 19.3.5. Vegetation shifts

Studies have documented recent changes in the vegetation in the Arctic. This has included treeline advancement in some areas, retreat in other areas, and an encroachment of tall, woody shrubs in the tundra. Treeline advancement and tall, woody shrub encroachment are likely due to a longer growing season with increases in temperature and moisture (Sturm *et al.* 2001, Lloyd *et al.* 2003). This replacement of tundra with boreal forest and increases of tall, woody shrubs will result in greater carbon uptake into the vegetation, acting as a negative feedback to climate warming. On an ecosystem scale, it is currently under study whether the vegetation shift will lead to releases of soil carbon that would affect magnitude or direction of this negative feedback. However, any event that causes an advance of treeline and shrubs will reduce albedo, causing a positive feedback to warming (Sturm *et al.* 2005, Euskirchen *et al.* 2009). In fact, research has shown that the net uptake or release of carbon associated with changes in treeline is likely a much smaller feedback to climate than the feedback due to changes in surface energy balance (Betts 2000).

Treeline retreat is likely in some areas due to drought stress under high temperatures, which then interacts with slow recruitment and reduced seed sources to decrease the success of tree regeneration following disturbance (McGuire *et al.* 2010). As a result, increased proportions of forests may regenerate as open forests or shrubland. In addition, permafrost degradation may also cause a decline of forest extent as forests may be replaced by bogs. Open forest, shrubland, or bogs would store less vegetation carbon but more soil carbon than a forest with the resulting net carbon feedback depending on the relative magnitude of these effects. However, the land surface of these less vegetated ecosystems would have a generally high albedo and act as a negative feedback to warming.

### 19.3.6. Changes in lake area

Methane emissions from Arctic lakes are substantial, and increases in their emissions act as a positive feedback to global climate warming (Walter *et al.* 2007). Changes in lake area in the Arctic have been documented due to permafrost thaw. Consequently, in the future, the amount of methane emissions may be highly dependent on changes in lake area. In southern areas of warm permafrost, studies have generally documented a decrease in lake area due to lake drainage following permafrost thaw (Smith *et al.* 2005, Riordan *et al.* 2006), whereas lake area tends to increase with permafrost thaw in northern ice-rich zones of cold permafrost (Smith *et al.* 2005; see also Wrona & Reist, Chapter 13). In addition to changing methane emissions, these increases or decreases in lake area would also impact albedo, with increases in lake area resulting in an increase in albedo and a negative climate feedback. Decreases in lake area will likely not have the opposite positive feedback effect, as the new surface can also have an increased albedo, dependent on the type of vegetation colonizing (Rouse *et al.* 2005). Overall, while the magnitude of the climate feedback due to changes in lake area has not been quantified, it would depend on the relative changes of methane emissions versus albedo.

### 19.3.7. Future prospects

In the coming decades, we will continue to observe changes in the sink strength of the Arctic in terms of carbon and methane, the duration of the snow and ice cover, the integrity of the permafrost, and vegetation shifts, all of which will generally promote positive feedbacks to climate. In fact, the number and strength of positive feedbacks to climate will likely continue to be larger than the number and strength of negative feedbacks (McGuire *et al.* 2006, Euskirchen *et al.* 2010), and there is indication that some positive feedbacks, such as albedo loss and permafrost thaw, accelerate each other (Canadell & Raupach 2009). Currently, the primary positive climate feedbacks are likely related to changes in surface albedo due to changes in ice and snow cover. While negative feedbacks to climate have been quantified, including increased carbon uptake by vegetation due to a longer growing season, these negative feedbacks are increasingly understood not be large enough – or last long enough – to counterbalance the larger and more sustained positive feedbacks. While models consistently simulate these feedbacks into the future, continuing to measure and monitor key indicators on integrated landscape and regional scales is extremely important. Key indicators to monitor include all those influencing energy fluxes and carbon cycling, for example, permafrost integrity, snow and ice cover duration, extent and thickness, landscape wetness and greenness, vegetation composition, as well as fire regimes and their related successional dynamics. The impacts of Arctic climate feedbacks will extend well beyond the Arctic, necessitating an integrated understanding of the Arctic ecosystem processes and their representation in global climate models.

## 19.4. CONSERVATION

### 19.4.1. Habitat protection

Protected areas have long been the foundation of biodiversity conservation programs. Although many of the first protected areas were established primarily for the purposes of recreation, they have evolved since that time to become important tools for habitat protection and species conservation. This is as true for the Arctic as it is elsewhere.

The first protected areas in the North were established in Sweden and Alaska at the beginning of the 20th century. It was not until the 1980s that there was a significant increase in number of areas under protection. Recent decades have seen an exponential growth in the number of protected areas in the circumpolar north. As of 2010, there are 1,127 protected areas in the region, covering approximately 3.5 million km$^2$ or 11% of the CAFF cooperation area (Tab. 19.2). These areas vary considerably in terms of size, type and nature of protection.

The International Union for the Conservation of Nature and Natural Resources (IUCN) has a classification system for protected areas as a means to help collate data from protected areas around the world. Since its inception, this international system has developed “to help provide a framework in which various protection strategies can be combined together, along with supportive management systems outside protected areas, into a coherent approach to conserving nature” (Dudley 2008). The categories, therefore, can help countries and regions assess their progress to meeting defined conservation goals. In the Arctic, the majority of protected areas fall into category II, Ecosystem Conservation and Protection (Tab. 19.2, Fig. 19.2).

**Table 19.2.** Total Arctic territories in IUCN protection categories (CAFF 2010). N.B.: The definition of Arctic for this table is the CAFF boundary, not the ABA boundary.

| Category | Title | Managed for | No. of protected areas | Total area (ha) | % of Arctic covered |
|---|---|---|---|---|---|
| **Ia** | Strict protection: strict nature reserve | Science | 350 | 273,000 | 0.8 |
| **Ib** | Strict protection: wilderness area | Wilderness protection | 111 | 795,000 | 2.5 |
| **II** | Ecosystem conservation and protection (e.g. national park) | Ecosystem protection or recreation | 102 | 1,530,000 | 4.7 |
| **III** | Conservation of natural features (e.g. natural monument) | Conservation of specific natural features | 103 | 52,600 | 0.2 |
| **IV** | Conservation through active management (e.g. habitat/species management area) | Conservation through management intervention | 125 | 154,000 | 0.5 |
| **V** | Landscape/seascape conservation and protection (e.g. protected landscape/ seascape) | Landscape/seascape conservation and recreation | 60 | 64,600 | 0.2 |
| **VI** | Sustainable use of natural resources (e.g. managed resource protected area) | Sustainable use of natural ecosystems | 120 | 648,000 | 2.0 |
| No category assigned | | | 156 | 30,800 | 0.1 |
| Total | | | 1,127 | 3,550,000 | 11.0 |

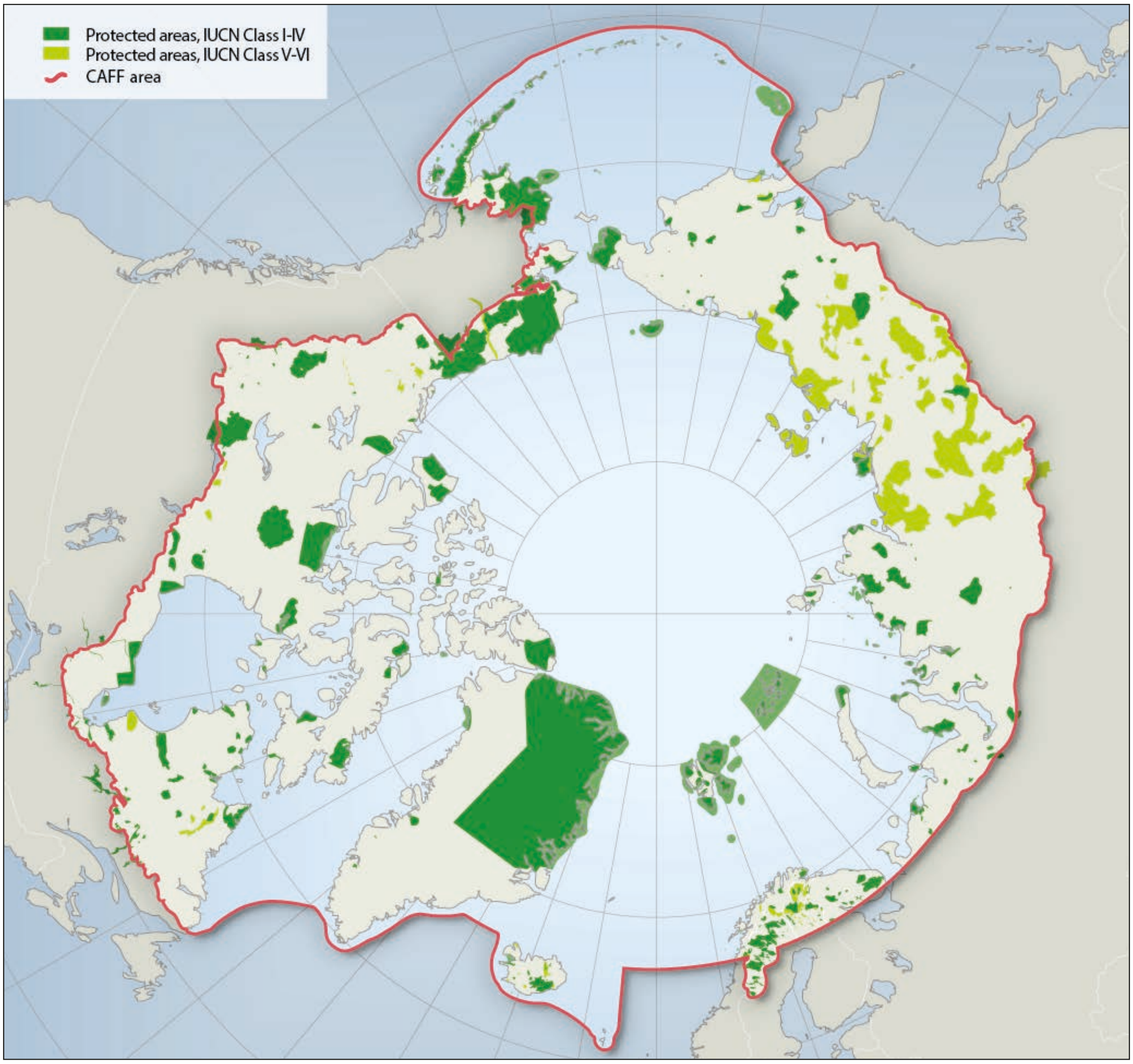

**Figure 19.2.** Protected areas within the political cooperation area of CAFF.

## Box 19.1. Aleut perspectives on national parks on the Kommandorskye Islands, Russia

*Tero and Kaisu Mustonen*

The methods of habitat protection are not always viewed favorably by Arctic residents. In some cases, this is due to an interest in resource development. In others, it is a result of real or perceived clashes between protection regulations and traditional practices. The Aleut region of the Kommandorskye Islands in the Bering Sea is one such example (Meschtyb 2008).

Dorfei Semionovich Berezin was born on Bering Island. In general, he says, in the past fishing was good in the rivers that the local population has always used for their subsistence. Today, park regulations only allow three fish species to be taken over the whole summer period. This means that local people have started to poach. Berezin notes that the underlying cause for the illegal fishing, an almost universal phenomenon on the island including the fishing inspection personnel, is the deteriorating standard of life of islanders.

Zinaida Ivanovna Kvasiuk lives in the village of Nikolskoe on the Bering Island. She believes that poorly thought out economic and administrative policies have upset the ecological balance on Bering Island and are damaging the traditional Aleut way of life. Zinaida says that the local community used to have a structured economic life based on fishing, hunting of marine mammals and a little bit of farming, so despite the harsh island conditions they were self-sufficient people. She says the park does not do enough for environmental protection but hinders traditional Aleut activities. Zinaida is adamant that the Aleut people cannot live without fish, seal and sea lion meat.

Gennadii Mikhailovich Yakolev was born on Mednyi Island in 1935, and now resides in the village of Nikolskoe. Traditional livelihoods have been the basis of his way of life: "The fat of a seal for Aleut people is like butter for others." For him, the traditional use of nature is not only a means of providing food, but is also a specific cultural legacy: "I try to take my grandsons with me so that they can become accustomed to real Aleut food." He feels that the bureaucracy, which for him represents the majority culture at its most absurd, has done far too much harm with its directives and policies. The overall impact of the national park in the center of Bering Island has placed traditional Aleut activities under a vast array of regulations.

Nikolai Nikolaevich Tiuterev has similar views. He describes how in the past the local community had hunted for seals in the summer and winter but now it is only permitted in the autumn and by specially accredited hunters. Tiuterev recalls earlier years when locals were permitted to hunt sea lions and seals but now this has been banned. He finds the official explanations difficult to understand:

"Our ancestors hunted these animals and their numbers never decreased. Yet, today, the authorities are afraid that we will exterminate them. In the past, when somebody needed a couple of seals for food, they would hunt for them. Why would we want to waste seals by over-hunting? It provides meat for the whole village.

"New regulations state that it is necessary to go to Lake Sarannoe, but this is a considerable distance from the community, and there is no transportation for local fishermen. Many people do not always receive any fish, especially pensioners."

All these regulations interfere with the practices of the traditional economy and Aleut livelihoods. Moreover, Tiuterev believes that they have a negative impact on the self-worth of the Aleut people as an indigenous culture.

While protected areas are a powerful conservation tool, they can also – depending on the exact rules in place – constrain some traditional activities, which can erode support for such conservation measures (see Box 19.1 for examples of indigenous views on conservation). Such a situation can be seen, for example, in the Malla nature reserve in Finland, where the removal of human activities has led to conflicts over the impacts of reindeer grazing, which can benefit some species as well as have negative impacts on others (Jokinen 2005). As with other forms of conservation measures, the establishment and management of protected areas needs to address traditional practices and potential conflicts to achieve the overall goals of habitat protection and biodiversity conservation.

#### 19.4.1.1. Aichi target 11

Target 11 of the Convention on Biological Diversity's (CBD) Aichi Targets states that: "By 2020, at least 17 per cent of terrestrial and inland water, and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes."

While terrestrial areas are relatively well represented in Arctic protected areas, the marine environment continues to be under-represented (CAFF 2010). Although over 40% of the protected areas inside the CAFF cooperation area have a coastal component, the extent to which the neighboring marine environment is incorporated is undetermined for most (Barry & McLennan 2010). The Arctic marine environment is one of the least understood regions of Earth, especially in the high Arctic. Historically, the harsh conditions of this area have made it difficult to study. With some projections indicating that the Arctic Ocean could be ice-free in late summer by mid-century or even before, the development pressure will increase. There is a critical need for identification of ecologically important and vulnerable marine areas in the Arctic and recommendations for their management. A recent effort in this direction has been the identification of ecologically and culturally important marine areas, following one of the recommendations of the Arctic Marine Shipping Assessment (AMSA 2009). This work is being carried out under three Arctic Council working groups: the Arctic Monitoring and Assessment Program (AMAP), CAFF and the Sustainable Development Working Group (SDWG).

### 19.4.1.2. Sacred sites

The IUCN broadly defines sacred sites as follows: "Sacred site – an area of special spiritual significance to peoples and communities; Sacred natural site – areas of land or water having special spiritual significance to peoples and communities" (Wild & McLeod 2008). They have been further described as "reflect[ing] the diversity of spiritual and cultural values that indigenous peoples attribute to their territories, landscapes, biota, and particular sites" (CAFF 2004).

In the Arctic, in particular, most sacred sites are natural areas, often high in biodiversity values, and so may contribute to biodiversity conservation with a strong link to customary livelihoods (CAFF 2004). A study by CAFF (2004) on the conservation values of sacred sites of indigenous peoples in the Arctic noted that "Not only are most sacred sites located on or in the vicinity to migration routes, fishing sites, or pastures; the active use, maintenance and protection of these sites depend largely on healthy livelihood systems."

Despite their conservation values, the role of sacred sites in habitat protection and biodiversity conservation has not received the same degree of attention as other types of protected areas. Ideally, sacred sites should be supported by national and regional protected area systems, but this is often not the case (Wild & McLeod 2008). While tangible sacred sites (e.g. human-built structures) tend to be afforded a reasonable degree of protection, intangible sites (e.g. holy rivers and lakes) are under-represented (Wild & McLeod 2008). While it may be that not all practices associated with sacred sites are in line with broader conservation objectives (e.g. conflicts between traditional reindeer herding practices and conservation of large predators), sacred sites have the potential to provide an important link in habitat conservation and protected area networks.

One of the challenges to fully incorporating sacred sites into formal protected area networks may be reluctance on the part of indigenous peoples to have their sacred sites formally classified. There are issues with the protection of cultural and intellectual property. The CAFF study also noted that the non-codified status of sacred sites, like traditional knowledge in general, leaves it open to abuse (CAFF 2004). Some of the key recommendations from that study include:

- developing an action plan for the further integration of sacred sites and indigenous territories of traditional nature use into broader protected areas networks;
- encouraging indigenous peoples to seek further reporting on sacred sites and their protection into national reporting on the implementation of the CBD;
- bringing to the attention of the World Intellectual Property Organization (WIPO) the need to accommodate within its work the knowledge about indigenous sacred sites, as this is a significant and important perspective for the intellectual property, traditional knowledge and genetic resources of indigenous peoples (CAFF 2004).

### 19.4.1.3. Potential for habitat shifts

One of the greatest challenges facing Arctic protected areas is climate change. The changes wrought by a warming climate are raising a number of questions regarding the effectiveness of protected areas as a conservation tool in the future. The changes to the physical environment are already well documented and include such effects as reductions in snow and ice and changes in precipitation patterns. The associated impacts as a result of these changes include a northward shift in species, 'greening' of the Arctic, changes in timing of key life cycle events and changing migration patterns, to name just a few.

Changes in habitat type, in particular, pose significant threats to protection efforts. Already there is evidence of significant shifts in Arctic vegetation in recent decades, and this is expected to continue with further warming (Henry & Elmendorf 2010). Henry & Elmendorf (2010) noted that treeline encroachment is threatening the southern margins of the tundra. According to some models, treelines may advance by as much as 500 km north over the next century with a resultant loss of 51% of tundra habitat (Callaghan *et al.* 2005).

A study assessing changes in biome types in Canada's protected areas networks under climate change found that the representation of northern biomes – tundra, taiga/tundra and boreal conifer forest – in protected areas was projected to decrease (Lemieux & Scott 2005). The study projected that 38-79% fewer protected areas will still have part of tundra biomes, and 81-87% fewer protected areas will contain at least part of the taiga/tundra biome (Lemieux & Scott 2005). These decreases are the result of decreases in these biomes overall, so that a lower proportion of tundra overall translates into a lower proportion of tundra within protected areas.

A similar and perhaps more dramatic change is occurring in the Arctic sea ice habitat. Changes are already being seen in the extent and thickness of the sea ice, with thicker multi-year ice being replaced by thinner first-year ice (NSIDC 2010). Current predictions indicate that the Arctic Ocean could be nearly ice-free in late summer by the middle of this century or even sooner (Wang & Overland 2009). Sea ice represents a unique ecosystem in the Arctic providing habitat for numerous ice-associated species (see Josefson & Mokievsky, Chapter 8 and Michel, Chapter 14). Changes in sea ice can be expected to have impacts throughout the marine food web, from phytoplankton and zooplankton to seabirds and marine mammals. Indigenous peoples of the Arctic will also be affected by these changes as many use sea ice for transportation and hunting. In response to the changes occurring in this important ecosystem, CAFF is conducting an Arctic Sea Ice Associated Biodiversity Assessment which will summarize the current status and trends of sea ice-associated biodiversity and recommendation actions that might to mitigate these changes.

Further complicating these habitat shifts and changes is the associated issue of invasive species. As the climate warms and more human activity takes place across the Arctic, both northward range expansions and biological invasions (i.e. transport by humans, intentionally or otherwise) are likely to increase (Lassuy & Lewis 2010; Lassuy & Lewis, Chapter 16).

There is a further issue of habitat fragmentation outside of formally protected areas that may further reduce the ability of species and ecosystems to adapt to change. Although such patterns are most likely a long ways off for the Arctic, protected areas can become isolated islands in a broader sea of development (industrial, agricultural, etc.) inhibiting the movement of species to more suitable habitats. The scale of development in most of the circumpolar Arctic is far below that seen in more southern regions, and some of the largest unaltered habitats are found here. The pressure to develop, however, is strong and will likely continue to grow as the Arctic becomes more accessible as a result of climate change.

#### 19.4.1.4. Future prospects

The scale of environmental change facing the Arctic forces us to ask whether protected areas can continue to be an effective conservation tool in the future. The majority of protected areas are selected on the basis of ecosystem representation, where there is an underlying assumption that they will remain static, unchanged. The rapid changes occurring in the Arctic, however, show that this is not guaranteed. With habitat shifts resulting from climate change, it will be more difficult to define ‘natural’ in the future (Lemieux & Scott 2005).

The question remains how protected areas can be used to help ecosystems and species adapt to stressors, climate change in particular. More systematic research and monitoring are needed to address the large uncertainties facing protected areas in light of climate change. In addition, more efforts are needed to place protected areas in the context of broader habitat conservation measures, i.e. conservation outside of protected areas. New tools will also be needed to help make sound management and policy decisions in a changing Arctic. The WWF project, Rapid Assessment of CircumArctic Ecosystem Resilience (RACER), is an example of a tool that has been developed to help identify and map places of importance in the Arctic, looking for areas of resilience that are likely to persist under the changes the Arctic is experiencing (Christie & Sommerkorn 2012).

While protected areas are facing clear threats as a result of climate change, they can also help mitigate some climate change impacts (e.g. carbon sequestration, flood control). They can also provide areas where natural processes can continue and potentially adapt to the impacts of climate change. For these reasons, protected areas will continue to be vital to habitat and biodiversity conservation efforts in the future (e.g. Livingston 2011).

### 19.4.2. Species protection

> “A recurring theme in wildlife and fisheries management over the centuries is that numerical abundance is not always a hedge against declines… We only have to think of salmon, northern cod, (and) bison... What determines persistence is rate of change not the size of the starting population. But numerical abundance carries the risk of over-confidence – ‘there’s still lots of caribou.’ Another contribution to over confidence among users is that the caribou, being cyclic in their abundance, have been low in number before and have come back. However, given changing environmental conditions, the past may not be a secure guide to the future” (CARMA 2010).

The Arctic embraces a wide variety of species of global importance. Almost a quarter of the world’s shorebird species are endemic to the Arctic, and all but three of the world’s 17 Arctic and sub-Arctic goose species have populations numbering in the hundreds of thousands or millions (Ganter & Gaston, Chapter 4). It is also home to several million reindeer and caribou and many unique marine mammals such as the polar bear *Ursus maritimus*, walrus *Odobenus rosmarus* and narwhal *Monodon monoceros*. Seasonal changes are extreme, with dark winters, snow, ice and temperatures plummeting to –50 °C. Summers bask in 24 hour daylight with temperatures soaring to above 20 °C. During this brief summer, several millions of birds and many thousands of terrestrial and marine mammals migrate into the area to breed and take advantage of the brief rich feeding grounds.

Historically, these dependable – albeit extreme – conditions helped protect Arctic species by limiting physical access. This in turn helped to reduce disturbance, slowed habitat fragmentation and generally limited other human activities. History, however, may no longer be an adequate guide to the future of the Arctic.

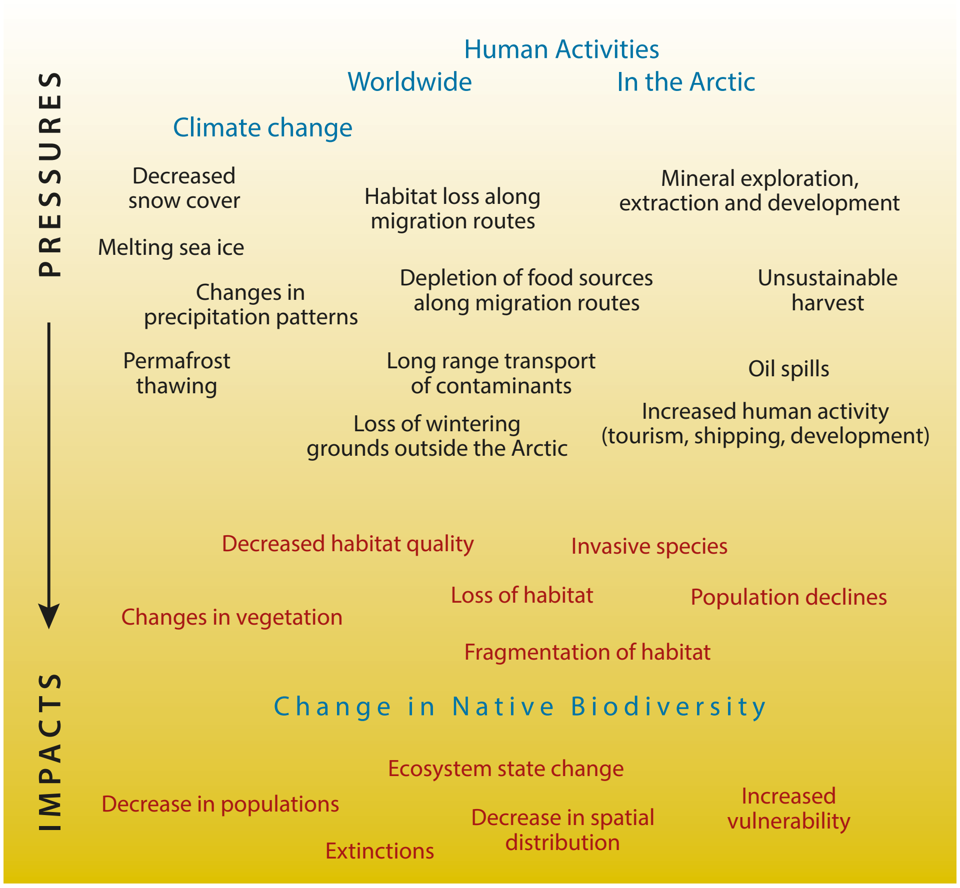

**Figure 19.3.** Currently, the environment in the circumpolar North represents one of the areas of the world with the least human impact. Pressures that exist and are on the increase are climate change, infrastructure development and the development of mineral resources – such as oil and gas and increased economic activity (CAFF 2010).

### 19.4.2.1. Challenges

The Arctic is one of the most rapidly changing regions on Earth. Increasing interest in developing natural resources there, coupled with rapid warming, will radically change this area once protected by its inaccessibility and the higher costs associated with extractive industrial development. These cumulative pressures create significant hurdles for conserving biodiversity (Fig. 19.3). The combination of rapid climatic warming and increasing human activities will require the development of new management tools, investment in basic scientific monitoring, and new governance agreements across the Arctic.

An entire marine ecosystem – from phytoplankton to polar bears and bowhead whales *Balaena mysticetus* – depends on the continued existence of Arctic sea ice. As temperatures increase and sea ice continues to decline, ice-associated species such as the ringed seal *Pusa hispida*, walrus and polar bear will find it more and more difficult to survive within historical ranges or current abundance. On land, thawing permafrost and shifting biophysical drivers will fundamentally alter current terrestrial ecosystems. Disturbance and fragmentation of habitats through increased human activities (primarily resource extraction) will further complicate conditions in this once relatively undisturbed region.

The conservation of species in the Arctic has traditionally focused on large mammals which are, or have been, commercially harvested. Examples are bowhead whales, walrus, caribou and polar bears. However, the basis for the rich marine and estuarine food webs has rarely, if ever, been acknowledged and protected. For example, the increasing loss of sea ice due to climate warming will have a dramatic impact on the plankton community living under the ice (see Michel, Chapter 14). That will alter the Arctic ecosystem as we know it today by affecting fish assemblages, ice-associated seals and polar bears (see Reid *et al.*, Chapter 3). The only long-term solutions for protecting this ecosystem and the species that have evolved with it are to decrease global greenhouse gas emissions and to manage human activities inside the Arctic.

In 2006, the polar bear was added to the IUCN's Red List as a vulnerable species, largely due to predicted impacts from climate change and the expected loss of sea ice habitat. Hudson Bay and southern Beaufort Sea polar bear subpopulations have shown significant declines (Regehr 2007) or metrics of pending decline including decreased adult size and decreased cub survival (Regehr 2010) over the last two decades. These changes in survival and condition have been directly linked to a decrease in summer sea ice habitat as a result of climate warming and are expected to affect polar bears across their range if warming trends continue unabated (Wiig *et al.* 2008; see also Reid *et al.*, Chapter 3).

While polar bears are often the face of Arctic warming, many species are or will become negatively affected by climate change. Hundreds of endemic Arctic species, from small beetles, ice associated algae and plankton, mushrooms, lichens, flowers and lemmings, to large mammals such as caribou, walrus and narwhal face an uncertain future. Barren Ground caribou numbers have dropped across their range in recent years, and experts suspect climate change is a significant contributing factor, though there are signs that the declining trend is reversing (Reid *et al.*, Chapter 3). Impacts include possible changes in the timing and availability of peak forage in the early summer and increased freezing rain events during winter that cover the vegetation in ice and decrease availability (Hummel & Ray 2008).

Many Arctic species are migratory and spend most of the year in much lower latitudes. For conservation, this often means protection of an Arctic species has to take place in areas far from the Arctic (Scott 1998). An example is the spoon-billed sandpiper *Calidris pygmeus* which breeds in the low hundreds in Chukotka, Russia and passes through coastal wetlands in China while migrating to overwintering grounds in SE Asia. During the last 30 years, the number of spoon-billed sandpipers has decreased dramatically from about 6,000 breeding pairs to just a few hundred pairs. Besides loss of habitat in staging and wintering areas, the most eminent cause of the decline appears to be indiscriminate hunting in Myanmar where the birds are caught in mist nets and sold to local markets as food (Zöckler *et al.* 2010). The only way to save this migrating Arctic species from extinction is to protect it outside the Arctic while safeguarding critical summer nesting areas within the Arctic (see Ganter & Gaston, Chapter 4).

Diminishing summer sea ice will also lead to an increase of human activities such as shipping, fishing, mining and oil and gas exploration. There is an urgent need for circumarctic management and governance that ensure a stewardship-first approach to these increasing demands for once inaccessible resources (e.g. Chapin *et al.* 2009a, 2009b). The Arctic remains one of the largest largely intact ecosystems on earth. Careful planning that incorporates future change and cumulative impact assessment prior to activities proceeding could reduce additional stressors to an already strained system (e.g. Meek 2011).

### 19.4.2.2. Management and regulation

The most effective way to protect the vast majority of species is to safeguard habitat, which often conserves representative ecosystems (see Section 19.4.1). More typically, species protection has focused on preventing overharvest, which has historically been the largest threat to Arctic biodiversity (e.g. Meltofte *et al.*, Chapter 1, Reid *et al.*, Chapter 3, Ganter & Gaston, Chapter 4, Christiansen & Reid, Chapter 6). Species protection in the Arctic is regulated at different levels. For example, The Agreement on the Conservation of Polar Bears from 1973 sets forth standards for polar bear conservation across its range. This landmark 'range state' agreement dramatically improved harvest management of polar bears and set up a framework to better coordinate and communicate scientific research and circumarctic management (Larsen & Stirling 2009).

Most species protection falls under national legislation, or a mix of national legislation, and bilateral and international agreements. In Greenland for example, the International Whaling Commission (IWC) sets national subsistence quotas for minke whales *Balaenoptera acutorostrata*. Narwhals and beluga whales *Delphinapterus leucas*, however, are regulated by the Canada-Greenland Joint Commission on the Conservation and Management of Narwhal and Beluga (DFO 2008).

As noted above, national parks and nature reserves are often created to protect a certain habitat for individual species. However, rapid climate change means the conditions for keeping these specific habitats (and inhabitants) within the reserve boundaries may be altered. In many cases the protected habitat itself will change over time. For example, the tundra in northernmost Scandinavia will shift to forest as the tree line moves north due to increasing temperatures (Heiskanen *et al.* 2008).

National legislation for typical nature reserves and protected areas is established to preserve what currently exists, but doesn't address what will happen in the future in the context of a rapidly changing world. Similar challenges exist with conservation constructs at the international level. While the IUCN's mission, for example, preserves the 'now', assuming stable conditions, it does not take into account future changes under unstable systems. Many national parks and nature reserves will not be able to meet the goals they set in terms of protecting viable populations of specific species or unique habitats. New tools and adaptive management strategies will be required as we move into uncharted territory.

### 19.4.2.3. Future prospects

The changing Arctic environment will put pressure on species as well as entire ecological processes. It is expected that high Arctic species, such as red knots *Calidris canutus*, will have fewer options in a changing environment, since the high Arctic zone in particular, will be 'squeezed in' between the northward expanding low Arctic biome and the Arctic Ocean (Meltofte *et al.* 2007; see also Ganter & Gaston, Chapter 4). Southern species, such as the red fox *Vulpes vulpes*, may see range expansions putting Arctic species under pressure (see Reid *et al.*, Chapter 3 and Ims & Ehrich, Chapter 12). Wildlife can try to adapt (an unlikely option given the current and expected rates of change), migrate or face a very uncertain future. Species that today are considered sentinel may be marginalized as ecosystems cross significant thresholds and shift into new phases. Single species protection will still be important, but it will likely become more important to preserve ecological processes over time.

A variety of regional, national and international legal mechanisms exist to help manage at-risk species such as the IUCN Red List, the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) and the various national legislation and regulations. Current and predicted impacts from rapidly warming climate scenarios have led to an almost preemptive push to list species as endangered or threatened at the regional, federal and international levels and often across species ranges. Listing of species under various legal articles provides increased public awareness of species status and threats, generally increases legal protections and can boost basic research and monitoring efforts as was seen following the 2007 US listing of the polar bear as threatened.

However, initiating increased protections indicates a failure to manage on other fronts and can have unintended consequences. The addition of species to higher categories of risk under constructs like the IUCN Red List is nothing to strive for or to celebrate. It measures the continued loss of biodiversity and societal or society's lack of understanding, will or ability to successfully manage the challenges facing species today. Range-wide listing decisions, as seen with both the polar bear and ice-associated species of seal listings in the US, may not adequately account for the varying rates of anticipated change across dramatically differing habitats within the Arctic. Existing legal structures, at the international and national levels, were not developed for pervasive, long term threats like climate change and often lack flexibility once enacted.

Polar bears provide one example. There are 19 subpopulations, or management units, of polar bears in the Arctic inhabiting a range of very different habitats. We are likely to see up to 19 different stories unfold as warming affects different areas at different times and in different ways. While scientists are already noting population declines or indices suggesting decline in the most southerly of polar bear populations, it is expected that populations in the higher Arctic will remain more resilient to change in the near term (Wiig *et al.* 2008; see also Reid *et al.*, Chapter 3). Prescriptive, one-size-fits-all solutions will challenge the acceptance of stakeholders and the people who rely on these species for their own survival both culturally and economically (Dowsley 2010).

Successful management of Arctic species will require new management tools and greater flexibility. The overarching threat posed by rapid climate warming will challenge our best efforts and existing legal mechanisms. It must also be recognized that people live in the Arctic and rely on its wildlife. Any plan to protect Arctic species must involve the people who live with them. It must understand the food and economic security challenges that come with increased legal protective status, and potential clashes with established indigenous rights. The situation is complex and demands well thought out and complex responses to the threats of today and the challenges of tomorrow.

## 19.4.3. Conservation through community involvement

The last several decades have seen continued interest in natural resource monitoring that involves both scientists and local stakeholders (Gofman 2010, Huntington 2011). This partnership, often referred to as community based monitoring (CBM), or community-based observations, continues to evolve and exert increased influence on decision making and resource management (Gofman 2010). The scope of CBM is diverse and complex and continues to develop as experiences of integration are shared. Moreover, the overwhelming connection of Arctic peoples to the land provides opportunities for strong conservation partnerships, for example initiatives related to ecological monitoring, food security or sacred sites.

In essence, CBM seeks to improve the ability to share observations and understanding of local changes that are occurring in a vast and remote region through the eyes of Arctic residents. The idea is that intimate and multi-generational knowledge held by local stakeholders can help governments and local organizations identify and address serious environment and development challenges at early stages (Harremoës *et al.* 2001).

### 19.4.3.1. Monitoring approaches

Monitoring approaches in all Arctic countries have some level of local involvement, and examples of CBM exist throughout the Arctic. These monitoring approaches range from programs involving local stakeholders only in data collection (citizen science) with the design, analysis and interpretation undertaken by professional researchers, to entirely autonomous monitoring schemes run by local people (see Gofman 2010 for full discussion).

The level of involvement by local peoples beyond project development and planning to include analysis can contribute to longer-term capacity and implementation benefits beyond just the collected data (Tab. 19.3). Although local residents can unquestionably monitor and report on certain observed changes, their interpretation of the changes and any policy implications they may have are sometimes left aside. However, this is not a problem limited to CBM. From a policy implementation perspective, opportunities to involve Arctic peoples in knowledge production, in an open and transparent manner, is critical when considering managing individual and commercial activities in the North.

### 19.4.3.2. Validity of CBM data

The struggle to break through the perceived limitations surrounding CBM is often linked to the approaches and skepticism at the heart of western approaches to knowledge production. Scientists have documented Arctic community members' detailed knowledge of key components of their environment, such as sea-ice (Laid-

**Table 19.3.** Arctic and sub-Arctic natural resource monitoring schemes across a spectrum of possible monitoring approaches based on the relative participation of different actors (modified from Danielsen *et al.* 2009).

| Category of monitoring | Arctic examples | Description | |
|---|---|---|---|
| Fully autonomous local monitoring | Customary conservation regimes, e.g. in Canada (Ferguson *et al*. 1998, Moller *et al.* 2004) | The whole monitoring process – from design, to data collection, to analysis, and finally to use of data for management decisions – is carried out autonomously by local stakeholders | ↑ Increasing role of local stakeholders |
| Collaborative monitoring with local data interpretation | Arctic Borderlands Ecological Knowledge Co-op, Canada (Eamer 2006, Russell *et al.* 2013); Community-based monitoring by Inuvialuit Settlement region, Canada (Huntington 2011); Opening Doors to the Native Knowledge of the Indigenous Peoples of the Nenet Autonomous Okrug, Russia (The Association of the Nenets People Yasavey and RAIPON); Piniakkanik Sumiiffinni Nalunaarsuineq, Greenland (Danielsen *et al.* in press) | Locally based monitoring involving local stakeholders in data collection, interpretation or analysis, and management decision making, although external scientists may provide advice and training. The original data collected by local people remain in the area being monitored, but copies of the data may be sent to professional researchers for in-depth or larger-scale analysis | |
| Collaborative monitoring with external data interpretation | Community Moose Monitoring Project, Canada (Gofman 2010); Integrated Ecosystem Management (ECORA), Russia (Larsen *et al.* 2011) | Local stakeholders involved in data collection and monitoring-based management decision making, but the design of the scheme and the data analysis and interpretation are undertaken by external scientists | |
| Externally driven monitoring with local data collectors | Bering Sea Sub Network, Alaska and Russia (Gofman & Smith 2009); Environmental Observations of Seal Hunters, Finland (Gofman 2010); Fávllis Network, Norway (Gofman 2010); Monitoring of breeding common eiders, Greenland (Merkel 2010); The Piniarneq fisheries catch and hunting report database, Greenland | Local stakeholders involved only in data collection stage, with design, analysis and interpretation of monitoring results for decision-making being undertaken by professional researchers, generally far from the site | |
| Externally driven, researcher executed monitoring | Multiple scientist-executed natural resource monitoring schemes with no involvement of the local stakeholders | Design and implementation conducted entirely by professional scientists who are funded by external agencies and generally reside elsewhere | |

ler 2006), weather patterns (Weatherhead *et al.* 2010) and caribou (Ferguson *et al.* 1998, Russell *et al*. 2013). Nevertheless, we know of no studies that have examined the accuracy of community-based monitoring of natural resources in the Arctic. Studies from other parts of the world provide cautious support for the idea that monitoring by community members can yield results that can be as reliable as those derived from professional, scientist-conducted monitoring (e.g. Danielsen *et al.* 2005, Jones *et al.* 2008, Rist *et al.* 2010).

Whereas scientists aspire to be impartial (Beardsley 2010), some fishermen, hunters and environmentally interested people may have a conflict of interest in their assessment of the status of those resources on which they depend for their livelihoods or that they are otherwise interested in (Root & Alpert 1994). For instance, a special local interest in certain resources or a preoccupation with certain challenges to resource management may influence which attributes are recorded, when and where. The community perspective is relevant too. Indigenous communities often view scientific initiatives with suspicion, if the scientists do not possess social and cultural skills to appreciate context and locality, creating a need to establish credibility in both directions.

Many of the potential limitations of CBM can be overcome by careful planning, by explicit consideration of likely biases, and by thorough training and supervision of the participants (Danielsen *et al.* 2009, Gofman 2010, Luzar *et al.* 2011). It is a challenge, however, that community monitoring can superficially appear low-tech and therefore primitive in a high-tech world. There remains a huge unexplored potential for strengthening monitoring efforts across the Arctic by engaging more communities and encouraging linkages with scientific monitoring programs (Huntington 2008). Often, an investment to build capacity to collect, interpret and manage data are central to maximizing such monitoring efforts (Gofman 2010).

### 19.4.3.3. Challenges

As the CBM record evolves and demonstrates continued improvement of accessible information on Arctic biodiversity, it is anticipated that there will be a delay between information production and use, accessibility and integration. In northwestern Canada and northeastern Alaska, for example, the reporting by the Arctic Borderlands Ecological Knowledge Co-op of CBM data on population health and body condition of the Porcupine caribou herd were largely dismissed and undervalued in favor of scientific models projecting substantive population declines (Gofman 2010, Russell *et al.* 2013). Moreover, such projected declines prompted government and decision makers to push for and build harvest regimes that limited northern residents' ability to harvest. Indeed in 2012, several years after the CBM results were released, scientific population surveys revealed record numbers of caribou actually existed. In this case, CBM would have limited harvest concerns and supported improved access to northern food. However, the combination of the potential for conflict of interest and the lack of demonstrable validation capacity may have contributed to placing limited value on the information from this source.

Such examples suggest that efforts to emphasize analysis and integration between the two knowledge production approaches should continue. Indeed, more recent biodiversity monitoring planning processes are proposing ways of integrating and coordinating the methods for knowledge co-production (Gofman 2010, Vongraven *et al.* 2012). The Circumpolar Biodiversity Monitoring Program's (CBMP) strategy for bridging some of the structural challenges over the next few years includes improving the access to CBM data via improved provision of and access to metadata, modeling and demonstrating integration examples of CBM with scientific monitoring processes (Gill *et al.* 2011, Culp *et al.* 2012).

#### 19.4.3.4. Contributions to biodiversity monitoring

Full participation in biodiversity monitoring programs continues to be a challenge for many Arctic peoples. Greenland's effort to increase involvement of CBM with management provides one of the promissong stories becoming more common in the Arctic. The Greenland government is piloting a natural resource monitoring system whereby local people and local authority staff are directly involved in data collection, interpretation and resource management. The scheme is called *Piniakkanik sumiiffinni nalunaarsuineq* (Opening Doors to Native Knowledge). Four communities in Disko Bay and Umanak/Uummannaq Fjord are involved: Akunnaaq, Kitsissuarsuit, Qaarsut and Jakobshavn/Ilulissat.

As in other parts of the Arctic, the communities in Greenland are widely distributed over a vast territory, and the opportunities for environmental monitoring and for implementing hunting and fishing regulations on the ground are limited. It has long been a priority of the Greenland government to increase the involvement of local citizens in the decision-making process related to natural resources (Greenland Government 1999, Haaland *et al.* 2005). However, there is limited funding available for monitoring Greenland's resources, and many species and populations are thus monitored infrequently or not at all (Nielsen 2009). There is therefore insufficient knowledge available about some wildlife populations to guide government decision making and consequently a need to supplement the existing scientist-led monitoring programs with low-cost monitoring, for example through CBM.

The following are examples of how the influence and impact of the data are increasing when it comes to Arctic resource management. In each of the examples, local community observations were central to effecting changes to management regimes.

Conservation of marine habitat: In Akunnaaq, Greenland, the Natural Resource Committee (NRC) recorded trawlers fishing for shrimp in a shallow sea area adjacent to their village on a daily basis. There were 4-5 vessels almost every day throughout April and May 2010. This number was the same as in 2009 but higher than in previous years. Moreover, the vessels were larger and used heavier fishing gear. The NRC in Akunnaaq was worried that potential degradation of the seafloor might affect the breeding and production of Atlantic wolf-fish *Anarhichas lupus*. The NRC therefore proposed that the municipality should issue an ordinance to restrict the size of vessels in the area.

Influencing marine harvest techniques: One of the attributes recorded by Qaarsut NRC concerned their catch of Greenland halibut *Reinhardtius hippoglossoides* in Umanak/Uummannaq Fjord. On the basis of their catch-and-effort data from long-line fishery, they estimated that the local Greenland halibut population was the same in May 2010 but higher in June-September 2010 than in the same months of 2009. Nevertheless, the NRC was concerned that many nets were being set over their longlines and that some nets were left at sea when the sea froze over. This resulted in many rotting fish, which attracted Greenland sharks *Somniosus microcephalus*. The NRC therefore proposed that the municipality should issue an ordinance to restrict net fishing in Umanak/Uummannaq Fjord. The fisheries legislation in Greenland allows municipalities – subject to ministerial approval – to prohibit the use of certain vessels and equipment in specific areas (Greenland Government 1996).

Influencing goose harvest pressure: Members of the Qaarsut NRC have observed that, over the past decade, the population of Canada goose *Branta canadensis* has risen sharply. Canada goose may out-compete the threatened Greenland white-fronted goose *Anser albifrons flavirostris* (Boyd & Fox 2008 *versus* Raundrup *et al.* 2012). Hunting seasons in Greenland are decided by the Ministry of Fisheries, Hunting and Agriculture on the basis of advice from scientists and from public input during a hearing process. The current hunting season for Canada goose is 15 August to 15 October (Department of Fisheries, Hunting and Agriculture 2011). The NRC proposed that the municipality should suggest to the Ministry that the hunting season for Canada goose be extended, for example by two weeks, to help keep the population from expanding further. However, a recent study has not found such competition between Canada geese and Greenland white-fronts during molt (Raundrup *et al.* 2012).

In all three examples, it is noteworthy that the proposals if implemented will benefit the people having put them forward. International experiences however suggest that

CBM also often leads to people suggesting restrictions in their own take of resources (Danielsen *et al.* 2007). CBM encourages people to take a long term perspective on the use of resources through facilitating agreements at community and municipal level to increase or reduce the use of resources.

#### 19.4.3.5. Future prospects

The Arctic environment is rapidly changing (e.g. Hinzman *et al.* 2005, CAFF 2010) and there is increasing pressure on its natural resources. There is therefore also an increased need for monitoring. To date, many examples exist of Arctic peoples describing the changes they witness related to climate, sea ice and especially to harvested wildlife species. There is a persistent need for more CBM that can detect change, interpret and integrate results, and lead to prompt decision-making to help tackle environmental challenges at operational levels of resource management (Huntington & Fox 2005, Danielsen *et al.* 2010).

Representatives of indigenous communities practice wildlife management guided by their indigenous knowledge, realizing that indigenous knowledge and western scientific knowledge are based on different knowledge generation systems or epistemologies (e.g. Agrawal 1995, Huntington *et al.* 2004). Through CBM, however, it may be possible to find a suitable means of cooperation and collaboration in which monitoring can be based on local observations and knowledge (Pulsifer *et al.* 2010, van der Velden 2010) and, at the same time, follow principles of data handling and data management in accordance with Western concepts of scientific accuracy (Yoccoz *et al.* 2001), which is what national government agencies and international conventions require. Several Arctic programs (including the CBMP) and Arctic peoples have already started to implement strategies to bridge this gap by building structures such as inventories and metadatabases to better access, use and integrate CBM knowledge in the arctic (e.g. Pulsifer *et al.* 2012).

In combination, the increased need for data and the necessity of promoting locally relevant knowledge and management actions suggest that there are substantial prospects in the coming decades for more CBM around the Arctic, and that such an increase will contribute to effective local conservation actions.

## 19.5. DISCUSSION AND CONCLUSIONS

The sections of this chapter have addressed a wide range of topics, quantitatively where possible and qualitatively otherwise. Evaluating the status and likely trends of disturbances, feedbacks and conservation efforts is not easy (see Tab. 19.4). For example, an increase in the number of species listed as threatened or endangered may indicate greater commitment to species protection, or it may indicate a greater number of species at risk. More extensive habitat protection will benefit biodiversity, but what occurs outside of protected areas may ultimately be more important, since protected areas are unlikely to cover a majority of the Arctic.

**Table 19.4.** Trends in the five indicators considered in this chapter. Note that 'Increasing' may be regarded as positive or negative depending on the indicator.

| Indicator | Trend | Notes |
|---|---|---|
| Disturbance | Increasing | Roads and industrial activity are expanding, creating more potential for disturbance |
| Feedbacks to ecosystems and climate | ? | Positive feedbacks, especially to climate, are exacerbating feedbacks from the Arctic to the globe |
| Habitat protection | Increasing | Parks and protected areas are more numerous, but additional designations may become harder; marine protection is nearly absent |
| Species protection | Increasing | Protective measures are increasing, but perhaps reflecting more species in need of protection |
| Conservation through community involvement | Increasing | Interest in this approach is growing, though the creation of new programs is slow |

Community involvement offers a number of clear benefits, but should not replace national and other monitoring and conservation efforts, since community practices may not always be consistent with the protection of biodiversity (see Huntington, Chapter 18). Disturbance is equally clearly a negative outcome of human-ecosystem interactions, though the causes vary from industrial exploitation of petroleum and minerals, heavy grazing and trampling, and the impacts of climate change. Determining how to address disturbance is thus not always straightforward, especially where large financial interests are at stake. The potential for climate feedbacks to magnify warming trends is worrisome, pointing to the need for global action to address threats with global causes. Action within the Arctic will not always be sufficient to conserve Arctic biodiversity.

To monitor trends in these indicators of human actions that affect biodiversity, a set of quantitative indicators should be developed. Other types of disturbance, feedbacks and conservation measures should also be considered. Noise and chemical pollution, including ocean acidification, may disturb the metabolism or behavior of many animals. The Arctic hydrological cycle, including the potential for sea level rise from melting of ice caps, has feedbacks to the global climate system, and the well-being of migratory species depends on the interrelationship of Arctic conditions with conditions elsewhere in the annual journeys of those species. Conservation outside of protected areas, the regulation of fishing and hunting, human population growth and the rate of consumption of non-renewable resources are all relevant to the success of biodiversity conservation generally.

Tracking all potential indicators is not possible, but a robust set of measures against which progress or decline can be monitored would greatly help in providing the public and policy makers with a means of assessing whether Arctic communities, Arctic countries and the world as a whole are contributing to the conservation of Arctic biodiversity or the opposite. Without timely and unambiguous measures of performance, uncertainty will provide an excuse for inaction or for accepting greater levels of risk than are consistent with a commitment to protecting the future of Arctic ecosystems and those who use them.

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Use in modern media is of decisive importance to the survival of indigenous languages.
Photo: Magnus Elander.

*Chapter 20*

# Linguistic Diversity

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## Contents

> **This silence we named "Qarrtsiluni" which means waiting for something to burst forth.**
>
> Inuit woman, Nunivak Island.

## SUMMARY

The future is bleak for the majority of the languages currently spoken in the North. If no action is taken, most are likely to become extinct in the next few generations. Twenty-one northern languages have become extinct since the 1800s and 10 of these extinctions have taken place after 1990, indicating an increasing rate of language extinction.

Twenty-eight languages classified as critically endangered are in dire need of attention before they, too, are lost forever. Over 70% of the northern indigenous languages are spoken only in single countries, and so are particularly exposed to the policies of a single government bringing with it the potential perhaps, for more effective conservation of these languages, as no cross border efforts are required. The remaining languages are spread across a number of jurisdictions and are therefore subject to differing approaches when it comes to addressing their revitalization.

Language revitalization in the North is possible, and there are multiple examples to prove it. However, whether it is sufficiently important to invest the time and resources needed to make revitalization a reality, is a question that politicians need to ask themselves sooner rather than later. They will face in the future increasing pressure from the indigenous peoples they represent to take action. Many indigenous groups have already begun working on language revitalization, viewing it as an important component of their identity. The Permanent Participants of the Arctic Council look to political leaders to implement policies which will help them promote and sustain their indigenous languages.

## 20.1. INTRODUCTION

Language provides the conceptual and cognitive mechanisms via which humans perceive their environment. Hence, understanding language as a culturally embedded system of meaning is an important guide to understanding how humans adapt and act within their environment. Language not only communicates, it defines culture, nature, history, humanity and ancestry (UNESCO 2009). The indigenous languages of the North have been formed and shaped in close contact with their environment. Languages are a valuable source of information, and a wealth of knowledge on human interactions with nature is encoded in languages (UNESCO 2003; see Box 20.1).

The preservation of languages is a crucial step in allowing us to benefit from traditional knowledge and form a better understanding of our environment. The Convention on Biological Diversity (CBD) recognizes that linguistic diversity is a useful indicator of the retention and use of traditional knowledge, including knowledge of biodiversity. It is, therefore, included in the suite of indicators used to assess progress towards meeting the CBDs 2020 biodiversity targets. With this in mind, this chapter considers the vitality of indigenous languages in the North and their current status and trends. We include indigenous languages of both the Arctic and boreal zones, and as this includes languages from outside the Arctic, we refer to the North instead. An indigenous language for the purposes of this chapter is defined as a language that is native to a region and spoken by indigenous people and with the exception of Greenlandic is a minority language.

The United Nations' Educational, Cultural and Scientific Organization (UNESCO) has developed a framework comprised of nine factors which can be used to determine the vitality and state of endangerment of a language (UNESCO 2003). Eight of these are critical to understanding language vitality in the North: (1) intergenerational transmission, (2) absolute numbers of speakers, (3) proportion of speakers within the total population, (4) trends in existing language domains, (5) response to new domains and media, (6) materials for language education and literacy, (7) governmental and institutional attitudes, and (8) community members' attitudes toward their own language.[1]

All of these factors are involved in situations of language shift and loss; they interact in complicated ways. For example, most linguists consider intergenerational transmission to be the single biggest indicator of language vitality, as children are future speakers. If a language has a large number of speakers and a relatively high proportion of the total ethnic population, then if a small percentage of the younger generation does not learn the language, it is not necessarily a sign of shift. The status of indigenous languages with even relatively large numbers of speakers, can change from 'safe' or 'vulnerable' to 'endangered' very rapidly, if a segment of the children cease learning the language; this is potentially the case with Inuktitut in Canada. In 2006, 64% of 32,200 Canadian Inuit reported Inuktitut as their mother language, representing a decline from 68% just 10 years earlier (Statistics Canada 2012). More to the point, only 50% report using Inuktitut as a home language (down from 58% in 1996), suggesting that children are not acquiring it (Statistics Canada 2012). These figures, along with other indicators, have led the Nunavut Language Commissioner to take specific actions, legislative and promotional, to foster the use of Inuktitut in *all* domains. As this suggests, efforts at strengthening indigenous languages need to take into account the multi-faceted nature of the contexts in which these languages are situated. Taken as a whole, these indicators are thus useful not only in assessing language vitality, but also in determining measures to revitalize them by pointing out areas in need of development.

This chapter looks at two of these criteria (absolute number of speakers and proportion of speakers within

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[1] The 9th factor proposed by UNESCO, amount and quality of documentation, is not an indicator of vitality, but rather was included in the report as a guide in determining which languages are in most urgent need of documentation.

## Box 20.1. Language and biodiversity

> *Lyee sakoowoo saawx' ch'a tleix ee jeedax goox la haash ee koosteeyi.*
>
> (If you don't know the names your [Tlingit] way of life will drift away forever; Grant 2006).

Indigenous peoples have adapted their lifestyles to live in the extreme Arctic climate. Many still maintain a subsistence or partial-subsistence lifestyle and survive by hunting, fishing and herding reindeer. The knowledge engendered by this intimate contact with their surroundings finds expression in languages and their vocabularies.

Languages provide windows into how cultures experience, interact and think about their environment (Nettle & Romaine 2001, Harrison 2007, Evans 2010). This knowledge and interconnectedness is expressed in song, everyday experiences, resource use, relationships with animals and other cultural expressions but especially in place names across the North. Place names of indigenous peoples reflect subsistence practices, histories, storytelling, dwelling sites, ecological significance and links to the sacred. Thornton (2008) provides a rich study of Tlingit place names, where he shows how place names encode information on history, geography and interactions between the Tlingit people and the places themselves. In Tlingit it is difficult to be introduced without reference to places.

Reindeer herding cultures have rich lexical means for referring to reindeer. The terms that are lexicalized tell much about the herding practices of peoples such as Saami, Nenets and Evenki, as they make specific reference to the age and status of reindeer, or lexicalize herding implements and practices. For example, the Evenki have separate words for a one-year old male reindeer (*avlakan*) versus a two-year old (*ektana*) versus a one-year old female (*sachari*), with over 30 words to distinguish different types of reindeer. These naming practices reflect differences which are relevant to maintaining healthy herds. The links between language, knowledge and environment are inseparable. Evenki maintain that they cannot herd reindeer in Russian; it must be done in Evenki. As elsewhere, the Evenki language is maintained by those who live a traditional lifestyle. As this lifestyle is lost – through climate change and/or cultural shift – so is the language, and vice versa. Harrison (2007) provides a compelling ethnolinguistic account of this process for a southern Siberian group, arguing for the same intertwining of language, knowledge and culture.

A very different sort of example is provided by ongoing studies of sea ice (see Krupnik *et al.* 2010; see also Gearhead *et al.* 2010, Aporta *et al.* 2011, Heyes 2011). Sea ice is fundamental to Arctic life; it is the heart of the circumpolar world. It provides a home to some and a landing pad to others. Sea ice has a social ontology and at the same time a life of its own. Knowledge of sea ice is encoded in the words and ways the Inuit speak of it, not only in terms of thickness and age, but also in terms of purpose. Thus the word *allu* 'seal breathing hole' is central to life: seals use it to breathe; polar bears and people use it for hunting seals. It forms the base for *alluaq* 'fishing hole' (or literally 'seal-breathing hole-alike'). Sea ice lexicon provides information about how people use and measure the ice; botanical terminology provides native taxonomies which can differ from Western science, creating classification systems according to features which provide different insights into the world; reindeer terminology informs us of herding and breeding practices.

Much can be deciphered about what cultures use and value by looking at their language.

a total population) and applies them to the North to provide an indication of the status and trends of indigenous languages. Scarcity of data did not allow for the remaining criteria to be applied at the circumpolar scale for all the languages considered in this chapter.

## 20.2. STATUS AND TRENDS

The development of circumpolar statistics for indigenous languages is a challenging task. Information on indigenous populations and their languages varies in coverage and extent. Statistics are often not collected consistently or are only recently being collected. The data used herein come from official and academic sources, as well as information provided by Arctic Council member countries and the six Permanent Participants (indigenous peoples' organizations participating in the Arctic Council). When attempting to compile circumpolar datasets, it must be remembered that even when cohesive national datasets are available, they may have been compiled at different times or use different approaches. Therefore, circumpolar statistics for languages such as Saami, Aleut and Inuit must be approached with caution. Attempts to address this gap in knowledge, however, are important, as they help to stimulate awareness of possible changes, encourage further research, draw attention to the challenges facing the long term vitality of many indigenous languages, and hopefully spur positive actions.

Appendix 20 shows a compilation of statistics on the status and trends of languages indigenous to the North.[2]

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[2] Although Appendix 20 summarizes the best available data on current language vitality; it should be treated with caution. The figures come primarily from census data and represent self-reporting of language knowledge, not the results of proficiency testing. In most cases, the figures are probably overly optimistic, with a higher estimate of speakers than is actually the case.

It undeniably indicates that the future is rather bleak for the majority of the languages currently spoken in the North. If no action is taken, most of them are likely to become extinct in the next few generations. It should be noted, however, that this doesn't necessarily mean that the communities or peoples speaking the languages in question become physically extinct. It is more common that language extinction can best be described as the end point of language shift, that a population ceases to speak its original language and replaces it with another through a gradual process. This situation is by no means unique to the North. The last century has seen a dramatic speeding up of the processes of language shift and extinction in most corners of the world, causing some researchers to talk about an ecological crisis of languages (Dahl 2000) or even claim that this century will see the extinction of 90% of all languages currently spoken (Krauss 1992).

### 20.2.1. Language trends

The North is inhabited by an array of peoples with different cultures and language groupings. For this report, information was compiled on 89 northern languages which accounts for a little more than 1% of the worlds living languages[3]. These can be grouped into six distinct language families plus three isolated languages presently unconnected to any other language grouping (Fig. 20.1).

It was possible to consider changes in populations for 46 languages (Fig. 20.2). Of these, 77% had populations of 10,000 or fewer, and 38% had populations of 1,000 or fewer. Between 1986 and 2010, 18 populations experienced decreases in size ranging from 5 to 50%, the

**Figure 20.1.** The distribution of languages and language families in the North.

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[3] Although it is difficult to determine, *The Ethnologue* lists 6,909 living languages (Lewis 2009).

**Table 20.1.** Languages displaying an increase in absolute numbers of speakers, proportion of speakers and net population.

| Languages | Current population estimates | Estimated population increase | Estimated increase in proportion of speakers (%) | Estimated increase in absolute numbers of speakers | Period |
|---|---|---|---|---|---|
| Inuit | 107,608 | 18,299 | 4 | 13,246 | 1989-2006 |
| Saami languages | 69,101 | 4,674 | 12 | 9,841 | 1995-2006 |
| Tsimshianic | 4,600 | 100 | 12 | 35 | 1997-2006 |

majority of these being located in Alaska and the Russian Federation. This implies either a decline in indigenous populations or alternatively a change in the methods used for census survey; Krauss (2007) provides a useful discussion of some of the challenges of such assessments. The indigenous population that experienced the greatest increase in net population was the Inuit, and the Veps experienced the greatest decrease in population.

It was possible to calculate change in the absolute number of speakers and proportion of speakers for 46 of the surveyed languages. Absolute numbers and percentage of speakers are two separate indicators of language vitality[4] (UNESCO 2003). Only three languages displayed an increase in absolute numbers of speakers, proportion of speakers and net population (Tab. 20.1).

Thirty-seven of the surveyed languages experienced a decrease both in numbers of speakers and in the proportion of speakers within their populations (Tab. 20.2). Only nine languages displayed an increase in proportion of speakers (Fig. 20.3).

## 20.2.2. Language vitality

UNESCO (2003) has classified the vitality of 87 of the northern languages on which data was collected (Fig. 20.4). It is striking to note that 21 of these languages have become extinct since the 1800s, and that 10 of these extinctions have taken place after 1990, indicating an increasing rate of language extinction. Of these extinctions, one was in Finland, one in Alaska, one in Canada and 18 in the Russian Federation (Fig. 20.5). With this in mind, the 30 languages classified as critically endangered are in dire need of attention before they, too, are lost forever.

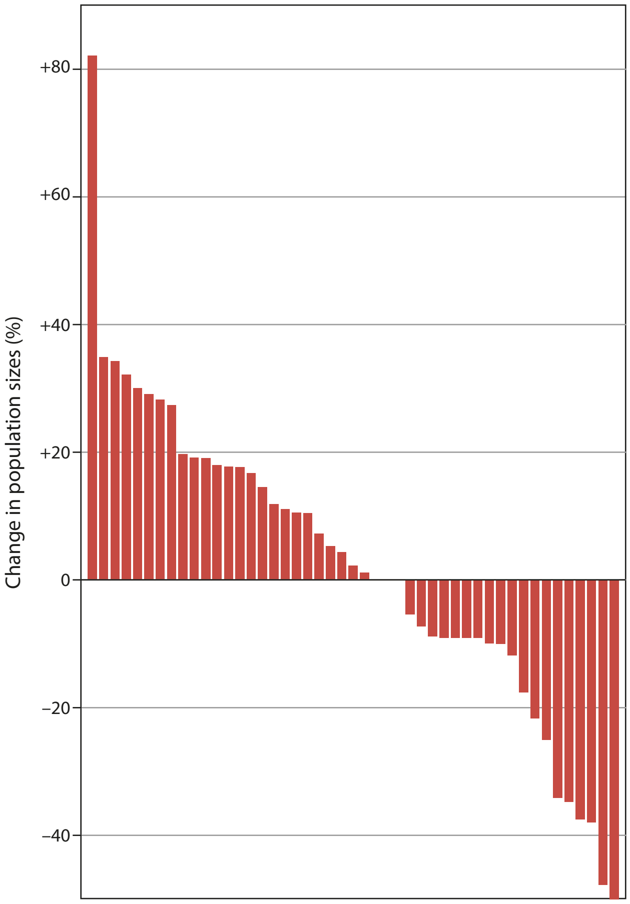

**Figure 20.2.** Change in population (estimated percentages) for 47 indigenous groups between 1989 and 2010.

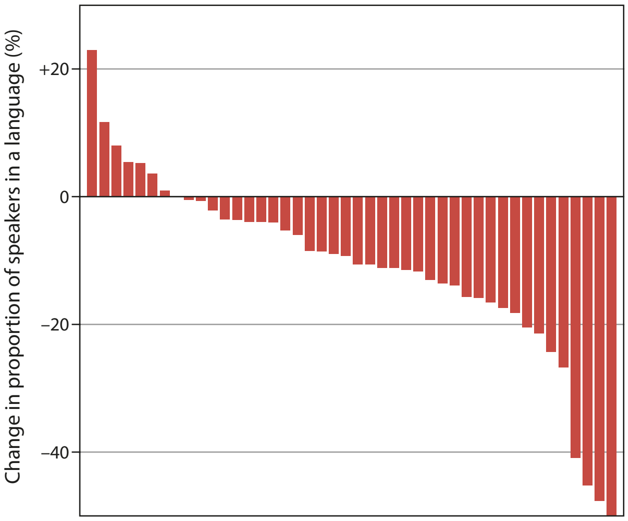

**Figure 20.3.** Estimated change in proportion of speakers for 46 northern languages between 1989 and 2006.

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[4] The smaller the numbers of speakers, the more at risk the language is, even if all community members are fluent in the language. Very small communities are simply vulnerable to rapid shift or even natural disaster. Percentage of speakers is an indicator of shift, not only because it shows that fewer people speak the language, but because the domains where it is spoken are diminished, since the non-speakers will use another language in all domains. Of course, the two combined can give a very good sense of overall vitality: a small population with less than half of its members retaining fluency indicates advanced language loss.

**Table 20.2.** Languages with the greatest increase and decrease in numbers of speakers.

| Language | Current population estimates | Estimated changes in numbers of speakers | Period |
|---|---|---|---|
| Nanai | 12,003 | 991 | 1997-2010 |
| Saami languages | 69,101 | 9,841 | 1995-2006 |
| Inuit | 107,608 | 13,246 | 1989-2006 |
| Chukchi | 15,908 | -6,355 | 1989-2010 |
| Nenets | 44,640 | -5,592 | 1989-2010 |
| Evenk | 38,396 | -5,089 | 1989-2010 |

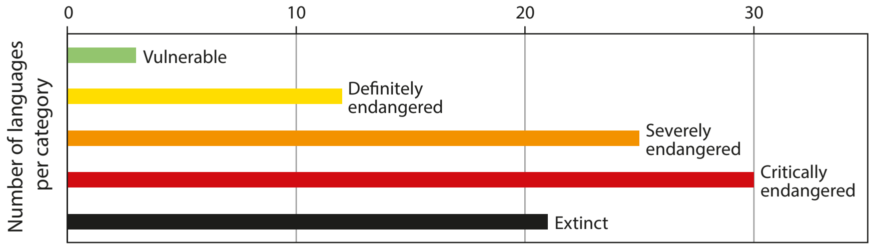

**Figure 20.4.** Vitality of northern languages as classified by UNESCO (2012).

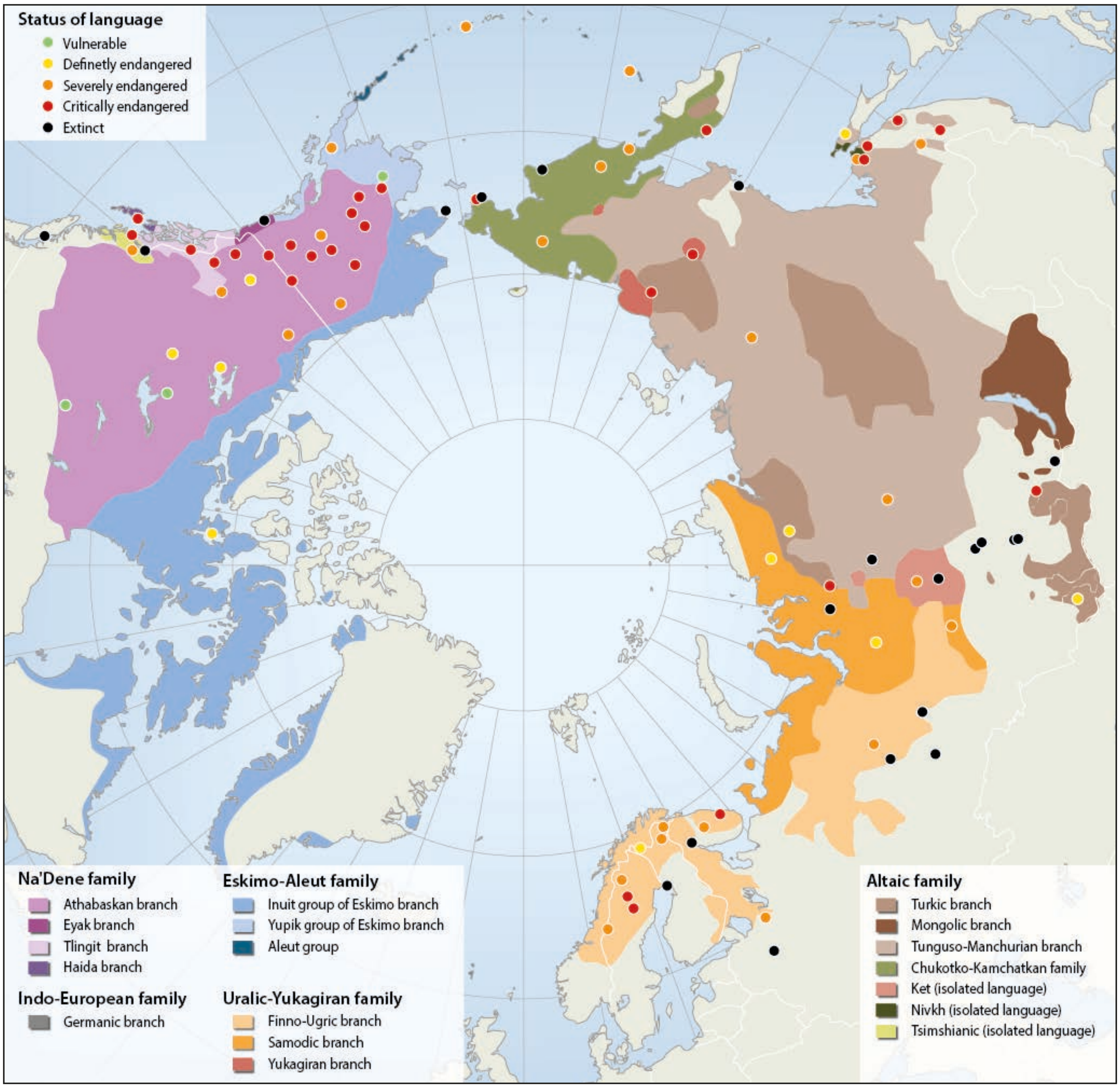

**Figure 20.5.** Map showing the languages colour coded after their vitality status as noted by UNESCO.

## Box 20.2. Language revitalization

> *In one of the coastal Saami villages where Saami is spoken as the mother tongue mainly by those over 50, a son came to his mother who was studying Saami at the university and said "Do I have to go to the University to learn Saami?" The mother realized that this should not be the case, which became a turning point for providing Saami as a subject in schools where it had never been offered before.*
>
> (Gunn-Britt Retter in Einarsson *et al.* 2004).

Revitalization efforts of various kinds are taking place throughout the North and are strong testimony to the interest of indigenous peoples in revitalizing and promoting their languages. Revitalization programs are largely grassroots movements with a variety of activities, such as intensive summer school programs, attempts to promote the language in the local schools and special courses aimed at adult second-language learners. A popular model in many parts of North America is the Master-Apprentice program (Hinton *et al.* 2002), which pairs an elder speaker with a single adult language learner. The Dena'ina language revitalization program in Alaska is one such example. Northern communities speaking an indigenous language are often spread over great distances, and many programs make a concerted effort to bring speakers and learners together to work on language revitalization together.

Aside from the special case of Greenland (see Box 20.3) there are a number of examples where revitalization efforts have the support of local governments e.g. the Nunavut Language Act, or language laws in the Republic of Sakha (Yakutia), Siberia, which grant official status to local indigenous languages (Chukchi, Dolgan, Even, Evenki and Yukaghir) in those regions where the populations are located. Coupled with legislative support are some active revitalization efforts, such as the nomadic school program in Sakha (Yakutia), aimed at delivering mother-tongue education to herding groups (Sakha (Yakutsk) Law on Nomadic Schools 2008, Semenova 2008, Sarviro n.d.). The model has gained popularity and spread to other regions of Siberia (such as the Krasnoyarsk Region and the Yamal Peninsula). The nomadic schools are founded on recognition of the fact that ensuring cultural and linguistic sustainability involves delivering mother-tongue education to children whose parents live a traditional lifestyle. For many indigenous groups in Siberia and elsewhere in the Arctic, this means traditional, nomadic reindeer herding and hunting. The nomadic schools (*kochevye shkoly*) are designed to provide education to children who are living with the herds, enabling them to grow up with their families rather than in boarding schools away from their parents and communities. There are a number of different variants: teachers can be sent to travel with the herds, or teachers may be located elsewhere and connect with their pupils through the internet. These schools are gaining ground among Evenki, in Sakha (Yakutia) and have been instituted in Evenki communities in other parts of Siberia (such as the Krasnoyarsk region) (Evenki Nomadic Schools 2011).

Despite the fact that the Saami peoples speak somewhat different languages and are living primarily in four separate Arctic Council member states (Norway, Sweden, Finland and Russia), they have found great strength in unity and collaboration. In March 2010, the DoBeS program (Dokumentation Bedrohter Sprachen, funded by Volkswagen Stiftung) sponsored a two-week long 'winter school' devoted to Saami language documentation and revitalization (Saami Winter School 2010). These efforts are not new, but have been reinvigorated in recent years. Inari Saami instruction was started in primary schools in the 1970s but vitality reached a critical point in 1997, with only four fluent speakers. Since then, active revitalization at the community level has had a positive impact on language prestige and on vitality, creating new speakers (Pasanen 2010).

These are just a sample of the many language revitalization programs taking place in the North today. Anecdotally, we hear that these programs do more than revitalize language: they create a sense of community and purpose. Although in some cases the actual number of new speakers which come from these programs is not great, many people learn some words, basic greetings and conversation. More importantly, they provide a source of increased ethnic pride and a sense of identity. Revitalizing language is an important part of revitalizing community. The fact that so many programs are happening today, despite lack of governmental or financial support, is testimony to the commitment of communities and the strong role that language plays in them.

## 20.3. CONCERNS FOR THE FUTURE

Since the 19th century, indigenous languages in the North have been subject to pressures and challenges from the colonial powers active in the North. In the early 20th century, this involved a process whereby indigenous languages were not incorporated within educational and civil systems. This often resulted in weakening ties to language and subsequently to culture and traditions. Today, the dominant languages in the North are Russian, English, Finnish and the Scandinavian languages. As documented above, the majority of northern indigenous languages have experienced significant decreases in the absolute number of speakers and the proportion of speakers. This indicates that northern languages are facing an uncertain future, and efforts to increase our understanding of the cultures and traditions contained within these languages should be amplified. However, some indigenous languages have gained stronger status in recent decades and been subject

## Box 20.3. Inuit – Greenland

The current position of Kalaallisut (or West Greenlandic, ISO 689-3 kal), an Inuit language, is often taken by other indigenous Arctic groups as a model for Arctic indigenous languages. An orthography for the language was established soon after Hans Egede, the Danish-Norwegian missionary, arrived in 1721. This comes from a key decision to make Kalaallisut the language of the Christian church in Greenland, and a decision to teach Greenlanders full literacy. 1739 saw publication of the first primer, and the Four Gospels were translated in 1744, followed by the New Testament in 1766, both translated by Poul Egede (Frandsen 2010). The orthography was standardized in 1851 by the Moravian missionary Samuel Kleinschmidt (Dorais 2010); Kleinschmidt also published a reference grammar of the language (Kleinschmidt 1851) and dictionary (Kleinschmidt 1871), which continue to be useful today. The Greenlandic newspaper *Atuagagdliutit* was established in 1861 (Langgård 2010) and is available online at the *Timarit.is* website (including the first issue; see Timarit n.d.). These measures paved the way for education in Kalaallisut, and meant that Greenland has been a highly literate society with a well-established tradition of reading and writing since the mid 1880s.

Since the first Inuit officials were elected in Greenland in the 1860s, their native language, Kalaallisut has been both a political issue and a source of empowerment for Inuit. This is reflected in the language reform initiatives started in 1925 through the institution of Home Rule in 1979 and the inception of self-government in 2009. The Danish system has long accommodated education in Greenlandic, for example through the establishment of a school for church catechists in 1845, which later became the Institute of Learning in the Greenland University. Initiatives in which young Inuit are provided support to pursue education abroad with a requirement that they return to Greenland to work have been influential in helping the language keep pace with modern developments. When these students return to Greenland they introduce new terms and ideas into Greenlandic so that the public can understand and follow their work.

A result of processes described above has been a consistent gain in the Greenlandic Inuit language in terms of concepts, words and usage. This gain has been further supported through the existence of a Language Committee which administers the usage of orthography in Greenlandic. Subcommittees include a Place Names Authority and a Committee on Personal Names. Legislation has also been enacted which establishes procedures for the adoption and authorization of new words and geographical names and personal names in Greenlandic. The usage of standardized language in written form is mandatory, while spoken language allows unlimited use of dialects.

The various forms of the Inuit language have similar typology, grammatical structure and cultural relevance (Dorais 2010). Semantic shifts, however, do occur and allow for dialectal variations. Despite the close proximity with various American Indian groups such as the Dene and Algonquin, there has been limited language borrowing. Encounters with other peoples can be traced through specific loan words and in lexical borrowings from Russian, Spanish, English, Danish, Old Norse, German, Portuguese, Hawaiian, French and other languages, reflecting the various explorers, whalers, fishermen, missionaries and colonizers who have come north. Similarly, Inuit have largely adopted the numbering systems of the majority languages of the nation-states in which they live today: Danish, Russian, English and French.

The education system has been the primary factor affecting the Inuit language, for example through new concepts which allowed for mutual benefits and cooperation between Inuit and Europeans. That said, climate change is a major source of social change, and is a crucial factor which impacts the cultural and linguistic survival of not only the Inuit, but also several other northern indigenous languages.

to sustained efforts to revitalize them both as tools of cultural heritage and as official languages, for example in Greenland and in Nunavut and the Northwest Territories, Canada (see Box 20.2).

No one single factor can be singled out as the main culprit of the increased rate of language shift and extinction. Rather, each language and the general conditions of the language community using it have to be considered separately in search of the cause – or a combination of causes – that weakens its position. This is a point underscored by linguistic research on language shift (Fishman 1991, Nettle & Romaine 2000, Grenoble & Whaley 2006). Nonetheless, a few factors emerge more often than others in this context, whether in the North or elsewhere. These factors include the increased rate of urbanization, which has meant that formerly rural populations which were largely isolated from the outside world have since become part of modern urban societies. This in turn places great pressure on indigenous languages, which tend not to be a viable means of social and economic advancement in the new urban environment. Hence, their speakers gradually abandon them and start using the majority language of the society in question.

Another common factor is a lack of institutional support for many of the smaller languages of the world. More often than not these languages are minority languages in the countries in which they are spoken. Even where the authorities in question hold a friendly view of minority languages, they simply do not have the means to support the use of them in fields such as administration, education and media. UNESCO (2003) targeted the use of language in these three spheres as critical to its vitality. Indeed, new media can even offer new possibilities for strengthening language use (Moriarty 2011). As a result, minority languages become, in a sense, invisible outside the communities using them, often compounding the effects of urbanization as mentioned above.

While a low number of speakers may seem to be a clear indicator of a language in risk of replacement, this is not necessarily the case as there are examples of languages where a small number of speakers is compensated for by strong loyalties to the language. A clearer indicator of the vitality of a language is probably "the ratio between the number of members of the ethnic group and the number of speakers of the ethnic tongue" (Brenzinger 1997). This means that a language that is used by 90% (e.g. 1,800) of speakers in an ethnic group with 2,000 members is likely in a healthier state than a language that is used by 20% (e.g. 40,000) of speakers in an ethnic group with 200,000 members. This should be kept in mind when examining Appendix 20.

The discussion above also raises the question as to what, if anything is lost with the disappearance of a language. After all, all languages change over time, and it could be suggested that the language extinction (and the possible emergence of new ones) is simply a natural change. Linguistic diversity is a possible source of conflict between populations or ethnic groups, as it may complicate communication between authorities on the one hand and segments of the population on the other e.g. with regards access to education, media and employment opportunities (Ostler 2005). Nonetheless, linguists tend to view the extinction of a language in a negative light. Here they point to the importance of language in the culture and identity of the ethnic group in question (Need 2010). Its history and traditions are encoded in and transmitted through its language, and the extinction of the language inevitably leads to the loss of a large part of the group's identity. It is also often claimed that linguistic diversity has a value in itself (Nettle & Romaine 2000, Maffi 2001, Abley 2003, Dalby 2003), though this may be difficult to support objectively other than pointing to the parallels between linguistic and biological diversity. Finally, the emotional value of language is sometimes brought to the fore in the defense of linguistic diversity (Hale *et al.* 1992, Grenoble & Whaley 1998, 2006). Preserving the language one grew up speaking may be just as important on a personal level as preserving one's family ties, and this can be transferred to the speech community as a whole.

A final question is whether anything can be done to reverse the trend of language shift and extinction, and instead to revitalize languages in danger of becoming extinct. The common consensus appears to be that something *can* be done, at least in theory, but there is less agreement on exactly what this is. One of the better known approaches in this respect is Fishman's (1991) program for reversing language shift. These actions include ensuring a language's survival as the language of the home to create a foundation for mother-tongue transmission; enabling and/or strengthening its use in education, mass media, the work sphere and governmental operations; and, in the case of languages which are on the brink of extinction, the reconstruction of the language and its acquisition by adults. There are multiple examples of ongoing efforts at language revitalization in the North today (see Box 20.2). These programs receive varying levels of support – institutional, financial and political – in varying regions. The situation in Greenland is a special case (see Box 20.3), as local (Inuit) concerns about language shift were an integral part of the popular support for the institution of Home Rule in 1979. The development of language policy to revitalize and support the use of West Greenlandic was an important achievement of the Home Rule government. Even today in Greenland, language maintenance and development is a central political and social issue.

Despite the plethora of such programs, they often struggle due to limited resources and inadequate means to address all the problems driving language shift. Northern indigenous language programs face serious challenges in creating domains for language usage, developing the language in media and new domains and changing attitudes toward not only the indigenous language, but often toward the indigenous peoples themselves. Almost all programs face struggle due to a lack of support from federal governments and even hostile policies and attitudes. Some national language and education policies (such as the *No Child Left Behind* Act in the United States or *Unified State Exam* in the Russian Federation) may require children to abandon their mother tongue in order to meet standardized test requirements. Financial resources are needed to create pedagogical materials, train teachers and create educational programs. Language attitudes at all levels can be a serious impediment to language revitalization. These issues were discussed at length at a meeting of the Permanent Participants of the Arctic Council in Tromsø 2008 (ICC 2008), resulting in several sets of recommendations to the Arctic Council and to the national governments in ways to assess, support and foster the use of circumpolar languages.

It is important to keep in mind that because language is one of a set of factors in social health and vitality, strengthening it is fundamental to strengthening the communities as well.

Over 70% of the northern indigenous languages are spoken only in single countries, and so are particularly exposed to the policies of a single government bringing with it the potential perhaps for more effective conservation of these languages as no cross border efforts are required. The remaining languages are spread across a number of jurisdictions and are therefore subject to differing approaches when it comes to addressing their revitalization.

Language revitalization is certainly possible, and there are multiple examples to prove it. Whether it is sufficiently important to invest the time and resources needed to make revitalization a reality is, however, a question which politicians in the North, as in most other parts of the world, need to ask themselves sooner rather than later.

## 20.4. RECOMMENDATIONS

- Encourage the development of improved methods for collecting data on language use and vitality in the North.
- Recognize the diverse richness of the northern indigenous languages, and acknowledge that their preservation is a crucial step in allowing us to benefit from traditional knowledge and form a better understanding of our environment.
- Encourage efforts to support language revitalization for the northern indigenous languages including sharing lessons from successful efforts.
- Undertake an assessment of the northern indigenous languages to allow for a better understanding of their status and what needs to be done to insure their future vitality.

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Appendix 20: www.abds.is/aba-2013-appendix-20

# Lead author biographies

**Tom Barry** is the Executive Secretary for the Conservation of Arctic Flora and Fauna (CAFF), which is the biodiversity working group of the Arctic Council. The CAFF Secretariat is based in Akureyri, Iceland. Tom has a broad range of experience at national and international levels dealing with strategic planning and organizational development, a primary focus of which has been Arctic issues, where he works with a diverse range of stakeholders throughout the Arctic. Tom was heavily involved in the Arctic Biodiversity Assessment, which creates a baseline for use in global and regional assessments of biodiversity and provide a basis to inform and guide future Arctic Council work. Tom is also closely involved in the implementation of the Circumpolar Biodiversity Monitoring Programme (CBMP), which is working to facilitate more rapid detection, communication and responses to the significant biodiversity-related trends and pressures affecting the circumpolar world.

**Professor Dominique Berteaux** was born in France in 1965 (where he grew up on the family farm) and immigrated to Canada as a student in 1991. After being trained in wildlife biology and animal ecology in several French and Canadian universities, he obtained in 1996 a PhD in biology at Sherbrooke University (Quebec). He is a university professor since 1999 and a Canada Research Chair on Northern Biodiversity at the University of Quebec in Rimouski since 2012. Over the years, he has developed an extensive experience of northern ecosystems and their wildlife, especially terrestrial mammals. He discovered the Canadian Arctic through the Swedish Tundra Northwest 1999 expedition and is leading since 2002 a study on Arctic fox ecology on Bylot Island, Nunavut. During the 2007-2008 International Polar Year, he was co-leader of the ArcticWOLVES (Arctic Wildlife Observatories Linking Vulnerable EcoSystems) project. He has authored or co-authored about 80 peer-reviewed scientific papers, but never counts the many hours he spends outdoors, enjoying with his family the wonders created through millions of years of Earth history.

**Dr. Helga Bültmann** developed an interest in flora especially of mountains and the Arctic early in her life. She studied biology in Münster, Germany and there started with lichens, a group of organisms highly diverse and important in marginal areas. A master about species richness in terricolous lichen vegetation of the Austrian Alps was followed by a PhD in 1999 on the terricolous lichen vegetation of Germany, Denmark, Finland and Greenland. Until 2006 she worked at the University of Münster teaching flora, vegetation science and lichenology; since 2007 as freelance ecologist mainly in lichen-related projects or in the Arctic. She participated in five expeditions to different parts of Greenland for research on Arctic vegetation.

**Professor Jørgen S. Christiansen** is full professor in Arctic fish biology at Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT-The Arctic University of Norway. He is presently guest professor at Åbo Akademi University, Environmental and Marine Biology, Turku, Finland. He grew up in Qeqertarsuaq and other settlements in Greenland. As student at Pinngortitaleriffik/Greenland Institute of Natural Resources, he gained experience from shrimp trawling and whaling during five seasons in W Greenland waters. He holds a BSc in biology, geography and geology at the University of Copenhagen (1980), a MSc on carotenoids in Arctic char (1985, UiT), and a DSc on swimming bioenergetics in salmonids (1991, UiT). His publication record comprises experimental studies in Arctic fish physiology and ecotoxicology involving species such as polar cod, capelin and Arctic char. Being Greenlander by inclination, he has turned to field studies on Arctic fish biodiversity, conservation and ecology. He has lead several research expeditions to Arctic waters (Jan Mayen, Svalbard and NE Greenland) and also worked in Arctic Russia (Kola and White Sea). He is member of the Norwegian Red List expert group on fishes and Head of the international TUNU Programme: Euro-Arctic marine fishes – diversity and adaptation (2002-). The latter activity has resulted in close collaboration with colleagues dedicated to Antarctic and Arctic marine biology.

**Professor Joseph A. Cook** is Director and Curator of Mammals and Genomic Resources, Museum of Southwestern Biology, University of New Mexico. Previously, he held faculty and curatorial positions at the University of Alaska Fairbanks and was Chair of Biology at Idaho State University. He is heavily involved in efforts to encourage greater participation of underrepresented students, especially Native Americans, in biology. His research in the Arctic built large museum collections (traditional and genomic) that are digitally web-accessible. He chairs the AIM-UP! Research Coordinating Network, which is exploring new ways to integrate environmental and genomic databases and infuse digital resources into education initiatives. His research focuses on conservation, molecular evolution and systematics of mammals and associated parasites, producing more than 125 peer-reviewed publications, including the Recent Mammals of Alaska. Over two decades, he led two international, specimen-based field projects aimed at understanding the biogeography of Beringia (Beringian Coevolution Project) and Alexander Archipelago (ISLES). Most recently, he co-founded Collaborative Integrated Investigations of Arctic Biomes to engage local communities, and resource managers together with botanists, parasitologists and mammalogists from academia in building site-intensive and spatially-extensive Arctic Archival Observatories to explore the relationships between environmental change, natural resource management and human health at high latitudes.

**Professor Anders Dahlberg** is doing research in fungal ecology. His research focus is analysis of spatiotemporal patterns and dynamics of mycorrhizal, other soil-dwelling and wood-inhabiting fungal populations and communities in boreal forests at natural and managed settings, presently primarily using mass-sequencing and DNA-barcoding. In the Arctic, he has researched arbuscular and ectomycorrhiza. He is also conducting mycological research in relation to sustainable forestry, global change biology and biodiversity conservation. One recent project is to integrate mycology, natural resource economics and forestry in order to evaluate interactions between fungal diversity and land management. Part-time, he works as a fungal conservation expert by the Swedish Species Information Centre, in charge of fungal red-listing in Sweden and conducting analyses of status, causes and in particular ways to facilitate desired developments of biological terrestrial diversity. The work is based on cooperation with scientists, NGOs, public authorities, land users, the educational systems and the public. He's working with global and European fungal conservation issues as a member of the Mushroom, Bracket and Puffball Specialist Group within the International Union for Conservation of Nature (IUCN) and the European Council for Conservation of Fungi (ECCF) and is one of the initiators to establish a global fungal Red List.

**Professor Fred J.A. Daniëls** was born 1943 in Arnhem, the Netherlands. His main interests are nature, music and soccer. He studied biology at the Utrecht University and was 1968 appointed as staff member of the Institute of Systematic Botany, later Botanical Ecology. He obtained his PhD degree in 1980 for a thesis on the vegetation of the Angmagssalik District, Southeast Greenland. In 1987 he accepted a university professor position in Geobotany at the University of Münster, Germany, from where he retired in 2008. His main research interests are patterns and dynamics of vegetation with special attention to bryophytes and lichens. He made 15 expeditions and research trips to Greenland (1966-2009), three to high Arctic Canada and two to the Aleutian Islands, Alaska, and one to the Russian Far East. In addition, he carried out fieldwork in many countries in Europe together with Kazakhstan, Egypt, North America and South Africa. He is (co)author of c. 130 scientific publications, almost half of these pertaining to the Arctic. He was involved in the CAVM project (1992-2005), is member of the CAFF Flora and Vegetation Group, involved in the ABA, CBVM and IAVD projects of CAFF. He is currently finishing a book project on the vegetation of Greenland. "May the beauty of Greenland's nature last forever"

**Dr. Dorothee Ehrich** is an Arctic ecologist. She was born in Geneva, Switzerland, in 1969 and studied biology at the University of Basel. In 1994 she participated in an ornithological expedition to Taimyr, Russian Arctic, and has since then worked with different aspects of Arctic ecology. She obtained her Ph.D. at University of Oslo, Norway, in 2001 with a thesis on population genetics of lemmings. In the following years she worked on genetics of cyclic small rodents and later on phylogeography and migration of Arctic plants. Since the beginning of the International Polar Year in 2007 she is working at the Department of Arctic and Marine Biology of the University of Tromsø. Her current research focuses on food web interactions in the Arctic tundra, ecosystem monitoring in the context of climate change, and natural resource use in Arctic terrestrial ecosystems. She works also on developing a collaborative monitoring program for the tundra ecosystem between northern Norway and several sites in Russia. Since 1994 she has worked in the field in the Arctic almost every year, mostly in Russia, but also in Canada, northern Norway and Svalbard.

**Professor Jon Fjeldså** was born in Norway in 1942 and grew up north of the Arctic Circle. A strong interest in nature goes back to the childhood. Early research activities were focused on grebes and other waterbirds, starting in Norway and Iceland, but soon shifting to South America. Employed since 1971 at the Zoological Museum, University of Copenhagen, where his DSc degree was obtained in 1975. With Copenhagen as a base he has since conducted fieldwork on all continents, mostly in the tropics, but with a preference for montane regions of South America and Africa, and the habitat mosaics on the transition between montane cloud forests and the barren alpine (or "Arctic") habitats. The current research, within the Center for Macroecology, Evolution and Climate, aims to understand the causes of global variation in biodiversity, with a strong focus on the phylogeny of birds and the role of evolution and Earth history in generating large-scale patterns of species diversity.

**Professor Finnur Friðriksson** is an associate professor of Icelandic at the University of Akureyri, Iceland. He is a trained sociolinguist who obtained his PhD from the Department of Linguistics at the University of Gothenburg, Sweden, in 2008. His main research interests are language variation and change, attitudes to language, the relationship between nationalism and language, language planning and policy and language education. He has been involved in projects on linguistic variation in both Icelandic and Scandinavian contexts as well as on the language ecology of multilingual children in Finland, Iceland and Sweden. Currently he co-leads a project on the teaching and usage of Icelandic in the Icelandic school system.

**Dr. Barbara Ganter** was born in Bonn, Germany, in 1965. She got hooked on the Arctic as a teenager during a hiking trip in Swedish Lapland, and got interested in birds during her training as a biologist at the University of Bonn. She did research on wintering Arctic-breeding geese on the German Wadden Sea coast before moving to Canada to do graduate work on population ecology of breeding snow geese on Hudson Bay. As a snow goose researcher, she was lucky to participate in two expeditions to Wrangel Island, Russia, in the 1990s. After returning to Europe she worked in projects on other Arctic goose species, based in The Netherlands and Denmark, and did field work in Greenland. She now works as a freelance ornithologist in northern Germany and, together with her husband, runs a small long-term shorebird research project on Norway's Barents Sea coast.

**Dr. Anthony J. Gaston** has been a Research Scientist with Environment Canada since 1979. His studies of Arctic marine birds have been an important source of evidence for climate change impacts on Arctic marine ecosystems, while his work on the impact of introduced mammals on marine and terrestrial birds in Haida Gwaii, British Columbia has alerted Canadians to the biodiversity losses created by such introductions. In addition to his work with Environment Canada he has acted as an advisor to Wildlife Institute of India on High Altitude Wildlife Monitoring and was instrumental in the creation of the Great Himalayan National Park. He is the author of four full-length books: two species monographs (Thick-billed Murre, 1981; Ancient Murrelet, 1992), an account of the Alcidae in the series Bird Families of the World (1998), and a general text on seabirds (Seabirds – a natural history, 2004). Tony is Research Director of the Laskeek Bay Conservation Society, an environmental organization specializing in citizen science, an Adjunct Professor with University of Ottawa, Editor-in-Chief of Marine Ornithology, a journal of marine birds, and an Associate Editor with Canadian Field-Naturalist. He has supervised a number of graduate students, some of whom now work with him at Environment Canada.

**Dr. Lynn J. Gillespie** is a Research Scientist at the Canadian Museum of Nature and Adjunct Professor in Biology at the University of Ottawa, Canada. She received a BSc from Carleton University, Ottawa, a Ph.D. from the University of California, Davis, with her dissertation on the systematics and phylogeny of a genus in the plant family Euphorbiaceae, and learned molecular techniques during postdoctoral studies at the Smithsonian Institution. Joining the Museum in 1994, she shifted her focus from the tropics to the Arctic, focusing on the Arctic flora and grass systematics. Since then she has made 10 research expeditions to the Canadian Arctic, and has also carried out fieldwork in Madagascar, Southeast Asia and Australia. Research projects include using molecular techniques to resolve the taxonomy and relationships of difficult Arctic species complexes, DNA-barcoding the Canadian Arctic flora and producing a worldwide phylogeny of *Poa* (meadow grasses) and relatives. She currently co-leads the

Arctic Flora of Canada and Alaska project. She is a lead editor for the Flora of North America project, a member of the CAFF Flora group, and has served on the Committee for the Status of Endangered Wildlife in Canada. She enjoys supervising undergraduate and graduate students, and has participated on three Students on Ice expeditions to the Canadian Arctic, an organization dedicated to educating and inspiring students.

**Professor Lenore Grenoble** is the Carl Darling Buck Professor of Linguistics and Slavic Linguistics at the University of Chicago and is a research associate at the Institute of Arctic Studies at Dartmouth College. She is a specialist in contact linguistics, language endangerment and shift, and language revitalization. Since the mid-1990s she has been engaged in the study of Evenki, a Siberian Tungusic language, with research focusing on the structure of Evenki and the impact of contact with Russian. Grenoble also studies Kalaallisut (W Greenlandic). In close collaboration with the Greenland Language Secretariat, she is involved in the creation of a bilingual English-Kalaallisut dictionary and a multi-media gazetteer, as well as the documentation of Greenlandic knowledge of plant use and ethnobotany. In addition, Grenoble serves as the Project Coordinator for the Arctic Indigenous Language Vitality Initiative, an initiative driven by the Permanent Participants of the Arctic Council and overseen by ICC Canada.

**Dr. Eric P. Hoberg** is Chief Curator and Zoologist at the US National Parasite Collection, among the largest archives of specimens and information documenting global parasite biodiversity. A native Californian, born in San Francisco in 1953, his early years were spent wandering the foothills of the Coast Ranges and Sierra Nevada. Arriving in Alaska in 1971, he studied biology, ornithology and parasitology at UA-Fairbanks, while discovering a passion for the North. Evolution of complex parasite faunas among seabirds became the focus for an MSc (Univ. Saskatchewan 1979), and PhD (Univ. Washington-1984). Career paths have taken him from Oregon State University (1984-1989), to the University of Prince Edward Island (1989-1990) and his current position with the USDA. A field biologist and biogeographer, he has traversed regions of Alaska, Canada, Siberia and Antarctica. Since 1999 he has been a principal of the Beringian Coevolution Project, an interdisciplinary exploration of historical processes, biodiversity and structure of host-parasite systems among northern mammals. He has authored or coauthored about 250 publications where parasites serve as a portal to historical/ecological insights about the biosphere, emphasizing the role of episodic events, climate, environmental perturbation and patterns of geographic colonization as determinants of diversity and emergent diseases in evolutionary and ecological time.

**Professor Ian D. Hodkinson** made his doctoral work (1968-71) on the population dynamics and energetics of jumping plant lice followed by a two-year postdoctoral fellowship at the Environmental Sciences Centre, University of Calgary, Canada. Back in the UK he took up a lectureship in Animal Ecology at Liverpool John Moores University in 1974 where he worked until retirement. Between 1976 and 1978 he was involved in the Research on Arctic Tundra Ecosystems project at Meade River, Alaska. Since then, he has worked extensively on invertebrate ecology in several Arctic and Alpine areas including Greenland, Svalbard and the Hardangervidda plateau of mainland Norway, as well as conducting studies on Tropical Rain Forest insects in Sulawesi and Central America. He has awarded his DSc from Newcastle University for his work on the taxonomy and ecology of insects in 1990. Since then, he was Principal Investigator on several large research grants examining the potential effects of climate change on Arctic and Alpine invertebrates with fieldwork on Svalbard, where he also taught for several years as a visiting lecturer on the Arctic Biology course at UNIS. Ian Hodkinson has published around 200 papers and books on invertebrate taxonomy and ecology, ranging from specialist monographs to a more general book entitled *Insect Herbivory*.

**Dr. Henry P. Huntington** was born in New York City in 1964. He worked in the Antarctic as a janitor before university, and then turned northwards, beginning his Arctic career by counting bowhead whales in Barrow, Alaska. His graduate work examined the management of subsistence hunting in Alaska. After completing his doctoral degree, he returned to Barrow, where he worked in a number of positions, and also met his wife Kathy. In 1994, he moved to Anchorage to work for the Inuit Circumpolar Council, which was his introduction to international Arctic work and the Arctic Council. In 1997, he started his own one-man business, specializing in Arctic research. He has conducted many research projects around the Arctic, and has written chapters (or more) of several major Arctic Council assessments, including the first AMAP Assessment, Arctic Flora and Fauna, the Arctic Climate Impact Assessment, the Arctic Oil and Gas Assessment and the Arctic Marine Shipping Assessment. In 2009, he became the Arctic science director for the Pew Environment Group. He has enjoyed several long trips by small boat, dog team and snowmachine in the Arctic. He and Kathy have two sons, and live in Eagle River, a suburb of Anchorage.

**Professor Rolf A. Ims** is based at the Department of Arctic and Marine Biology, University of Tromsø, and is the leader of the Terrestrial Flagship Program of the High North Research Centre for Climate and the Environment (the 'FramCentre'). He received his PhD from the University of Oslo in 1989 and was a professor of landscape ecology there for 10 years before he moved permanently to Tromsø, northern Norway in 2001. Currently, his research focusses on climate change impacts on Arctic terrestrial ecosystems. He has been responsible for research projects at a range of localities in Arctic Norway and Russia. Examples of results from his more than 200 scientific publications are demonstrations of ecosystem state shift resulting from expanding insect pest outbreaks in the transition zone between Arctic tundra and the boreal forest, collapsed population dynamics of key-stone herbivores with cascading impacts on Arctic food webs and adaptive management of endemic Arctic biodiversity under climate warming. Ims was a coauthor of the Arctic Climate Impact Assessment (ACIA), and he chairs the recently launched Climate-ecological Observatory for Arctic Tundra (COAT). COAT is a fully ecosystem-based, adaptive monitoring system that presently includes sites in high Arctic Svalbard and low Arctic Varanger Peninsula in Norway.

**Dr. Alf B. Josefson** was born in 1947 in northern Sweden, c. 300 km south of the Arctic Circle. He took his doctor degree in Zoology at the University of Gothenburg, Sweden in 1985. After a 17 year period affiliated as scientist to the Swedish Environmental Protection Agency conducting the marine benthic fauna monitoring program on the Swedish west coast, he moved to Denmark in 1989, where he now holds a position as Senior Scientist at the Aarhus University. His field is benthic ecology with focus on invertebrates in marine and estuarine sediments, which has involved the role of benthos in biogeochemical cycling and benthos biodiversity with focus on macroecology. He has field work experience from the Baltic Sea, North Sea, Northern Atlantic and the Arctic. He has, as author and co-author, numerous publications of which more than 50 peer reviewed papers (of these 42 are cited c. 1,400 times with H-index = 23, in Web of Science as of Feb. 2013). He uses a significant part of his time for reviewing, with reviews for more than 30 scientific journals and scientific boards in Europe and the US (including Subject editor of Marine Biology Research).

**Dr. Susan J. Kutz** fell in love with the North after spending a summer in the Yukon at 'squirrel camp', Arctic Institute of North America, Kluane Research Station in 1988. She has traveled and worked in the Arctic every year since. Susan completed her degree in veterinary medicine at the University of Saskatchewan in 1992 and then entered small animal veterinary practice based in Yellowknife and providing services to outlying communities in the Northwest Territories and Nunavut. Pursuing her interests in wildlife health, she did a PhD investigating the impacts of climate change on lungworms in muskoxen and carried on to do a Post-doctoral fellowship at the University of Alaska Fairbanks, contributing to the Beringian Coevolution Project field activities in the Russian Far East and Alaska. In 2005, she joined the Department Ecosystem and Public Health at the Faculty of Veterinary Medicine, University of Calgary as a founding member for this new veterinary school. She is also the Director of the Alberta Node of the Canadian Cooperative Wildlife Health Centre. Her research interests lie in understanding the impacts of climate and other landscape change on parasitic diseases in Arctic wildlife. To do this she works closely with northerners exchanging information on wildlife health, engaging youth and developing tools and capacity for wildlife health monitoring.

**Dr. Sergius L. Kuzmin** was born in 1959 and educated from Moscow State Pedagogical Institute (1982). He earned his PhD at the USSR Academy of Sciences in 1987 and has been Senior Scientist at the Institute of Ecology and Evolution, Russian Academy of Sciences since 1993. He is member of the IUCN/Species Survival Commission member, chairman of the IUCN/SSC/Amphibian Specialist Group/Regional Group for the Commonwealth of Independent States and Mongolia, and editor of *Advances in Amphibian Biology in the former Soviet Union*. His research interests are amphibian ecology, systematics, distribution and conservation (population number and dynamics), habitat preferences, life history regulation, development, feeding, competition, reproduction, assemblage structure and dynamics, anthropogenic influences and protection – mainly on the territory of the former Soviet Union and Mongolia, including Arctic regions. But he also has an interest in the history of Mongolia and Tibet. Sergius Kuzmin worked in more than 25 expeditions in different areas of the former USSR, Mongolia, India etc. He is author and co-author of more than 200 publications on amphibians and reptiles, including 15 monographs.

**Dr. Kristin L. Laidre** is a marine mammal ecologist at the University of Washington, Seattle, USA working at the Polar Science Center/APL and the School of Aquatic and Fishery Sciences. She is partially supported by the Greenland Institute of Natural Resources in Nuuk, Greenland. She received her PhD in 2003 from the University of Washington and worked as NSF-funded post-doctoral fellow at the Greenland Institute of Natural Resources between 2004 and 2006. Kristin's research is field-based and focused on studying the behavior, ecology, and population dynamics of Arctic marine mammals. She is a member of the IUCN Species Survival Commission Cetacean Specialist Group and the IUCN Species Survival Commission Polar Bear Specialist Group, and has worked on the North Atlantic Marine Mammal Commission Beluga and Narwhal scientific working group and the International Whaling Commission. She has participated in over 30 field expeditions in Greenland and authored or co-authored over 70 peer-reviewed articles and two books on high-latitude marine mammals.

**Dr. Dennis R. Lassuy** wandered across much of the Pacific Rim before settling into Arctic issues as the Deputy Director of the North Slope Science Initiative. Denny studied intertidal and desert ecology along the shores of the Sea of Cortez, coral reef fish behavior in Micronesia, marine algae in Japan and the ecology freshwater herbivores in the Pacific Northwest. He completed his PhD in Fisheries Science at Oregon State University, and then went to work as an endangered species biologist for the U.S. Fish and Wildlife Service (USFWS). It did not take him long to realize that most endangered fish cases could not be resolved without dealing with the damages done and continuing threats posed by invasive species. That launched him into a decades long affiliation with invasive species issues, mixed in with a number of other interesting posts like research coordinator, science editor and even as the USFWS liaison to the U.S. Congress. After spending the past 10 years as the Invasive Species Program Manager for the USFWS Alaska Region, Denny took a fateful temporary assignment as the Acting Deputy Director of North Slope Science Initiative (NSSI). He so enjoyed his interactions with the whaling culture of Barrow (Alaska) that he joined the NSSI on a permanent basis in April of 2012 and plans a long and happy stint working on Arctic science coordination.

**Dr. Patrick N. Lewis** grew up in the outback of Australia and from an early age was fascinated by nature and wild places. He completed his PhD at the University of Tasmania examining pathways and management options for marine invasive species in the sub-Antarctic islands and Antarctica. Patrick has worked throughout Australia as a consultant engaged in various marine ecology projects specializing in marine invasive species issues. As the Assistant Manager for the Invasive Marine Species Programme of the Australian Government he was responsible for coordinating national response and monitoring programs. Patrick has spent eight seasons working in the Antarctic conducting marine and terrestrial science and sharing his passion for the icy continent as a guide with Antarctic tourism operations. He recently shifted attention to the Arctic when he accepted a position with the WWF Arctic Program where he was responsible for mitigating threats posed by developing fisheries, shipping and oil and gas industries in the vulnerable polar environment. Patrick is currently engaged in an independent project examining marine biodiversity and conservation during a two year pole-to-pole sailing expedition. He has spent the past six months on a 35 foot yacht sailing around Svalbard and Greenland.

**Professor Connie Lovejoy**, originally from the eastern side of Washington State (USA), did her BS in Botany at University of California, Davis. As an undergraduate she identified phytoplankton from Lake Tahoe, and was a lead in a student originated study of Mono Lake. She later lived in New Zealand and participated in two expeditions studying lakes in the Antarctic Dry Valleys. She also spent a year on the altiplano of Peru working on Lake Titicaca. Following her move to Québec City, Canada, she changed her preferred environment from lakes to oceans. She completed a PhD in 2002 at Laval University, her dissertation focused on microbial food web interactions and taxonomy of protists in the North Water Polynya, Northern Baffin Bay. Following a post-doctoral fellowship in Barcelona, Spain, where she learned techniques in molecular biology, she was engaged as a professor at Laval University in 2004. Since then her work has been mostly in the Canadian Arctic, with projects both in marine and freshwater ecosystems. She has authored or co-authored over 80 publications and enjoys supervising graduate students and turning post-doctoral fellows into colleagues. Her current interests include microbial biogeography and dispersion, biological connections within the cryosphere, and the use of genomics and metatranscriptomics as indicators of the state of an environment.

**Dr. Hans Meltofte** was born in Copenhagen, Denmark in 1946. Since childhood, nature, birds, people and travelling were his main interests. Originally trained as a radio technician and meteorological assistant, he worked at weather stations in NE Greenland for several years. This was followed by more than 35 expeditions and travels to the Arctic and five travels to the Antarctic. Since 1973, he has worked as a freelance ornithologist. He has volunteered at a number of NGOs including positions as board member of the Danish Ornithological Society and Wetlands International and earned a DSc degree from the University of Copenhagen in 1994 on a thesis analyzing Western Palearctic/African shorebird migration strategies. He was a driving force behind the establishment of the Zackenberg Research Station in NE Greenland in 1995, where he worked for 11 seasons, initially as station manager, and during the entire period as head of the biological monitoring program. Currently, he is Senior Scientist at the Department of Bioscience at Aarhus University, Denmark, primarily engaged with research in Arctic ecology and waterbird biology. He has authored or co-authored about 600 scientific and popular articles/reports and produced 14 books. Privately and professionally, he has visited more than 100 states on all continents.

**Dr. Christine Michel** grew up in Quebec City, Canada, and obtained a PhD in Marine Biology at Laval University in 1995. She pursued a post-doctorate at the National Institute of Polar Research in Tokyo, with a fellowship from the Japanese Society for the Promotion of Science. Christine joined the Department of Fisheries and Oceans Canada in 1999, where she holds a position as research scientist. Her research investigates processes that influence primary production and energy transfers in Arctic marine ecosystems. Over the past 25 years, Christine has been involved in several national and international multidisciplinary Arctic research programs and networks, working in various Arctic regions such as the Beaufort Sea, the Canadian Arctic Archipelago, Baffin Bay and Hudson Bay. She published more than 60 primary papers, and her research was presented at more than 100 national and international conference in the past five years only. In addition to the Arctic Biodiversity Assessment, Christine also co-led the sea ice biology section in the recent Arctic Council Assessment *Snow, Water, Ice, Permafrost in the Arctic* (SWIPA). She currently leads a multidisciplinary program exploring mesoscale forcings on sea ice biogeochemistry in the Canadian high Arctic. A focal point of Christine's current research is to address impacts of climate-related change on sea ice-associated production and impacts to Arctic food webs.

**Dr. Vadim Mokievsky** is head of Laboratory of Coastal Benthos Ecology in P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow. His main scientific interests are community ecology with special references to meiobenthos (microscopic metazoan associations). He is an expert in taxonomy of marine nematodes and tardigrades and has participated in a number of expeditions in the marine Arctic from the coastal zone to the deep waters. His primary research area is the White Sea, where the White Sea Biological Station of Moscow State University is situated. Apart from the White Sea, Dr. Mokievsky participated in a number of expeditions to the Barents and Kara Seas, where research was focused on the Svalbard archipelago, Novaya Zemlya, Kola Peninsula, eastern Barents and western Kara sea shores and islands. Since 2011, Vadim Mokievsky is a member of CAFF Marine Steering Group.

**Dr. Tero Mustonen**, a passionate defender of traditional worldview and cosmology of his people, is a Finn and the head of village of Selkie in North Karelia, Finland. He is the traditional knowledge coordinator for Eurasia for the Arctic Biodiversity Assessment. Professionally, he works for the award-winning Snowchange Cooperative, which is a non-profit organization based in Finland with members across the Arctic, including the communities of Eastern Sámi, Chukchi, Yukaghir, Sakha, Evenk, Even, Inuit, Inuvialuit, Gwitchin and many more. Mustonen is well-known scholar of the Arctic biodiversity, climate change and indigenous issues, having published over a dozen publications on the topics, including the ground-breaking Eastern Sámi Atlas and Snowscapes, Dreamscapes. He lives in the middle of the last old-growth forest in Selkie with his wife, Kaisu, two goats and 10 chicken without running water. He is a winter seiner. Mustonen has won several human rights and environmental awards for the work with Snowchange and indigenous peoples of the Arctic. He is also an adopted full status member of the Kwakwakwala First Nation based in British Columbia, Canada.

**Dr. David Payer** was born in Massachusetts, USA in 1959. He inherited his mother's love for nature and his father's love for adventure. David earned a Doctor of Veterinary Medicine degree from Cornell University in 1986, worked in private veterinary practice, then travelled to Alaska to study damages to wildlife from the Exxon Valdez oil spill. Dedicating himself to wildlife conservation, he earned M.S. (Oregon State University, 1992) and Ph.D. (University of Maine, 1999) degrees in wildlife ecology. His doctoral research focused on effects of forestry practices on the American marten. David has published numerous scientific and popular articles related to the ecology of desert ungulates, forest carnivores and Arctic birds. Since 2001 he has worked for the U.S. Fish and Wildlife Service as the Supervisory Ecologist at the Arctic National Wildlife Refuge, which comprises 7.8 million ha in north-eastern Alaska. He is currently investigating factors causing declines of Arctic-breeding shorebirds, and effects of climate change on Arctic wildlife and habitats.

**Dr. Michel Poulin** obtained a PhD in marine biology from Université Laval, Quebec City, Canada in 1982. His thesis dealt with the taxonomy and ecology of sea-ice microalgae communities in southeastern Hudson Bay. His main research interests focus on the taxonomy, systematics and biodiversity of brackish and marine microalgae from mid- and high latitudes. He joined the Canadian Museum of Nature in 1984 as the Curator of the National Algal Collection, became Chief of the Botany Division in 1989 and Director of the Research Division in 1990 before returning to active science in 1996. He conducted field work in the St. Lawrence Estuary, across the Canadian high Arctic and in East Antarctica. He led a multidisciplinary research project on the impacts of natural and human-induced disturbances on the biodiversity of the Rideau River in eastern Ontario, Canada. He participated in three Canadian-led international research programs on climate change affecting the Arctic as an expert on marine phytoplankton and sea-ice algae. He is also a Canadian representative in the Marine Expert Monitoring Group of the Circumpolar Biodiversity Monitoring Program under CAFF. He is an Adjunct Professor at Université Laval and at Université du Québec à Rimouski. He published three books and more than 50 primary papers in the last 15 years. He is presently Editor-in-Chief of *Diatom Research* and Associate Editor of *Botanica Marina*.

**Dr. Donald Reid** is an Associate Conservation Zoologist with Wildlife Conservation Society (WCS) Canada, based in Whitehorse, Yukon. His interest in the natural world was nurtured by frequent childhood adventures in the wilds of Kenya and central

Canada, leading to academic studies in animal ecology. His first experiences of the Arctic came as a technician on Canadian Wildlife Service colonial seabird studies. The allure of research in a setting where ecological interactions are so open to observation later drew him back to the Arctic for a doctoral degree studying lemming population dynamics with Dr. Charles Krebs, and subsequently to collaboration on International Polar Year food web studies on the tundra of northern Yukon. The Arctic is one theme in a career spent working for government, the private sector, and non-government organizations. His research and applied conservation work have also taken him to the eastern Himalaya of China, and the boreal and montane environments of western Canada. Working for WCS in the taiga and tundra regions of northwest Canada, he currently leads projects aimed at increasing the scope of protected areas, developing scientifically-derived land and marine management regulations, and understanding the likely effects of climate change on key species.

**Dr. James D. Reist** has researched northern and Arctic fishes since 1975 (MSc, 1978, University of Alberta; evolutionary ecology of sticklebacks; PhD, 1983, University of Toronto; systematics of esocoid fishes; Visiting Fellowship in Government of Canada Laboratories 1983-1985, Freshwater Institute, Winnipeg; stock structure of whitefishes). He has been employed as a research scientist by Fisheries and Oceans Canada in Winnipeg, Canada for the past 28 years. His scientific output includes author and co-authorship on about 180 formal publications, many of which were produced by graduate students supervised through adjunct professorships at nine Canadian universities. Past contributions have included Arctic Council (e.g. Arctic Climate Impact Assessment; Snow, Water, Ice and Permafrost in the Arctic), national (Climate Change) and international (International Panel on Climate Change fourth report) assessments, and as lead investigator for an International Polar Year project on Char Diversity and Climate Change. Presently he leads the following projects in the Canadian Arctic: Beaufort Sea Offshore Marine Fishes Survey, Climate Change Effects on Freshwater and Anadromous Fishes, and Conservation Status Assessments of Arctic Fishes. Over-arching themes of his research have been the origin and maintenance of diversity in northern fishes, consequences of anthropogenic stressors on that diversity, and conservation and sustainability of fishes. Other than fishes, his interests include nature photography and sampling old world single-malt whiskeys and Guinness Stout.

**David F. Tessler** is the Regional Wildlife Biologist for the Wildlife Diversity Program at Alaska Department of Fish and Game. David was born in Colorado in 1967 where his passions for nature and conservation were nurtured, and he has spent his life since in the mountains and the high latitudes. He earned his B.S. in Wildlife Biology from Colorado State University in 1989. His early professional career as a biologist was spent in the mountains of Colorado, Wyoming and New Mexico, where he also worked as a mountaineering and wilderness guide and instructor. David moved to Alaska in 1994 and earned his M.S. in Ecology in 1999 from the University of Alaska Anchorage studying the responses of Arctic and alpine plant communities to a changing climate. David has a broad and varied background in conservation biology and ecological research, most of it focused on rare and threatened species, or species of special conservation concern. His research experience spans a broad swath of taxa and topics, including the movements, behavior and ecology of the Pacific walrus in Alaska and the Russian Far East, the ecology of high latitude shorebirds, seabirds, and passerines, anadromous salmonids, alpine bird assemblages, ungulates, bats and – of course – amphibians.

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The eyes of the world are turning northwards. In recent years, interest in the Arctic has increased dramatically within and outside of Arctic countries. This is reflected in the amount of attention given to Arctic biodiversity. While the landscapes and wildlife have been the subject of explorers, scientists, artists and photographers as well as the home of a variety of peoples for a long time, until recently Arctic biodiversity did not feature very prominently in national or international policy work. This, however, is changing, as the unique values of Arctic nature are increasingly discussed at high levels. At the same time, more and more attention has been paid to the interface between science and policy to ensure that policy is built on the best science available.

Biodiversity is life. It is the very foundation of our existence on Earth. In the Arctic, links between biodiversity and traditional ways of life are often seen more clearly than in many other parts of the world. These are examples of ecosystem services, the benefits that we receive from nature. Many ecosystems and ecosystem functions in the Arctic remain largely unstudied and involve little-known organisms, especially microbes. The Arctic Biodiversity Assessment presents current knowledge also on these processes and organisms and thus provides a base for further work.

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