Marine Biology Research, 2013
Vol. 9, No. 4, 337–357, http://dx.doi.org/10.1080/17451000.2012.756982

INVITED REVIEW

Impacts of climate variation and potential effects of climate change on South American seabirds – a review

PETRA QUILLFELDT* & JUAN F. MASELLO

Justus Liebig University Giessen, Department of Animal Ecology & Systematics, Germany

Abstract

The coastal and oceanic waters around the South American coasts provide rich foraging grounds for breeding and wintering seabirds, but there is growing concern that climate change will provide additional pressures to the seabirds around South America. As in many other coastal ecosystems, seabirds around South America are already faced with threats to their breeding habitats such as human disturbance and introduced predators, and threats at sea such as persistent pollutants and pesticides and direct mortality risks due to fisheries and oil spills. The sensitivity of South American marine ecosystems to ocean climate anomalies is well known from the dramatic population collapses caused by El Niño Southern Oscillation (ENSO) events. However, longer-term climate change effects have been explored less often and few long-term data sets exist for South American seabirds. Seven Large Marine Ecosystems (LME) border South America. While all LMEs experienced warming during the last 50 years, their climate dynamics have differed in recent decades. Climate models suggest that potential climate change effects may be important, especially due to changes in ENSO intensity and frequency and associated changes in the ocean climate of Atlantic and Pacific marine ecosystems. In this review, we found that the best studied seabird communities are those of the Patagonian Shelf and the Humboldt Current, but overall, our knowledge on climate effects on South American seabirds is scarce.

Key words: *Aves, climate change, ENSO, South America, coastal ocean ecosystems*

Introduction

Anthropogenic climate change affects the physical environment of seabirds through increasing air and ocean temperatures (Levitus et al. 2000, 2005) and associated changes in patterns of precipitation and changes in frequency and severity of extreme events (e.g. Timmermann et al. 1999; Holmgren et al. 2001; Cobb et al. 2003). Rising atmospheric greenhouse gas concentrations have increased global average temperatures by about 0.2°C per decade over the past 40 years (Hansen et al. 2010), and much of this added energy is absorbed by the world's oceans. As a result, the average temperature of the upper layers of the ocean has increased by 0.6°C over the past 100 years (IPCC 2007). Measurable impacts of this ocean climate change so far include decreased ocean productivity, altered food web dynamics, reduced abundance of habitat-forming species, shifting species distributions, and a greater incidence of disease (Hoegh-Guldberg & Bruno 2010). Several recent reviews suggested that global warming has a profound bottom-up impact upon marine top-predators (e.g. Grémillet & Boulinier 2009; Chambers et al. 2011). Climate change also increasingly affects seabirds. It has been estimated that adverse weather and climatic events at breeding sites and the potential impact of sea level rise negatively influence the conservation status of 40% of the 97 globally threatened seabird species, making it the third most common threat after invasive alien species and bycatch (Croxall et al. 2012, fig. 7).

Long-term observations of seabirds show that increases in sea surface temperature (SST) typically cause low availability of seabird prey, and consequently deferred reproduction, lowered growth rates and high mortality of chicks in different oceans such as the Antarctic (Jenouvrier et al. 2005b; Le Bohec et al. 2008), the Indian Ocean (Monticelli et al. 2007),

---

*Correspondence: Petra Quillfeldt, Justus Liebig University Giessen, Department of Animal Ecology & Systematics, Heinrich-Buff-Ring 38, D-35392 Giessen, Germany. E-mail: Petra.Quillfeldt@bio.uni-giessen.de

Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark

(Accepted 22 November 2012; Published online 18 February 2013)

the North Atlantic (Durant et al. 2004; Riou et al. 2011) and the Southern Ocean (Weimerskirch et al. 2003). Thus, global ocean warming places an added burden on many seabird species (e.g. Ainley et al. 2010), although some seabirds have also been shown to benefit from climatic change (e.g. Hamer 2010; Rivalan et al. 2010; Weimerskirch et al. 2012).

Most seabirds feed at a relatively narrow range of trophic levels, mainly taking larger zooplankton or small pelagic fish or squid. Most seabird prey is thus strongly influenced by climate-driven changes in phytoplankton productivity (e.g. Behrenfeld et al. 2006), which cause changes in the abundance and fecundity of small grazing zooplankton such as copepods and euphausiids and in consequence, carnivorous zooplankton and pelagic fish or squid. The dynamics of small pelagic fish has been studied intensively in upwelling ecosystems, such as the Humboldt and Benguela currents, where collapses of small pelagic fish populations are often accompanied by sharp declines in marine bird populations (Crawford & Jahncke 1999; Crawford et al. 2008a).

Most seabirds have life-history characteristics that buffer their populations against interannual fluctuations in their food sources, such as high survivorship and longevity. However, longevity comes at the cost of low fecundity, such that population recovery is usually low. Furthermore, seabirds are restricted to specific breeding sites such as predator-free islands, from where they act as central-place foragers. Depending on their mode of locomotion (gliding or flapping flight, or underwater pursuit diving), foraging is more or less energetically costly and the foraging range more or less restricted. Thus, seabird guilds would be expected to differ in their ability to respond to a shift in prey distribution. Few studies have tested this hypothesis (e.g. Jaksik & Fariña 2010).

Climate change effects can also be significant for high-latitude seabirds. Antarctic penguin species adapted to sea-ice habitat are among those where large effects are expected. For example, a simulation of a 2°C warmer climate predicts that 50% of emperor penguin (*Aptenodytes forsteri* Gray, 1844) colonies (40% of breeding population) and 75% of Adélie penguin (*Pygoscelis adeliae* (Hombron & Jacquinot, 1841)) colonies (70% of breeding population) will disappear (Ainley et al. 2010).

Changes in climatic conditions can therefore cause dramatic changes in food availability, followed by changes in population size, distribution or reproductive ecology of seabirds (e.g. Kitaysky & Golubova 2000; Jaksic 2004). There are signs that ocean warming and acidification decreases the carrying capacity of many marine ecosystems and this is reflected in the decreasing population sizes of seabirds (e.g. California Current: Ainley & Hyrenbach 2010).

Responses of seabirds to either climate change or, more specifically, warm SST, include increased mortality levels (e.g. southern fulmar *Fulmarus glacialoides* (Smith, 1840), in 1964–2002: Jenouvrier et al. 2003; emperor penguin in 1962–2001: Jenouvrier et al. 2005a; King penguin *Aptenodytes patagonicus* Miller, 1778, in 1997–2005: Le Bohec et al. 2008; Northern Atlantic seabirds in 1989–2003: Sandvik et al. 2005; Galápagos penguins *Spheniscus mendiculus* Sundevall, 1871, in 1971–2004: Vargas et al. 2006), changes in migration patterns (sooty shearwater *Puffinus griseus* (Gmelin, 1789), in 1987–1994: Veit et al. 1996) and changes in the distribution of species (e.g. non-breeding species in the California upwelling system: Ainley et al. 2005; South Africa: Crawford et al. 2008b), changes in the phenology of breeding (e.g. kittiwakes *Rissa tridactyla* (Linnaeus, 1758), in 1955–1987: Aebischer et al. 1990; and in 1970–2008: Moe et al. 2009; blue-footed booby *Sula nebouxii* Milne-Edwards, 1882, in 1989–2006: Ancona et al. 2011; Antarctic seabirds in 1950–2004: Barbraud & Weimerskirch 2006; little auks *Alle alle* (Linnaeus, 1758), in 1963–2008: Moe et al. 2009), reduced breeding participation (e.g. blue-footed booby in 1989–2006: Ancona et al. 2011; red-footed booby *Sula sula* (Linnaeus, 1766), in 1983–2002: Cubaynes et al. 2011), reduced breeding success (e.g. kittiwakes in 1955–1987: Aebischer et al. 1990; tufted puffins *Fratercula cirrhata* (Pallas, 1769), in 1975–2002: Gjerdrum et al. 2003) and reduced offspring quality (e.g. tufted puffins in 1975–2002: Gjerdrum et al. 2003).

From the list above, it becomes clear that long-term data sets have been crucial for understanding these changes; and that these long-term data sets are mainly concentrated around Antarctica, North America and Northern Europe (e.g. Sandvik & Erikstad 2008 for a meta analysis in the North Atlantic; Sydeman et al. 2012 for a global analysis), while only one of these data sets originates from South America (Vargas et al. 2006). However, South America also harbours important breeding sites for seabirds (e.g. Yorio et al. 1999; Simeone et al. 2003) and oceanic and/or coastal areas offer wintering sites for Antarctic and Sub-Antarctic seabirds (reviewed by Costa et al. 2011) as well as Northern Hemisphere seabirds (e.g. Spear & Ainley 2008). In the subsequent sections, we summarize the state of knowledge on seabird responses to climatic variability in South American waters, using the units of the Large Marine Ecosystems (LMEs) to structure the review. We give a detailed account on three LMEs (Humboldt Current, Patagonian Shelf and

South Brazil Shelf), from where some studies of seabird responses to climate have been reported.

South American Large Marine Ecosystems and climate

Large Marine Ecosystems are ocean areas of approximately 200,000 km^2 or greater, adjacent to the continents in coastal waters where primary productivity is generally higher than in open ocean areas (e.g. Sherman 1991). The extent of the LME is defined by four linked ecological criteria: bathymetry, hydrography, productivity and trophic relationships. A total of 64 distinct LMEs have been delineated around the world's ocean coasts, 7 of them around South America (Figure 1). South America is bordered by the Pacific Ocean with the southernmost portion of the Pacific Central-American coastal LME and the cold Humboldt Current LME in the west. Several northwestern South American countries border the Caribbean Sea, and the Atlantic Ocean coasts are separated into four LMEs embracing the cold Falkland/Malvinas and the warmer Brazil currents.

In an analysis of LMEs, there was a widespread, global pattern of warming in the period 1957–2006 (Sherman & Hempel 2009). This also affected all seven South American LMEs, although to varying degrees.

There is growing awareness that environmental variability plays a crucial role in marine ecosystems. Global climatic phenomena cause environmental variability in South American waters. In particular, the El Niño Southern Oscillation (ENSO) and the Antarctic Oscillation (AAO) are climatic cycles that greatly affect vast regions of South America and the surrounding oceanic waters (e.g. Ropelewski & Halpert 1987, 1989; Silvestri & Vera 2003). Research in the last two decades has shown that ENSO has major implications for the functioning of ecosystems and pulses of primary productivity that can cascade upward through the food web invoking unforeseen feedbacks (e.g. terrestrial ecosystems: Jaksic et al. 1997; Holmgren et al. 2001, 2006).

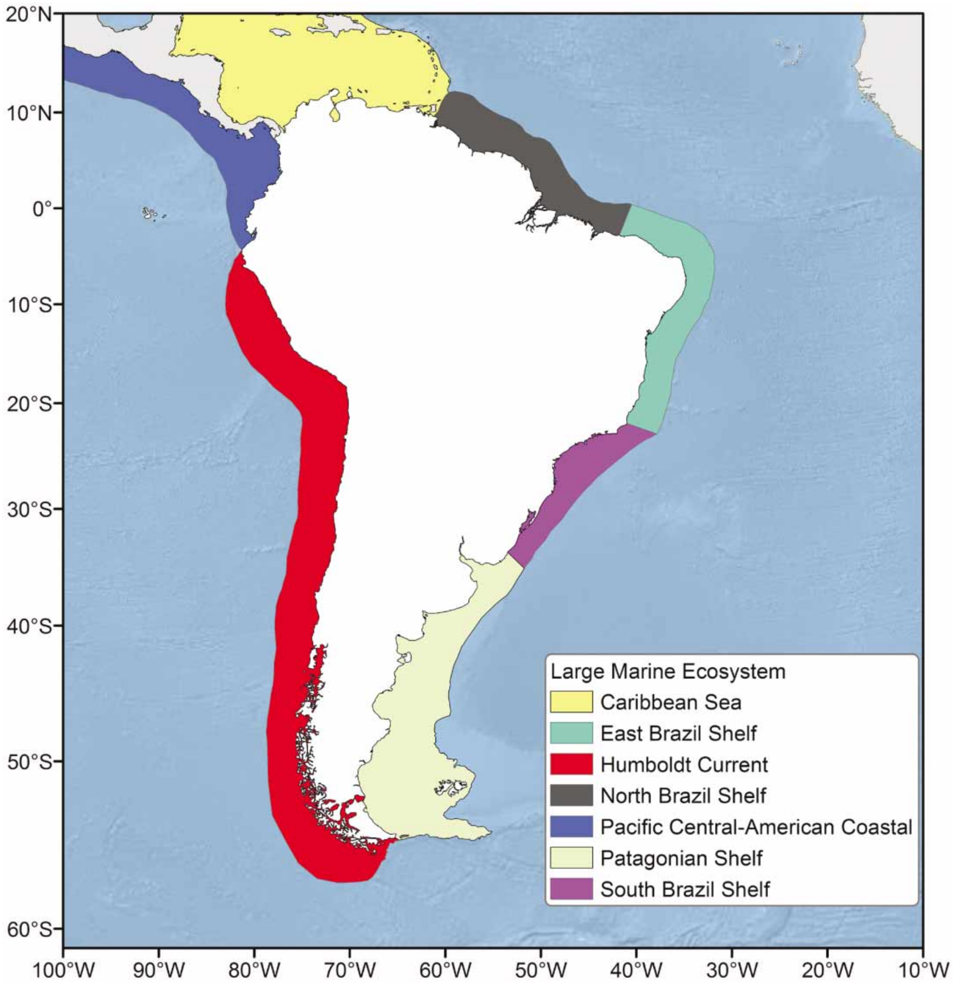

Figure 1. Large Marine Ecosystems bordering South America, as defined by Sherman & Hempel (2009) (see also http://www.lme.noaa.gov/).

ENSO is the strongest climate signal of global impact that affects marine ecosystems, by changing patterns of upwelling with a frequency of 3–7 years (e.g. Timmermann et al. 1999; Dijkstra 2006; Ashok & Yamagata 2009; Yeh et al. 2009). El Niño years are defined by warmer than normal SSTs in the eastern tropical Pacific, depressing primary productivity and consequently the trophic web depending on primary production. Although El Niño is the classic example of the impact of climate variability on ocean ecosystems (Barber & Chavez 1983), longer and more gradual changes in marine environments are also important and can cause profound changes on marine living resources (e.g. Alheit & Niquen 2004) leading to the so-called 'regime-shifts' once they reach a tipping point.

While we will discuss impacts of ENSO cycles mainly within the Humboldt Current LME, it is important to notice that changes in SST related to the ENSO cycle occur also in places far from the source of the phenomenon, i.e. outside of the Pacific (e.g. Ropelewski & Halpert 1987; Holmgren et al. 2001, 2006), and that several climate models predict an increased frequency or change in the pattern of ENSO cycles with climate change (e.g. Timmermann et al. 1999; Yeh et al. 2009).

The ENSO cycle is present in all relevant paleoclimate records. It was systematically weaker during the early and middle Holocene, and data from corals show substantial decadal and longer variations in the strength of the ENSO cycle within the past 1000 years (Cane 2005). Models used for future climate projections provide an indeterminate picture of ENSO's future. Some predict more ENSO activity (e.g. Timmermann et al. 1999), but some also less (reviewed in Cane 2005). A puzzling shift in the ENSO cycle behaviour was observed over recent years (Yeh et al. 2009), with a distinction among 'classic' Eastern Pacific (EP) El Niño and the new phenomenon the Central Pacific (CP) El Niño, where the maximum SST anomaly persists in the central Pacific from the boreal summer through to the winter. The occurrence ratio of the CP-El Niño to the EP-El Niño is expected to increase in response to global warming (Yeh et al. 2009), and the importance of this change for seabirds remains to be explored.

Impacts of ENSO on reproduction of seabird populations have been detected in places far from the equatorial Pacific, where they often occur after a lag of few months or years (e.g., Ainley et al. 1995; Guinet et al. 1998; Chambers 2004; Quillfeldt et al. 2007), depending on the distance of the site from the equatorial Pacific and on the time required for bottom-up processes to cascade to upper trophic levels (Monticelli et al. 2007). The Southern Oscillation Index (SOI) summarizes the state of the ENSO on a global scale, and appears to be strongly related to the breeding success and survival of seabirds ranging widely, such as albatrosses and many petrels (e.g. Nevoux et al. 2007; Rolland et al. 2010).

Chambers et al. (2011) pointed out further potential impacts of climate change, including effects of rises in sea level and storms, ocean acidification, changing wind patterns, increased land temperature and extreme precipitation events.

Rises in sea level may cause flooding of seabird colonies on low-lying islands and atolls, or increased competition for nesting space as island size is reduced. Urban developments of islands and coastal areas will constrain the ability of seabirds to find alternative nesting locations, or lead to seabirds breeding on artificial structures (e.g. Erwin 1980; Coulson & Coulson 2008). However, some birds may also benefit from climate-driven habitat modifications. Some indirect evidence comes from coastal waterbirds: several species of herons breeding in mangrove habitats recently expanded southwards in Brazil (Gianuca 2007; Gianuca et al. 2008).

Altered wind patterns can have effects on food availability, especially for far-ranging, surface-feeding seabirds (e.g. wandering albatross *Diomedea exulans* Linnaeus, 1758: Weimerskirch et al. 2012). Storms, increased land temperature and extreme precipitation events may lead to increased breeding failures if they affect the breeding sites. Taken together, these parameters could profoundly alter biodiversity and ecosystem functioning in many regions of the world, as populations may not be able to respond as fast as the changing conditions might require.

Seabirds face a number of imminent threats, which may seem more urgent than gradual climate change and its associated climatic phenomena. In particular, fisheries over-exploitation, pollution (especially oil), introduced species, habitat destruction and human disturbance through coastal development, guano harvesting and tourism are especially relevant (e.g. Yorio et al. 1999; Petry & Fonseca 2002; Tourinho et al. 2010). Offshore fishing operations may provide food in the form of discards (Bugoni et al. 2010), but also lead to incidental mortality of penguins, albatrosses, petrels, shearwaters and cormorants (e.g. Favero et al. 2003; Phillips et al. 2006; González-Zevallos & Yorio 2006; Bugoni et al. 2008a; Jiménez et al. 2009; Cardoso et al. 2011) and to increased intake of heavy metals (Carvalho et al. 2013). While some of these threats are locally restricted or could be remedied through political decisions, climatic phenomena have the potential to influence the whole region profoundly and add to the cumulative pressure affecting many seabird species.

Humboldt Current LME

The Humboldt Current along the Pacific coasts of Chile and Peru is the world's largest coastal upwelling system. Intense wind-induced upwelling cells along the coast result in unusually cool surface waters, relative to latitude. For example, the SST at 5°S off Peru is as cool as 16°C when most other tropical locations are in excess of 25°C (Chavez et al. 2008). In addition, the surface oxygenated waters in the Humboldt Current overlie an intense and extremely shallow Oxygen Minimum Zone that forms a barrier and concentrates living resources near the surface, thus making them available for seabirds.

Characteristic resident seabirds (Figure 2) include Humboldt penguins (*Spheniscus humboldti* Meyen, 1834), Peruvian diving petrels (*Pelecanoides garnotii* (Lesson, 1828)) and the so-called guano birds: Peruvian booby (*Sula variegata* (Tschudi, 1845)), guanay cormorant (*Phalacrocorax bougainvilii* (Lesson, 1837)) and Peruvian pelican (*Pelecanus thagus* Molina, 1782) (e.g. Croxall et al. 1984). In addition, over 90 species of seabirds were recorded offshore (Spear & Ainley 2008), composed of 18 endemics, 10 residents (species breeding in the study area and elsewhere), 41 Southern Hemisphere migrants (most numerous: black-browed albatross *T. melanophris* (Temminck, 1828), white-chinned petrel *Procellaria aequinoctialis* Linnaeus, 1758, Juan Fernandez petrel *Pterodroma externa* (Salvin, 1875), thin-billed prion *Pachyptila belcheri* (Mathews, 1912), blue-footed booby *Sula nebouxii*, 18 Northern Hemisphere migrants (most numerous: red phalarope *Phalaropus fulicarius* (Linnaeus, 1758), Franklin's gull *Larus pipixcan* (Wagler, 1831) and 6 migrants that breed in both hemispheres. The most common species was the sooty shearwater (Spear & Ainley 2008).

The southern part of the Humboldt Current LME differs in several aspects from the more northern coasts with their relatively linear, arid coastline and few rocky islands. The southern Chilean waters are characterized by many islands, fjords and channels, but which remain poorly studied and inaccessible,

Figure 2. Humboldt Current LME seabirds: Humboldt penguins (upper left), Peruvian boobies (upper right), Chilean pelicans (lower left) and red-legged cormorants (lower right). Choros and Chungungo Islands, Northern Chile. Photographer: Petra Quillfeldt.

with a cold–humid climate and partly dense vegetation (e.g. Croxall et al. 1984). The seabirds are clearly more Sub-Antarctic, with similar species to seabirds in the Patagonian shelf LME. For the purposes of this review, we also count the Galápagos Islands as part of the Humboldt LME, as its climate variability is similar to that of the coast, being part of the extended Humboldt Current upwelling system.

The average primary productivity in the Humboldt Current LME is moderate, however, the northern Humboldt Current system off Peru produces more fish per unit area than any other region in the world oceans (Chavez et al. 2008), representing less than 0.1% of the world ocean surface but presently producing about 10% of the world fish catch. The fishery, as well as the seabirds, depend on a crucial intermediate trophic level of small, plankton-feeding pelagic fish dominated by a few schooling species, especially Peruvian anchoveta (*Engraulis ringens* Jenyns, 1842) and Pacific sardines (*Sardinops sagax* (Jenyns, 1842)). Their massive populations may vary radically in size, depending on the available primary productivity. About 94% of the variation in guanay cormorant and Peruvian booby numbers from 1925 to 2000 were explained by two factors governing primary production in the Humboldt upwelling system, namely wind stress and SST, and the competitive effect of the fishery that limits prey availability (Jahncke et al. 2004). The Humboldt Current is affected by strong seasonal, interannual and longer-term variability. In particular, the Humboldt Current is well known for the periodic occurrence of ENSO. During the warmest phase, El Niño conditions, the upwelling can be interrupted and primary productivity depressed. Occurrences of ENSO are associated with large-scale changes in seabird geographic distribution, survival, and reproductive success in the Humboldt Current (reviewed by Jaksik & Fariña 2010). Strong declines of seabird populations along Peruvian and Chilean coasts and in the Galápagos Islands have been associated with El Niño events (e.g. Anderson 1989; Boersma 1978; Kalmbach et al. 2001). This link between oceanographic events and seabird breeding failures and die-offs has been observed for a long time (Murphy 1926), and has more recently been studied intensely, when one of the most severe El Niño events occurred during 1982–1983, as well as during the El Niño event of 1997–1998. Responses included movement away from Peruvian waters during El Niño events (e.g. Mackiernan et al. 2001) and large numbers of dead and dying birds at several places throughout the eastern Pacific (Ainley et al. 1988, Duffy 1990). ENSO-related southward migration of top-predators relying on the Humboldt Current ecosystem has been observed in guano birds (Arntz & Fahrbach 1991) as well as Humboldt penguins (Culik 2001). Adult seabirds often did not attempt to breed (e.g. Jahncke & Goya 1998; Zavalaga et al. 2008), and if so, chicks were fed less than usual (e.g. Ainley et al. 1988). In Galápagos penguins, breeding attempts failed during most El Niño events, and the strongest events in 1982–1983 and 1997–1998 caused mortality of adults from starvation and a population decline by an estimated 77% and 65%, respectively (Rosenberg & Harcourt 1987; Vargas et al. 2006), followed by slow recovery (Boersma 1998). Today, Galápagos penguin numbers are only about 25% of what they were in the 1970s (Boersma 2008). In central Chile, the number of breeding pairs of Neotropic cormorants (*Phalacrocorax brasilianus* (Gmelin, 1789)) declined by 71% during El Niño, laying started 15 days later, was less synchronized and ended 35 days later (Kalmbach et al. 2001). Not only did the pelagic fish migrate to deeper, inaccessible waters, reducing the food availability, but an increase in rainfall (e.g. Kane 1999; Andreoli & Kayano 2005) and rising sea levels also contributed to seabird breeding failures (e.g. Valle et al. 1987). In central Chile, 55–85% fewer breeding pairs of Humboldt penguins were present at the breeding colonies during the 1997/98 El Niño episode, the onset of nesting was delayed, and abnormally heavy rainfall flooded nests (Simeone et al. 2002). While the number of breeding pairs was significantly related to sea surface temperature anomalies (SSTA), breeding success was not.

There is some evidence that the ecology and life history of seabirds influences the degree to which El Niño events affected different species. Seabirds with a narrow dietary range (e.g. those eating fish and fish larvae) were the most severely affected by El Niño 1982–1983 (Jaksik & Fariña 2010). This relationship is also found within species, for example SSTAs were negatively correlated with diet diversity in Peruvian diving petrels, suggesting that warm conditions decrease prey options (García-Godos & Goya 2006). Further, seabird populations can recover rapidly after El Niño if they have large clutch sizes, fast body growth rates and early reproductive ages. In the Humboldt Current system, the seabird assemblages are dominated by species with these life history characteristics (Luna-Jorquera et al. 2003). Thus, response to El Niño could be an important selective factor for breeding biology and life-history patterns of seabirds.

El Niño events have always had a negative influence on guano bird populations, but severe crashes have only been apparent since fishing activities intensified (Croxall et al. 1984). In addition, it has been observed that anchovy can recover even from strong ENSO events within 1–2 years and, therefore, periods of warm and cold temperature anomalies on the decadal scale seem to play a more important role for long-term anchovy dynamics than ENSO events (Alheit & Niquen 2004). Furthermore, a recent model simulates a cooling trend of the SST off Peru, with an increase in the occurrence of the CP El Niño events but a reduction of EP El Niño and, thus, mesoscale El Niño activity in the northern Humboldt Current region (Dewitte et al. 2012). If these model predictions are correct, seabirds in this region may have a favourable time ahead.

In the 1950s–1970s, seabird numbers collapsed after a large-scale commercial fishery reduced anchoveta stocks in the northern Humboldt Current. However, at the same time, waters became warmer, most likely causing a regime shift (e.g. Cahuin et al. 2009). Thus, it has been proposed that the long-term dynamics of the Humboldt Current ecosystem are controlled by shifts between alternating anchovy and sardine regimes (Alheit & Niquen 2004). Such regimes are caused by lasting periods of warm or cold temperature anomalies and restructure the entire ecosystem from phytoplankton to the top predators. Phases with colder water temperatures parallel anchovy regimes (termed 'La Vieja', e.g. 1950–1970; 1985 to the present). During a warmer period from 1970 to 1985 (termed 'El Viejo'), sardines became dominant as anchovy populations were restricted to smaller coastal upwelling cells for feeding and spawning, increasing egg and larval cannibalism and predation, and anchovy catchability (Alheit & Niquen 2004; Chavez et al. 2008). The example shows how small pelagic fish such as sardine and anchovy respond dramatically and quickly to changes in ocean climate, causing dramatic changes in abundance over a few decades. A number of seabird species (e.g. Salvin's *Thalassarche salvini* (Rothschild, 1893), and black-browed albatrosses, southern fulmars, white-chinned and pintado (Cape) petrels *Daption capense* (Linnaeus, 1758), Wilson's storm-petrels *Oceanites oceanicus* (Kuhl, 1820) and thin-billed prions) moves into the LME mostly from the Antarctic and Sub-Antarctic, appearing during winter and then remaining in colder, less saline waters (Spear & Ainley 2008). On a smaller spatial scale, a major upwelling area with low SST in the southern part of the Coquimbo area in northern Chile attracted Juan Fernandez petrels, Antarctic prions *Pachyptila desolata* (Gmelin, 1789), and white-chinned petrels (Weichler et al. 2004). Likewise, cold-water areas in the Galápagos Archipelago attracted a number of seabirds, such as storm petrels and boobies (Hayes & Baker 1989). Given these preferences for cold-water areas, interannual variability in ocean climate would affect the offshore distribution and abundance of seabirds in the LME.

In summary, Humboldt Current seabird work has mainly concentrated on the impact of extreme El Niño events, while systematic long-term data sets on seabird demographics in the Humboldt Current are lacking. It has been pointed out that by concentrating efforts only on El Niño years (e.g. 12 years during the last century: Jaksik & Fariña 2010), we are missing the information of the 'normal' years, which is essential for understanding not only the responses of birds during the ENSO cycle, but also the influence of the warm and cold temperature anomalies on the decadal scale.

Patagonian Shelf LME

The waters of the Patagonian Shelf, one of the widest shelves in the world, support a highly productive marine ecosystem ($>$ 300 gC/m^2-yr based on SeaWiFS global primary production estimates, e.g. Carranza et al. 2008; Sherman & Hempel 2009). The Patagonian Shelf extends from Tierra del Fuego in the south to the Rio de la Plata River in the north, encompassing the Atlantic coast of Argentina, and large islands in the south (Staten Island, Falkland/Malvinas Islands; e.g. Glorioso 2002; Piola 2008). In the southern part of the Patagonian Shelf, high primary production is supported by upwelling of cold Antarctic waters. The cold, northward Falkland/Malvinas Current extends along the Patagonian Shelf break and provides an ecological border to the east. The northern part of the Patagonian Shelf is dominated by the subtropical, southward Brazil Current, which is higher in temperature and salinity and supports lower productivity (e.g. Stramma 1989; Piola 2008). Where the two currents meet, they form an extensive and highly productive confluence zone (e.g. Gordon 1989; Peterson & Stramma 1991; Seeliger et al. 1991), which is also influenced by the outflow of the Rio de la Plata River, the second largest drainage in South America. In addition to these boundary currents, the extent of the Patagonian Shelf allows for the development of a great diversity of mesoscale fronts (Acha et al. 2004), including a number of year-round and seasonal tidal fronts, such as the Bahía Grande Front and the Valdés Front. These fronts play a paramount role in ecological processes, allowing for high biological production, offering feeding and/or reproductive habitats for fishes, squids, and birds (Acha et al. 2004; Orgeira 2001).

Argentine anchovy (*Engraulis anchoita* Hubbs & Marini in Marini, 1935) is the main pelagic species in the northern Patagonian shelf LME and the preferred food of many seabirds from southern Brazil to Patagonia (e.g. Skewgar et al. 2003). The Patagonian stock spawns during late spring and summer in association with tidal frontal systems. The annual anchovy larval density off Patagonia depends on the formation of these systems, and varies interannually by an order of magnitude (Pájaro et al. 2009). Further south, squid share the ecological niche of epipelagic fish on the Falkland Shelf and Slope (Laptikhovsky et al. 2010). The hyperiid amphipod *Themisto gaudichaudii* Guérin-Méneville, 1825 is a crucial food item for many of the fish and squid species distributed in the region (e.g. Padovani et al. 2012) and thus, along with the Chilean sprat (*Sprattus fuegensis* (Jenyns, 1842)), it is another key species in the trophic dynamics of Austral Patagonia (Sabatini & Álvarez-Colombo 2001).

Due to the complex oceanography, the biological diversity of the Patagonian shelf LME is high, with cold- and warm-water adapted species. Characteristic breeding seabirds (Figure 3) thus include (Sub-)Antarctic species such as black-browed

Figure 3. Patagonian Shelf LME seabirds. Upper row left to right: imperial shag, gentoo penguin, dolphin gull, southern rockhopper penguin. Second row: breeding sites on cliffs (left, New Island) and beaches (right, Península Valdéz). Third row: mixed breeding colonies (here, southern rockhopper penguins, black-browed albatrosses and imperial shags). Lower row left to right: Falkland skua, Magellanic penguin, black-browed albatross, thin-billed prion. Falkland Islands/Islas Malvinas and Península Valdéz. Photographer: Petra Quillfeldt.

albatross, imperial shags (*Phalacrocorax atriceps* King, 1828), Wilson's storm-petrels, southern rockhopper penguins (*Eudyptes chrysocome* (Forster, 1781)) and gentoo penguins (*Pygoscelis papua* (Forster, 1781)), temperate species such as Magellanic penguins (*Spheniscus magellanicus* (Forster, 1781)), dolphin gulls (*Larus scoresbii* Traill, 1823) and rock shags *Phalacrocorax magellanicus* (Gmelin, 1789)) (e.g. Croxall et al. 1984; Yorio 2000). Penguin populations are especially important, an order of magnitude larger than the rest on the coasts of Argentina (Yorio et al. 1999), but many populations have declined in the last decades both in Argentina (Boersma 2008) and in the Falkland/Malvinas Islands (Pütz et al. 2003). At the same time, some actually show an increase and the breeding range is expanding to the north, suggesting that these regional differences potentially depend on oceanographic–climatic factors.

Petrels also breed in large numbers, especially in the Falkland/Malvinas Islands. Of five regularly observed albatross species, only the black-browed albatross breeds in the area and is resident year-round. The Patagonian shelf LME further offers important foraging areas for seabirds breeding at adjacent island groups such as South Georgia in the Atlantic and Diego Ramirez in Chile (e.g. wandering albatross, grey-headed albatross *Thalassarche chrysostoma* (Forster, 1785), light-mantled albatross *Phoebetria palpebrata* (Forster, 1785) and white-chinned petrels: Croxall & Wood 2002). Birds from more distant island groups, e.g. Tristan da Cunha and Gough, also feed in Patagonian shelf waters during both breeding and non-breeding seasons (Croxall & Wood 2002). Further wintering seabirds include southern fulmars and Cape petrels from Antarctic and Sub-Antarctic breeding sites and northern royal albatross (*Diomedea sanfordi* Murphy, 1917) from New Zealand, while other species such as Wilson's storm petrels and great shearwater (*Puffinus gravis* (O'Reilly, 1818)) use it as a staging ground on migration. Even birds of the Northern Hemisphere winter here, such as Arctic terns (*Sterna paradisaea* Pontoppidan, 1763), Manx shearwaters (*Puffinus puffinus* (Brünnich, 1764)), Cory's shearwaters (*Calonectris borealis* (Cory, 1881)) and several Arctic skuas/jaegers (Favero & Silva-Rodríguez 2005).

The southern Patagonian Shelf waters are dominated by strong westerly winds. Wind-driven cold-water current systems such as the Falkland/Malvinas Current are strongly affected by climate forcing. For example, ENSO-mediated SSTAs generated in the Pacific propagate to the Southwest Atlantic with a lag of 2–3 years via the Antarctic Circumpolar Current (Waluda et al. 1999); furthermore, the Antarctic Oscillation, i.e. fluctuations in the strength of the circumpolar vortex, may also have an influence (Silvestri & Vera 2003).

SSTAs have been shown to influence seabirds in the Sub-Antarctic Falkland/Malvinas Islands. SST anomalies were negatively correlated with provisioning rates and chick growth in thin-billed prions (Quillfeldt et al. 2007, 2010b) and showed a quadratic relationship with southern rockhopper penguin survival rates (Dehnhard et al. in press). Winters that are colder than the current average provide optimal oceanographic conditions, where southern rockhopper penguins were able to find enough food to survive and prepare for the following breeding season (Raya-Rey et al. 2007). A study of the influence of SST on gentoo penguin numbers indicated a non-linear response and differences among areas (Baylis et al. 2012). This might reflect the differences in trophic level and foraging ecology, but also in the timescale of measurements taken. Gentoo penguins mainly feed on fish and squid that occur close to their breeding sites (e.g. Masello et al. 2010), and the abundance of their prey is influenced by environmental variability (Waluda et al. 1999, 2004), which may vary locally across the archipelago. In contrast, thin-billed prions and rockhopper penguins feed on zooplankton and range widely over the Patagonian Shelf and, in the case of the prions, into the Drake Passage to the south. Thus, they are able to buffer the adverse effects of poor food availability with lower provisioning and growth rates. Moreover, due to flexible growth rates the chick survival to fledging is not necessarily affected by poor conditions (Quillfeldt et al. 2007), and thus any effect on numbers of breeding birds would depend mainly on the survival rate of fledglings and might not be apparent for several years.

Some evidence suggests that seabirds of the central and northern Patagonian Shelf are also influenced by climate change. The largest Magellanic penguin colony is located in temperate waters, at Punta Tombo, Argentina. The breeding population here declined in the last decades (Boersma 2008). In the 1980s and 1990s, petroleum pollution was a major source of Patagonian penguin mortality, but even though this is now less important, the decline continues. Climate-driven factors may now become more important. On one hand, high mortality here was observed in years with severe rains, as many chicks die during flooding of nesting burrows (Boersma 2008). The area experiences increased rain during El Niño years (e.g. Ropelewski & Halpert 1987; Holmgren et al. 2001; Andreoli & Kayano 2005). On the other hand, longer foraging trips during incubation more than a decade ago indicate reductions in prey abundance closer to the colony (Boersma 2008). This may be due to shifts in prey location or a general reduction in productivity in response to climate change, but also due to commercial fishing. These causal relationships still need to be better understood.

As in Argentina, severe weather can also impact seabird colonies in the Falkland/Malvinas Islands. Storms with severe rain caused breeding failures affecting southern rockhopper penguins, imperial shags and black-browed albatross at New Island in January 2008 (Demongin et al. 2010), and black-browed albatross and southern rockhopper penguins at Steeple Jason and Beauchêne islands in December 2010 (Crofts et al. 2011). For example, the breeding success of black-browed albatrosses at Steeple Jason fluctuated between 40.5% in 2005 and 62% in 2009 and decreased to 20% in 2010 due to the impacts of the storm, while southern rockhopper penguins at Steeple Jason failed completely (Crofts et al. 2011). With a predicted increase in storm events and precipitation due to climate change (e.g. Wentz et al. 2007; D'Onofrio et al. 2008), an increase in frequency of these impacts and the cumulative effects of other threats is possible.

Historical changes in at-sea distribution provide another line of evidence for climate change effects acting in this area. In winter, most thin-billed prions breeding at the Falkland/Malvinas Islands move towards more polar waters (Quillfeldt et al. 2008). Carbon stable isotope ratios in recent and historical feather samples indicated that poleward winter movements of thin-billed prions were less common historically (45% in 1913–1915) and have only recently become dominant (92% in 2003–2005), apparently in response to warming sea temperatures and less favourable conditions over the Patagonian Shelf (Quillfeldt et al. 2010a).

Thus, the most relevant datasets on seabird responses to climate in the Patagonian Shelf LME come from thin-billed prions and gentoo penguins of the Falkland/Malvinas Islands and from Magellanic penguins in Argentina. Although the Patagonian Shelf experienced only a slight gradual warming during the last 50 years (Table I), the seabird data collectively suggest significant changes in the food base for top-predators of the Patagonian Shelf LME. These have so far mainly been interpreted as a consequence of top-down effects due to commercial fisheries (e.g. Foro para la Conservación del Mar Patagónico y Áreas de Influencia 2008).

However, several papers suggested changes of the low atmospheric circulation in the Southwest Atlantic during recent decades, such as a poleward shift of 3° in the maximum wind zone associated with the circumpolar westerlies during the period 1976–1991 (Gibson 1992) and an increase in wave height (Dragani et al. 2010). Strengthening of the circumpolar westerlies and their poleward movement during the past 50 years has been shown to favour wandering albatrosses in the Sub-Antarctic Indian Ocean (Weimerskirch et al. 2012), while their impact on seabirds in the southwest Atlantic merits attention. Also, an increase in primary productivity has

Table I. Overview of the oceanographic characteristics of the LMEs (as in Abstract) treated in detail in this review.

LME	Geographic position	Key oceanographic characteristics	Surface area (million km^2)	Protection (%)	Productivity	Sea surface temperature trend (warming since 1957; 1982)[1]
Humboldt Current LME	West coast of Chile (55°S) to Peru (5°S)	World's largest coastal upwelling system, intense wind-induced upwelling cells result in productive cold water masses	2.5	0.1	Moderate (150–300 gC/m^2-yr)	Variable: 0.41°C, −0.10°C
Patagonian Shelf LME	Coast of Argentina to Uruguay (34°S)	wide, shallow shelf, with mesoscale tidal mixing fronts (e.g. Valdéz f., Bahía Grande f.) and boundary currents (Brazil C., Malvinas/Falkland C.), influence of Sub-Antarctic and estuarine waters	1.2	0.18	Moderate (150–300 gC/m^2-yr)	Very gradual warming: 0.15°C, −0.08°C
South Brazil Shelf LME	From central Brazil (22°S) to Uruguay (34°S)	Wide (up to 220 km) Shelf, 3 parts: a. Southern Shelf influenced by estuarine outflows, most productive in summer b. South Brazil Bight (seasonal upwellings and cold intrusions) c. Eastern slope (mesoscale eddies, fronts best defined April to September)	0.6	1.7	Moderate (150–300 gC/m^2-yr)	Moderate warming: 1.12°C, 0.53°C

[1] Linear SST trend since 1957 and 1982 (Sherman & Hempel 2009).

been suggested for the Patagonian Shelf (Gregg et al. 2005), which may be attributed, at least in part, to high nutrient input from glacial flour (as Patagonian glaciers undergo melting: Rignot et al. 2003) and wind-driven land degradation processes (e.g. del Valle et al. 2010) following the clearance of natural vegetation in Northeastern Patagonia (Pezzola et al. 2004). Differences in primary productivity can change the zooplankton distribution, as can temperature changes (Spinelli 2012), for example by an influence on the relative abundance of copepods and appendicularians. In one reported instance, massive blooms of gelatinous zooplankton occurred when the water temperature rose by 2°C, rendering the tidal fronts off Patagonia less prominent and depressing copepod populations (Sabatini & Martos 2002). Much work remains to be done in order to understand bottom-up effects in this ecosystem, and put them into perspective with top-down effects due to the massive fisheries.

South Brazil Shelf LME

The South Brazil Shelf LME extends from central Brazil (22°S) to Uruguay (34°S, Figure 1), and has a wide shelf, extending up to 220 km (Sherman & Hempel 2009). The oceanography of the South Brazil Shelf LME is complex. It is influenced by the oligotrophic, southward-flowing Brazil Current, by two sources of nutrient-rich Sub-Antarctic water (the Falkland/Malvinas Current and the South Atlantic Central Water) and by estuarine outflows.

Seasonal variability in the southern part of the LME depends on seasonal migration of the Brazil–Malvinas Confluence region. This confluence, also termed the Subtropical Convergence, shows a typical northern limit around 30°S in winter (reaching the South Brazil Shelf LME) and 46°S in summer (in the Patagonian Shelf LME: Ciotti et al. 1995). The Sub-Antarctic waters and northward extensions of the La Plata River plume cause peaks in chlorophyll and primary production in winter (August–September) in the southern part of the South Brazil Shelf LME (Garcia et al. 2004). However, another source of productivity acts in the austral summer, as the shelf edge and wind-driven upwellings of nutrient-rich waters are intensified by the trade winds, and the overall productivity in the LME is thus higher in summer.

Furthermore, large coastal lagoons and wetlands such as the Patos/Mirim Lagoon system support a very rich biodiversity, and the freshwater outflow is an important source of nutrients for the shelf waters (Ciotti et al. 1995).

This LME provides important reproduction and feeding grounds for pelagic and demersal fish, marine turtles, cetaceans and seabirds (Neves et al. 2006). The seasonally high productivity results in a considerable biomass of potential seabird prey (for, e.g. common tern *Sterna hirundo* Linnaeus, 1758: Bugoni & Vooren 2004), such as small pelagic fish, especially orangespot sardine (*Sardinella brasiliensis* (Steindachner, 1879)) and anchovy, pelagic juvenile stages of demersal fish species and flying fish *Cypselurus* sp. (for, e.g. Cory's shearwater: Bugoni et al. 2010). The slope, between 400 and 900 m deep, harbours vast and continuous deep-sea coral reefs. The region is also home to more than 30 species of cephalopods (Haimovici & Perez 1991), which are important in seabird diet (e.g. Magellanic penguins: Fonseca et al. 2001; Pinto et al. 2007; Baldassin et al. 2010; albatrosses and shearwaters: Santos & Haimovici 2002; Petry et al. 2007, 2008, 2009; southern fulmar: Fonseca & Petry 2007; southern giant petrels (*Macronectes giganteus* (Gmelin, 1789)): Petry et al. 2010). Migratory species such as Argentine shortfin squid (*Illex argentinus* (Castellanos, 1960)) use the South Brazil Shelf as a spawning and nursery ground in winter (June–September), while spending the summer in the colder waters of the Patagonian Shelf (Perez et al. 2009), utilizing the Brazil and Falkland/Malvinas Currents for long-distance transport.

Breeding seabirds on coastal islands and sandy beaches (Figure 4; Antas 1991) include brown boobies (*Sula leucogaster* (Boddaert, 1783)), neotropic cormorants, magnificent frigatebirds (*Fregata magnificens* Mathews, 1914), kelp gulls (*Larus dominicanus* Lichtenstein, 1823), brown-hooded gulls (*L. maculipennis* Lichtenstein, 1823), snowy-crowned tern (*Sterna trudeaui* Audubon, 1838), South American terns (*S. hirundinacea* Lesson, 1831), Cabbot's tern (*Thalasseus acuflavidus* (Cabot 1847)) and royal tern (*Thalasseus maximus* (Boddaert, 1783)).

Although Procellariiformes do not breed in the South Brazil Shelf LME, the region provides important foraging grounds for Procellariiformes such as wandering albatross, Tristan albatross (*Diomedea dabbenena* Mathews, 1929), black-browed albatross, northern royal albatross, southern royal albatross (*D. epomophora* Lesson, 1825) and shy-type albatross (*Thalassarche cauta/steadi*), Atlantic yellow-nosed albatross (*T. chlororhynchos* (Gmelin, 1789)), spectacled petrel (*Procellaria conspicillata* Gould, 1844), white-chinned petrel, Cape petrel, southern fulmars, great shearwaters, sooty shearwater, Manx shearwaters, Cory's shearwaters and Wilson's storm petrels (e.g. Neves et al. 2006; Bugoni et al. 2008b). Ring recoveries have indicated that seabirds reach the area for the non-breeding season from places such as the British Isles, Iceland, Finland and North

Figure 4. South Brazil Shelf LME seabirds: spectacled petrel (upper left), juvenile black-browed albatross (upper right), Atlantic yellow-nosed albatross (lower left) and a mixed group of royal terns, Cabbot's tern, and snowy-crowned tern in breeding plumage, with non-breeding South American terns (lower right). Photographer: Leandro Bugoni.

America in the Northern Hemisphere, as well as from southern breeding sites such as New Zealand, South Georgia, South Orkneys and Tristan da Cunha (Olmos 2002). Magellanic penguins migrate north from their breeding sites in Patagonia, many of them reaching up to Uruguay and Brazil (Boersma et al. 1990), which is also important for juveniles (García-Borboroglu et al. 2006). Olrog's Gull (*Larus atlanticus* Olrog, 1958), royal and Cabbot's terns also migrate north, reaching the coasts of Uruguay and even Brazil (Escalante 1984; Collar et al. 1992; Bugoni & Vooren 2005).

The variability of phytoplankton biomass in the South Brazil Shelf LME has been related to the seasonal latitudinal displacement of the Subtropical Convergence and to the freshwater outflow of La Plata River and Patos Lagoon. As the amount of chlorophyll in shelf waters is related to nutrients supplied by the freshwater outflow, strong inter-annual variability in line with the ENSO conditions is observed (Ciotti et al. 1995; Garcia & Garcia 2008), due to the relationship between precipitation rates in southern Brazil and the ENSO cycle (e.g. Ropelewski & Halpert 1987; Kane 2002; Grimm & Tedeschi 2009). Warm episodes of ENSO in the Pacific cause abundant rainfall in southern Brazil, Uruguay and northeastern Argentina, mainly due to an increased frequency of extreme rainfall events (e.g. Ropelewski & Halpert 1987, 1989; Grimm & Tedeschi 2009). Thus, in El Niño years, the freshwater outflow is greater and the productivity is enhanced. For example, the high precipitation in the El Niño spring 1977 resulted in nutrient-rich Coastal Water (i.e. the waters formed by freshwater outflow) extending over the entire shelf from Uruguay at 36°S to north of Rio Grande at 32°S, and in the El Niño spring 1987, Coastal Water occupied a large extension over the shelf reaching 130 km offshore near 33°S, compared with only 20–30 km in 1988 (Ciotti et al. 1995). Apart from nutrient input by freshwater, the El Niño events influence wind patterns. Cold (warm) SST anomalies in the tropical Pacific Ocean are associated with an intensification of the southeasterlies (northwesterlies) over the Rio de la Plata Estuary (Simionato et al. 2005). Thus, ENSO events have an important impact on the variability of phytoplankton production in the southern Brazilian coastal areas, and the magnitude of the

La Plata impact on the southern Brazil Shelf (north of the river mouth) can show high interannual variations, depending on the combined (sometimes opposing) effects of both alongshore wind stress and magnitude of river discharge (Garcia & Garcia 2008).

Variability is also caused by differences in the prominence of Sub-Antarctic waters. For example, onshore (southeasterly) winds can cause a greater dominance of Sub-Antarctic waters over the shelf. On the other hand, northwesterly offshore winds and consequent offshore transport following periods of high precipitation during El Niño conditions can cause upwelling of deeper waters, rich in nutrients, to the euphotic zone on the mid shelf (Ciotti et al. 1995). Cold SST anomalies may be related to ENSO events (Lentini et al. 2001). In particular, anomalous cold (warm) waters occur via northward-propagating anomalies generally in every warm (cold) ENSO + 1 year in the present climatology (Lentini et al. 2001). These events can radically change the local ecosystem dynamics. For instance, recruitment failures of the Brazilian sardine may be linked to the occurrence of cold or warm SST anomalies (Lentini et al. 2001).

Furthermore, with freshwater and SST, an increase in red tide occurrences with climate change (e.g. Edwards et al. 2006) might be relevant for seabirds. Dinoflagellate dominance causing red tides (harmful algal blooms) is a recurring phenomenon along the southern Brazilian and Uruguayan coasts that seems to be related to the oceanographic conditions offshore. In 1993, massive mortality of intertidal benthic fauna was related to the accumulation of dinoflagellates in the surf zone, due to the action of onshore winds (Odebrecht et al. 1995).

Despite a rich literature on environmental variability in the region, there are very few studies on the responses of seabirds to environmental conditions in this LME. Different habitat preferences were found in two closely related *Procellaria* petrels (Bugoni et al. 2009). While spectacled petrels prefer warm, offshore and mesotrophic or oligotrophic waters of the southwest Atlantic Ocean, coastal cold and productive waters are used extensively by wintering white-chinned petrels (Phillips et al. 2006), but were avoided by spectacled petrels (Bugoni et al. 2009). Studies such as this should be followed up over several years to link with environmental variability and, more importantly, with global climate change.

Mäder et al. (2010) observed that the years with highest numbers of carcasses of Magellanic penguins washed up on southern Brazilian coasts were years of outstanding ocean climate, with either 'El Niño' or 'La Niña' phenomena. Together with oiling, the ENSO index explained 35% of the annual variation in Magellanic penguin mortality. Mäder et al. (2010) propose two possible mechanisms: an increase in storms, or poor food availability. Penguin carcasses appear on Brazilian beaches after strong storms. Studies suggest that storms may be coupled to ENSO and increases in frequency in the area (e.g. Escobar et al. 2004; D'Onofrio et al. 2008). In March 2004 the first ever reported hurricane in the South Atlantic hit southern Brazil and displaced Atlantic petrels (*Pterodroma incerta* (Schlegel, 1863)) inland, up to 420 km from the coast and 1100 m above sea level (Bugoni et al. 2007). On the other hand, poor food availability for the penguins may be the result of current displacement, in particular in conditions when the warm and oligotrophic waters of the Brazil Current prevail at the southern Brazilian coasts and displace the colder Falkland/Malvinas waters southwards (Mäder et al. 2010).

In summary, it seems crucial to study the interannual variability in seabird abundance in this globally important wintering area, ideally in connection with studies using dataloggers to follow individual birds. Due to the very different requirements of the species, any effects of climate change on seabirds in the South Brazil LME would be expected to affect birds with cold-water preference differently to those with a warm-water preference.

Summary and research priorities

Overall, seabird responses to climatic variability suggest that many seabirds will be vulnerable to at least some of the environmental changes affecting South American waters due to anthropogenic climate change (Table II). While several studies have considered the effects of global climatic cycles, like ENSO, on seabird populations in South America, only a few long-term studies have investigated the effects of global warming in South American seabirds. Seabird conservationists have not seen climate change as the most immediate threat, and uncertainties in future climates and their consequences are high in marine environments. Enough is known, however, to suggest that the impacts could be severe. Accordingly, a comprehensive review on seabird conservation concludes that enhanced research is desirable on the potential effects on seabirds of climate change (e.g. Croxall et al. 2012). In particular, the authors emphasized a need to identify the seabird species and populations that are likely to be most susceptible to sea-level rise as a more immediate threat, and pointed out that a better understanding of the effects of major shifts in ocean conditions on seabirds might assist in developing management actions (e.g. Croxall et al. 2012).

Long-term monitoring is needed to understand these connections between climate and the population

Table II. Overview of the seabird associations, proposed climatic trends and seabirds' responses of the LME treated in detail in this review. The number of seabird species correspond to species whose distribution at sea overlaps with each Large Marine Ecosystem, as given by Croxall et al. (2012, supplement, table S3).

LME	Number of seabird species and examples	Climatic factors that may influence seabirds	Evidence for climatic influences
Humboldt Current LME	105 species Breeding/resident: Humboldt penguin, sooty shearwater, wedge-rumped storm-petrel, Elliot's storm petrel, Markham's storm petrel, Peruvian diving petrel, Peruvian pelican, Peruvian booby, guanay cormorant, Peruvian tern, Inca tern, band-tailed gull, grey gull Non-breeding/wintering: black-browed albatross, Salvin's albatross, white-chinned petrel, Juan Fernandez petrel, thin-billed prion, blue-footed booby, red phalarope, Franklin's gull	Strong seasonal, interannual and longer-term variability, periodic occurrence of ENSO, leading to very variable productivity Models forecast reduced Eastern Pacific ENSO activity, in line with recent cooling trend	Seabird breeding failures and emigration during strong El Niño events well documented, otherwise climate influences little known
Patagonian Shelf LME	73 species Breeding/resident: black-browed albatross, Wilson's storm petrel, thin-billed prion, common diving petrel, Magellanic diving petrel, southern rockhopper penguin, gentoo penguin, Magellanic penguin, kelp gull, imperial shag, rock shag, dolphin gull, South American tern Non-breeding/wintering: wandering albatross, grey-headed albatross, light-mantled albatross, white-chinned petrel, Wilson's storm petrel, great shearwater, Manx shearwater, Cory's shearwater, Arctic tern	No clear trends proposed, possibly LME is affected by a poleward shift in the maximum wind zone associated with the circumpolar westerlies and an increase in productivity	SST anomalies affect seabird provisioning (e.g. thin-billed prion) and survival (rockhopper penguin, gentoo penguin) Severe rains frequently cause breeding failures (Magellanic penguin, southern rockhopper penguin, black-browed albatross)
South Brazil Shelf LME	51 species Breeding/resident: brown booby, neotropic cormorant, magnificent frigatebird, kelp gull, brown-hooded gull, snowy-crowned tern, South American tern, Cabbot's tern, royal tern Non-breeding/wintering: wandering albatross, Tristan albatross, black-browed albatross, northern royal albatross, southern royal albatross, shy-type albatross, Atlantic yellow-nosed albatross, spectacled petrel, white-chinned petrel, Cape petrel, southern fulmar, great shearwater, sooty shearwater, Manx shearwater, Cory's shearwater, Wilson's storm petrel, Magellanic Penguin	Southern Shelf: in El Niño years, the freshwater outflow is greater and the productivity is enhanced South Brazil Bight and Eastern slope: stronger upwelling in El Niño years, resulting in more productive Sub-Antarctic water	Climate influences little known, few case studies: e.g., ENSO anomalies related to Magellanic penguin mortality

dynamics of seabirds. Long-term studies with individually known animals would be particularly desirable, as they allow for detecting and understanding the temporal trends in life-history traits and to estimate the inheritability of life-history traits (e.g. Visser 2008). Although long-term data sets only exist for a few species and sites around South America, hopefully more data sets from previous multi-year research and data from reports can be compiled. A retrospective analysis of guanay cormorant and Peruvian booby population numbers (Jahncke et al. 2004) shows that such data, combined with data from fisheries landings and environmental proxies, can be used to reconstruct the mechanisms governing seabird dynamics. About 94% of the variation in seabird numbers from 1925 to 2000 were explained by two factors governing primary production in the Humboldt upwelling system, namely wind stress and sea-surface temperature, and the competitive effect of the fishery that limits prey availability (Jahncke et al. 2004).

Our understanding of the processes would also benefit from more coordinated research efforts. For example, Peruvian boobies have been studied in Peru (Jahncke et al. 1997; Jahncke & Goya 1997, 2000; Zavalaga et al. 2010) where their distribution at sea is strongly correlated with the distribution of their near-exclusive prey, anchovies (Jahncke et al. 1998). In northern Chile, in contrast, the diet has been found to be more variable (Ludynia et al. 2010), but it remains unclear whether the observed differences reflect differences among years or sites.

Some previous studies also have shown a great potential to reflect environmental variability. For example, a study of the weight of dark-rumped petrel (*Pterodroma phaeopygia* (Salvin, 1876)) chicks in the Galapagos Archipelago has been conducted in 1981–1985, showing high variability (e.g. at age 45 days chicks weighed 290 ± 69 g during the 1983 El Niño, compared with 415 ± 52 g in 1981, 1984 and 1985: Ainley et al. 1988). Studies such as this should be continued in combination with modern biotelemetry methods, such as miniature GPS and geolocation loggers to follow the at-sea distribution and with diet analyses.

The challenge is further to join forces with marine biologists working on lower trophic levels and increase joint systematic sampling efforts, in order to detect functional links between seabird and prey dynamics and distribution. For example, climate change can lead to decoupling of phenological relationships (also termed match–mismatch: Cushing 1990), with important ramifications for trophic interactions, including altered food-web structures and eventually ecosystem-level changes (e.g. Edwards & Richardson 2004). A climate-forced seasonal mismatch between the hatching of seabird chicks and the availability of prey has been detected in zooplanktivorous and piscivorous auks (Hipfner 2008; Watanuki et al. 2009).

Thus, measurements on lower trophic levels and on the mechanisms underlying phenotypic plasticity are needed to predict the rate of microevolution of seabirds under changing conditions. As in seabirds, climate change responses at lower trophic levels, such as poleward range shifts of planktonic organisms and changes in timing of peak biomass, have been particularly well documented off the coasts of western North America and the UK (e.g. Beaugrand et al. 2002; deYoung et al. 2004; Richardson & Schoeman 2004; Hays et al. 2005). Over 90 years, the timing of annual migration of squid and fish followed decadal trends in ocean temperature, being later in cool decades and up to 1–2 months earlier in warm years (Southward et al. 2005). Some copepod communities have shifted as much as 1000 km northward (Beaugrand et al. 2002). Seabird species with a rather fixed timing of breeding or prey choice would be expected to experience such decoupling from the peaks of food availability. The combined impact of bottom-up effects due to climate change and top-down effects due to fisheries further merits attention. On the other hand, as dataloggers become ever smaller, seabird-deployed dataloggers might be used to supplement the study of marine environmental variables (e.g. Wilson et al. 2002, 2007).

In an advanced stage, these data can be combined with future climate scenarios for marine habitats. Thus, species distribution models (i.e. spatially explicit habitat modelling applied to data obtained from biotelemetry) based on current ecological niche constraints can be used to project future species distributions and predict seabird responses to top-down and bottom-up food web changes. Such models would ideally be refined with data on phenotypic plasticity within seabird spatial responses to climate change (e.g. Grémillet & Boulinier 2009; Lescroël et al. 2010).

More detailed information on the responses of seabirds to climate variability and climate change will finally enable wildlife managers to plan measures for assisting seabirds to adapt to climate change (e.g. Chambers et al. 2011), for example by informed decisions to define marine protected areas and to regulate fisheries (e.g. Grémillet & Boulinier 2009).

Acknowledgements

PQ was supported by grants provided by the Deutsche Forschungsgemeinschaft DFG (Qu 148/1ff). We would like to thank the editors and three anonymous referees for helpful comments on the manuscript.

References

Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava J. 2004. Marine fronts at the continental shelves of austral South America: Physical and ecological processes. Journal of Marine Systems 44:83–105.

Aebischer NJ, Coulson JC, Colebrook JM. 1990. Parallel long-term trends across four marine trophic levels and weather. Nature 347:753–55.

Ainley D, Russell J, Jenouvrier S, Woehler E, Lyver PO, Fraser WR, et al. 2010. Antarctic penguin response to habitat change as Earth's troposphere reaches 2°C above preindustrial levels. Ecological Monographs 80:49–66.

Ainley DG, Carter HR, Anderson DW, Briggs KT, Coulter MC, Cruz F, et al. 1988. Effects of the 1982–83 El Niño–Southern Oscillation on Pacific Ocean bird populations. Proceedings of the International Ornithological Congress 19:1747–58.

Ainley DG, Hyrenbach KD. 2010. Top-down and bottom-up factors affecting seabird population trends in the California Current system (1985–2006). Progress in Oceanography 84:242–54.

Ainley DG, Spear LB, Tynan CT, Barth JA, Pierce SD, Ford RG, et al. 2005. Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. Deep-Sea Research II 52:123–43.

Ainley DG, Sydeman WJ, Norton J. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California current food web. Marine Ecology Progress Series 118:69–79.

Alheit J, Niquen M. 2004. Regime shifts in the Humboldt Current ecosystem. Progress in Oceanography 60:201–22.

Ancona S, Sánchez-Colon S, Rodríguez C, Drummond H. 2011. El Niño in the warm tropics: Local sea temperature predicts breeding parameters and growth of blue-footed boobies. Journal of Animal Ecology 80:799–808.

Anderson DJ. 1989. Differential responses of boobies and other seabirds in the Galápagos to the 1986–87 El Niño-Southern Oscillation event. Marine Ecology Progress Series 52:209–16.

Andreoli R, Kayano M. 2005. ENSO-related rainfall anomalies in South America and associated circulation features during warm and cold Pacific Decadal oscillation regimes. International Journal of Climatology 25:2017–30.

Antas PTZ. 1991. Status and conservation of seabirds breeding in Brazilian waters. In: Croxall JP, editor. Seabird Status and Conservation: A Supplement. International Council for Bird Preservation. Norwich: Page Bros., p 141–58.

Arntz WE, Fahrbach E. 1991. El Niño – Klimaexperiment der Natur. Basel, Switzerland: Birkhäuser Verlag. 264 pages.

Ashok K, Yamagata T. 2009. The El Niño with a difference. Nature 461:481–84.

Baldassin P, Santos RA, Cunha JMM, Werneck MR, Gallo H. 2010. Cephalopods in the diet of Magellanic penguins *Spheniscus magellanicus* found on the coast of Brazil. Marine Ornithology 38:55–57.

Barber RT, Chavez FP. 1983. Biological consequences of El Niño. Science 222:1203–10.

Barbraud C, Weimerskirch H. 2006. Antarctic birds breed later in response to climate change. Proceedings of the National Academy of Sciences of the United States of America 103:6248–51.

Baylis AMM, Zuur AF, Brickle P, Pistorius PA. 2012. Climate as a driver of population variability in breeding Gentoo penguins *Pygoscelis papua* at the Falkland Islands. Ibis 154:30–41.

Beaugrand G, Reid PC, Ibanez F, Lindley JA, Edwards M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296:1692–94.

Behrenfeld MJ, O'Malley R, Siegel DA, McClain CR, Sarmiento JL, Feldman GC, et al. 2006. Climate-driven trends in contemporary ocean productivity. Nature 444:752–55.

Boersma PD. 1978. Breeding patterns of Galapagos penguins as an indicator of oceanographic conditions. Science 200: 1481–83.

Boersma PD. 1998. Population trends of the Galapagos penguin: impacts of El Niño and La Niña. Condor 100:245–53.

Boersma PD. 2008. Penguins as marine sentinels. Bioscience 58:597–607.

Boersma PD, Stokes DL, Yorio P. 1990. Reproductive variability and historical change of Magellanic penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. In: Davis L, Darby J, editors. Biology of Penguins. NY: Macmillan, p 15–43.

Bugoni L, D'Alba L, Furness RW. 2009. Marine habitat use of wintering spectacled petrels *Procellaria conspicillata* and overlap with longline fishery. Marine Ecology Progress Series 374: 273–85.

Bugoni L, Mancini PL, Monteiro DS, Nascimento L, Neves TS. 2008a. Seabird bycatch in the Brazilian pelagic longline fishery and a review of capture rates in the southwestern Atlantic Ocean. Endangered Species Research 5:137–47.

Bugoni L, McGill RAR, Furness RW. 2010. The importance of pelagic longline fishery discards for a seabird community determined through stable isotope analysis. Journal of Experimental Marine Biology and Ecology 391:190–200.

Bugoni L, Neves TS, Peppes FV, Furness RW. 2008b. An effective method for trapping scavenging seabirds at sea. Journal of Field Ornithology 79:308–13.

Bugoni L, Sander M, Costa ES. 2007. Effects of the first southern Atlantic hurricane on Atlantic petrels (*Pterodroma incerta*). Wilson Journal of Ornithology 119:725–29.

Bugoni L, Vooren CM. 2004. Feeding ecology of the common tern *Sterna hirundo* in a wintering area in southern Brazil. Ibis 146:438–53.

Bugoni L, Vooren CM. 2005. Distribution and abundance of six tern species in southern Brazil. Waterbirds 28:110–19.

Cahuin S, Cubillos L, Ñiquen M, Escribano R. 2009. Climatic regimes and the recruitment rate of anchoveta, *Engraulis ringens*, off Peru. Estuarine, Coastal and Shelf Science 84: 591–97.

Cane MA. 2005. The evolution of El Niño, past and future. Earth and Planetary Science Letters 230:227–40.

Cardoso LG, Bugoni L, Mancini P, Haimovici M. 2011. Gillnet fisheries as major mortality factor of Magellanic penguins in wintering areas. Marine Pollution Bulletin 62:840–44.

Carranza MM, Romero SI, Piola AR. 2008. Concentración de clorofila. In: Foro para la Conservación del Mar Patagónico y Áreas de Influencia, editor. Estado de conservación del Mar Patagónico y áreas de influencia. Puerto Madryn, Argentina: Edición del Foro, p 766–75.

Carvalho PC, Bugoni L, McGill RAR, Bianchini A. 2013. Metal and selenium concentrations in blood and feathers of petrels of the genus *Procellaria*. Environmental Toxicology and Chemistry 32: in press.

Chambers LE. 2004. The impact of climate on little penguin breeding success. BMRC Research Report 100. Melbourne, Australia: Bureau of Meteorology. 51 pages.

Chambers LE, Devney CA, Congdon BC, Dunlop N, Woehler EJ, Dann P. 2011. Observed and predicted effects of climate on Australian seabirds. Emu 111:235–51.

Chavez FP, Bertrand A, Guevara R, Soler P, Csirke J. 2008. The northern Humboldt Current system: Brief history, present status and a view towards the future. Progress in Oceanography 79:95–105.

Ciotti AM, Odebrecht C, Fillmann G, Möller OO. 1995. Freshwater outflow and Subtropical Convergence influence on phytoplankton biomass on the southern Brazilian Continental Shelf. Continental Shelf Research 15:1737–56.

Cobb KM, Charles CD, Cheng H, Eduards RL. 2003. El Niño/ Southern Oscillation and tropical Pacific climate during the last millennium. Nature 424:271–26.

Collar NJ, Gonzaga LP, Krabbe N, Madroño Nieto A, Naranjo LG, et al. 1992. Threatened Birds of the Americas. Cambridge: International Council for Bird Preservation. 1150 pages.

Costa ES, Ayala L, Ivar Do Sul JA, Coria NR, Sánchez-Scaglioni RE, Alves MAS, et al. 2011. Antarctic and Sub-Antarctic seabirds in South America: A review. Oecologia Australis 15:59–68.

Coulson JC, Coulson BA. 2008. Measuring immigration and philopatry in seabirds; Recruitment to black-legged kittiwake colonies. Ibis 150:288–99.

Crawford RJM, Jahncke J. 1999. Comparison of trends in abundance of guano-producing seabirds in Peru and southern Africa. South African Journal of Marine Science 21:145–56.

Crawford RJM, Sabarros PS, Fairweather T, Underhill LG, Wolfaardt AC. 2008a. Implications for seabirds of a long-term change in the distribution of sardine: A South African experience. African Journal of Marine Science 30:177–84.

Crawford RJM, Tree AJ, Whittington PA, Visagie J, Upfold L, Roxburg KJ, et al. 2008b. Recent distributional changes of seabirds in South Africa: Is climate having an impact? African Journal of Marine Science 30:189–93.

Crofts S, Wolfaardt A, Baylis A. 2011. Storm damage to colonial seabirds at Beauchêne Island and Steeple Jason Island during 13–14 December 2010. Stanley: Falklands Conservation. 20 pages.

Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, et al. 2012. Seabird conservation status, threats and priority actions: A global assessment. Bird Conservation International 22:1–34.

Croxall JP, Evans PGH, Schreiber RW (editors). 1984. Status and Conservation of the World's Seabirds. Cambridge: ICBP. 778 pages.

Croxall JP, Wood AG. 2002. The importance of the Patagonian Shelf for top predator species breeding at South Georgia. Aquatic Conservation: Marine and Freshwater Ecosystems 12:101–18.

Cubaynes S, Doherty Jr PF, Schreiber EA, Gimenez O. 2011. To breed or not to breed: A seabird's response to extreme climatic events. Biology Letters 7:303–06.

Culik B. 2001. Finding food in the open ocean: Foraging strategies in Humboldt penguins. Zoology 104:327–38.

Cushing DH. 1990. Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. Advances in Marine Biology 26:249–93.

Dehnhard N, Poisbleau M, Demongin L, Ludynia K, Lecoq M, Masello JF, Quillfeldt P. in press. Survival of rockhopper penguins in times of global climate change. Aquatic Conservation: Marine and Freshwater Ecosystems (accepted 30 Dec 2012).

del Valle HF, Blanco PD, Metternicht GI, Zinck JA. 2010. Radar remote sensing of wind-driven land degradation processes in northeastern Patagonia. Journal of Environmental Quality 39:62–75.

Demongin L, Poisbleau M, Strange IJ, Quillfeldt P. 2010. Effects of severe rains on the mortality of southern rockhopper penguin (*Eudyptes chrysocome*) chicks and its impact on breeding success. Ornitología Neotropical 21:439–43.

D'Onofrio EE, Fiore MME, Pousa JL. 2008. Changes in the regime of storm surges at Buenos Aires, Argentina. Journal of Coastal Research 24:260–65.

Dewitte B, Vasquez J, Goubanova K, Illig S, Takahashi K, Cambon G, et al. 2012. Change in El Niño flavours over 1958–2008: Implications for the long-term trend of the upwelling off Peru. Deep Sea Research II 77–80:143–56.

deYoung B, Harris R, Alheit J, Beaugrand G, Mantua N, Shannon L. 2004. Detecting regime shifts in the ocean: Data considerations. Progress in Oceanography 60:143–64.

Dijkstra HA. 2006. The ENSO phenomenon: Theory and mechanisms. Advances in Geosciences 6:3–15.

Dragani WC, Martin PB, Simionato CG, Campos MI. 2010. Are wind wave heights increasing in south-eastern South American Continental Shelf between 32°S and 40°S? Continental Shelf Research 30:481–90.

Duffy DC. 1990. Seabirds and the 1982–1984 El Niño. Elsevier Oceanography Series 52:395–415.

Durant JM, Stenseth NC, Anker-Nilssen T, Harris MP, Thompson PM, Wanless S. 2004. Marine birds and climate fluctuation in the North Atlantic. In: Stenseth NC, Ottersen G, Hurrell JW, Belgrano A, editors. Marine Ecosystems and Climate Variation: The North Atlantic – A Comparative Perspective. Oxford: Oxford University Press, p 95–105.

Edwards M, Johns DG, Leterme SC, Svendsen E, Richardson AJ. 2006. Regional climate change and harmful algal blooms in the Northeast Atlantic. Limnology and Oceanography 51: 820–29.

Edwards M, Richardson AJ. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881–84.

Erwin RM. 1980. Breeding habitat use by colonially nesting waterbirds in two mid-Atlantic US regions under different regimes of human disturbance. Biological Conservation 18: 39–51.

Escalante R. 1984. Problemas en la conservación de dos especies de Láridos sobre la costa atlántica de Sud América (*Larus (belcheri) atlanticus* y *Sterna maxima*). Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Zoología 13:147–52.

Escobar G, Vargas W, Bischoff S. 2004. Wind tides in the Rio de la Plata estuary: Meteorological conditions. International Journal of Climatology 24:1159–69.

Favero M, Khatchikian CE, Arias A, Silva Rodríguez MP, Cañete G, Mariano-Jelicich R. 2003. Estimates of seabirds by-catch along the Patagonian Shelf by Argentine longline fishing vessels, 1999–2001. Bird Conservation International 13:273–81.

Favero M, Silva Rodriguez MP. 2005. Estado actual y conservación de aves pelágicas que utilizan la Plataforma Continental Argentina como áreas de alimentación. Hornero 20:95–110.

Fonseca VSS, Petry MV 2007. Evidence of food items used by *Fulmarus glacialoides* (Smith, 1840) (Procellariiformes: Procellariidae) in southern Brazil. Polar Biology 30:317–20.

Fonseca VSS, Petry MV, Jost AH. 2001. Diet of the Magellanic penguin on the coast of Rio Grande do Sul, Brazil. Waterbirds 24:290–93.

Foro para la Conservación del Mar Patagónico y Áreas de Influencia. 2008. Estado de conservación del Mar Patagónico y áreas de influencia. Puerto Madryn, Argentina: Edición del Foro. 810 pages. Available at: http://www.marpatagonico.org/libro/sintesis-mar-patagonico.pdf (accessed 11 November 2012).

Garcia CAE, Garcia VMT. 2008. Variability of chlorophyll-a from ocean color images in the La Plata continental shelf region. Continental Shelf Research 28:1568–78.

Garcia CAE, Sarma YVB, Mata MM, Garcia VMT. 2004. Chlorophyll variability and eddies in the Brazil–Malvinas Confluence region. Deep-Sea Research Part II 51:159–72.

García-Borboroglu P, Boersma PD, Ruoppolo V, Reyes L, Rebstock GA, Griot K, et al. 2006. Chronic oil pollution harms Magellanic penguins in the Southwest Atlantic. Marine Pollution Bulletin 52:193–98.

García-Godos I, Goya E. 2006. Diet of the Peruvian diving petrel *Pelecanoides garnotii* at La Vieja Island, Peru, 1997–2000: Potential fishery interactions and conservation implications. Marine Ornithology 34:33–41.

Gianuca D. 2007. Ocorrência sazonal e reprodução do socó-caranguejeiro *Nyctanassa violacea* no estuário da Lagoa dos Patos, novo limite sul da sua distribuição geográfica. Revista Brasileira de Ornitologia 15:464–67.

Gianuca D, Quintela FM, Barros JA, Gomes A, Gianuca NM. 2008. Ocorrência regular da garça-azul *Egretta caerulea* (Ciconiiformes, Ardeidae) no estuário da Lagoa dos Patos, Rio Grande do Sul, Brasil. Pan-American Journal of Aquatic Sciences 3:328–34.

Gibson T. 1992. An observed poleward shift of the Southern Hemisphere subtropical wind maximum: A greenhouse symptom? International Journal of Climatology 12:637–40.

Gjerdrum C, Vallée AMJ, St Clair CC, Bertram DF, Ryder JL, Blackburn GS. 2003. Tufted puffin reproduction reveals ocean climate variability. Proceedings of the National Academy of Sciences of the United States of America 100:9377–82.

Glorioso PD. 2002. Modelling the South West Atlantic. Aquatic Conservation 12:27–37.

González-Zevallos D, Yorio P. 2006. Seabird use of discards and incidental captures at the Argentine hake trawl fishery in the Golfo San Jorge, Argentina. Marine Ecology Progress Series 316:175–83.

Gordon AL. 1989. Brazil Malvinas Confluence – 1984. Deep-Sea Research I 36:359–84.

Gregg WG, Casey NW, McClain CR. 2005. Recent trends in global ocean chlorophyll. Geophysical Research Letters 32:3606–10.

Grémillet D, Boulinier T. 2009. Spatial ecology and conservation of seabirds facing global climate change: A review. Marine Ecology Progress Series 391:121–37.

Grimm AM, Tedeschi RG. 2009. ENSO and extreme rainfall events in South America. Journal of Climate 22:1589–609.

Guinet C, Chastel O, Koudil M, Durbec JP, Jouventin P. 1998. Effects of warm sea-surface temperature anomalies on the blue petrel at the Kerguelen Islands. Proceedings of the Royal Society of London B 265:1001–06.

Haimovici M, Perez JAA. 1991. Abundância e distribuição de cefalópodes em cruzeiros de prospecção pesqueira demersal na plataforma externa e talude continental do sul do Brasil. Atlântica 13:189–200.

Hamer KC. 2010. The search for winners and losers in a sea of climate change. Ibis 152:3–5.

Hansen J, Ruedy R, Sato M, Lo K. 2010. Global surface temperature change. Reviews of Geophysics 48:RG4004, p 1–29.

Hays GC, Richardson AJ, Robinson C. 2005. Climate change and marine plankton. Trends in Ecology and Evolution 20: 337–44.

Hayes FE, Baker WS. 1989. Seabird distribution at sea in the Galapagos Islands: Environmental correlations and associations with upwelled water. Colonial Waterbirds 12:60–66.

Hipfner JM. 2008. Matches and mismatches: Ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. Marine Ecology Progress Series 368:295–304.

Hoegh-Guldberg O, Bruno JF. 2010. The impact of climate change on the world's marine ecosystems. Science 328: 1523–28.

Holmgren M, Scheffer M, Ezcurra E, Gutiérrez JR, Mohren GMJ. 2001. El Niño effects on the dynamics of terrestrial ecosystems. Trends in Ecology and Evolution 16:89–94.

Holmgren M, Stapp P, Dickman CR, Gracia C, Graham S, Gutiérrez JR, et al. 2006. Extreme climatic events shape arid and semiarid ecosystems. Frontiers in Ecology and the Environment 4:87–95.

IPCC. 2007. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Pachauri RK, Reisinger A, editors. Geneva, Switzerland: IPCC. 104 pages.

Jahncke J, Goya E. 1997. Variación latitudinal y estacional en la dieta del guanay (*Leucocarbo bougainvillii*) y el piquero peruano (*Sula variegata*) en la costa peruana. Boletín del Instituto del Mar del Perú 16:23–41.

Jahncke J, Goya E. 1998. Las dietas del guanay y piquero peruano como indicadoras de la abundancia y distribución de anchoveta. Boletín del Instituto del Mar del Perú 17:15–34.

Jahncke J, Goya E. 2000. Responses of three booby species to El Niño 1997–1998. Waterbirds 23:102–08.

Jahncke J, García-Godos A, Goya E. 1997. Dieta del guanay *Leucocarbo bougainvillii*, del piquero peruano *Sula variegata* y otras aves de la costa peruana, abril y mayo de 1997. Informe del Instituto del Mar del Perú 126:75–86.

Jahncke J, Ayala L, Mendoza C. 1998. Abundancia relativa y distribución de aves marinas frente a la costa peruana y su relación con la abundancia de anchoveta. Crucero BIC Humboldt 9808–09, de Piura a Lima. Informe del Instituto del Mar del Perú 141:85–95.

Jahncke J, Checkley Jr DM, Hunt Jr GL. 2004. Trends in carbon flux to seabirds in the Peruvian Upwelling system: Effects of wind and fisheries on population regulation. Fisheries Oceanography 13:208–23.

Jaksic FM. 2004. El Niño effects on avian ecology: Lessons learned from the southeastern Pacific. Ornitología Neotropical 15:61–72.

Jaksic FM, Fariña JM. 2010. El Niño and the birds: A resource-based interpretation of climatic forcing in the southeastern Pacific. Anales Instituto de la Patagonia 38:121–40.

Jaksic FM, Silva SI, Meserve PL, Gutiérrez JR. 1997. A long term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. Oikos 78: 341–54.

Jenouvrier S, Barbraud C, Weimerskirch H. 2003. Effects of climate variability on the temporal population dynamics of southern fulmars. Journal of Animal Ecology 72:576–87.

Jenouvrier S, Barbraud C, Weimerskirch H. 2005a. Long-term contrasted responses to climate of two Antarctic seabird species. Ecology 86:2889–903.

Jenouvrier S, Weimerskirch H, Barbraud C, Park YH, Cazelles B. 2005b. Evidence of a shift in the cyclicity of Antarctic seabird dynamics linked to climate. Proceedings of the Royal Society of London B 272:887–95.

Jiménez S, Domingo A, Brazeiro A. 2009. Seabird bycatch in the southwest Atlantic: Interaction with the Uruguayan pelagic longline fishery. Polar Biology 32:187–96.

Kalmbach E, Ramsay SC, Wendeln H, Becker PH. 2001. A study of Neotropic cormorants in central Chile: Possible effects of El Niño. Waterbirds 24:345–51.

Kane RP. 1999. Rainfall extremes in some selected parts of Central and South America: ENSO and other relationships reexamined. International Journal of Climatology 19:423–55.

Kane RP. 2002. Precipitation anomalies in southern South America associated with a finer classification of El Niño and la Niña events. International Journal of Climatology 22:357–73.

Kitaysky AS, Golubova EG. 2000. Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. Journal of Animal Ecology 69: 248–62.

Laptikhovsky V, Arkhipkin A, Brickle P. 2010. Squid as a resource shared by fish and humans on the Falkland Islands' Shelf. Fisheries Research 106:151–55.

Le Bohec C, Durant JM, Gauthier-Clerc M, Stenseth NC, Park YH, Pradel R, et al. 2008. King penguin population threatened by Southern Ocean warming. Proceedings of the National Academy of Sciences of the United States of America 105:2493–97.

Lentini CAD, Podestá GG, Campos EJD, Olson DB. 2001. Sea surface temperature anomalies on the western south Atlantic from 1982 to 1994. Continental Shelf Research 21:89–112.

Lescroël A, Ballard G, Toniolo V, Barton KJ, Wilson PR, Lyver PO, et al. 2010. Working less to gain more: When breeding quality relates to foraging efficiency. Ecology 91:2044–55.

Levitus S, Antonov J, Boyer T. 2005. Warming of the world ocean, 1955–2003. Geophysical Research Letters 32: L02604, p 1–4.

Levitus S, Antonov JI, Boyer TP, Stephens C. 2000. Warming of the world ocean. Science 287:2225–29.

Ludynia K, Garthe S, Luna-Jorquera G. 2009. Distribution and foraging behaviour of the Peruvian booby (*Sula variegata*) off northern Chile. Journal of Ornithology 151:103–11.

Luna-Jorquera G, Simeone A, Aguilar R. 2003. Ecofisiología de animales endotermos en un desierto cálido y un mar frío: El caso de las aves marinas de la Corriente de Humboldt. In: Bozinovic F, editor. Fisiología Ecológica y Evolutiva: Conceptos y Casos de Estudio en Animales. Santiago: Ed. Univ. Católica de Chile, p 297–316.

Mackiernan G, Lonsdale P, Shany N, Cooper B, Ginsburg P. 2001. Observations of seabirds in Peruvian and Chilean waters during the 1998 El Niño. Cotinga 15:88–94.

Mäder A, Sander M, Casa Jr G 2010. Ciclo sazonal de mortalidade do pinguim-de-magalhães, *Spheniscus magellanicus* influenciado por fatores antrópicos e climáticos na costa do Rio Grande do Sul, Brasil. Revista Brasileira de Ornitologia 18:228–33.

Masello JF, Mundry R, Poisbleau M, Demongin L, Voigt CC, Wikelski M, et al. 2010. Diving seabirds share foraging space and time within and among species. Ecosphere 1: 19.1–28.

Moe B, Stempniewicz L, Jakubas D, Angelier F, Chastel O, Dinessen F, et al. 2009. Climate change and phenological responses of two seabird species breeding in the high-Arctic. Marine Ecology Progress Series 393:235–46.

Monticelli D, Ramos JA, Quartly GD. 2007. Effects of annual changes in primary productivity and ocean indices on the breeding performance of tropical roseate terns in the western Indian Ocean. Marine Ecology Progress Series 351: 273–86.

Murphy RC. 1926. Oceanic and climatic phenomena along the west coast of South America during 1925. Geographical Review 16:26–54.

Neves T, Vooren CM, Bugoni L, Olmos F, Nascimento L. 2006. Distribuição e abundância de aves marinhas na região sudeste-sul do Brasil. In: Neves T, Bugoni L, Rossi-Wongtschowski CLB, editors. Aves oceânicas e suas interações com a pesca na região sudeste-sul do Brasil. São Paulo: USP, p 11–35.

Nevoux M, Weimerskirch H, Barbraud C. 2007. Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. Journal of Animal Ecology 76:159–67.

Odebrecht C, Rörig L, Garcia V, Abreu P. 1995. Shellfish mortality and a red tide event in southern Brazil. In: Lassus P, Arzul G, Erard E, Gentien P, Marcaillou C, editors. Proceedings of the Sixth International Conference on Toxic Marine Phytoplankton. Harmful Algal Blooms. Paris: Lavoisier Science Publishers, p 213–18.

Olmos F. 2002. Non-breeding seabirds in Brazil: A review of band recoveries. Ararajuba 10:31–42.

Orgeira JL. 2001. Distribución espacial de densidades de aves marinas en la plataforma continental argentina y Océano Atlántico Sur. Ornitología Neotropical 12:45–55.

Padovani LN, Viñas MD, Sánchez F, Mianzan H. 2012. Amphipod-supported food web: *Themisto gaudichaudii*, a key food resource for fishes in the southern Patagonian Shelf. Journal of Sea Research 67:85–90.

Pájaro M, Macchi GJ, Leonarduzzi E, Hansen JE. 2009. Spawning biomass of Argentine anchovy (*Engraulis anchoita*) from 1996 to 2004 using the Daily Egg Production Method. Journal of the Marine Biological Association of the United Kingdom 89:829–37.

Perez JAA, Silva TN, Schroeder R, Schwarz R, Martins RS. 2009. Biological patterns of the Argentine shortfin squid *Illex argentinus* in the slope trawl fishery off Brazil. Latin American [checked] Journal of Aquatic Research 37:409–27.

Peterson RG, Stramma L. 1991. Upper-level circulation in the South Atlantic Ocean. Progress in Oceanography 26:1–73.

Petry MV, Fonseca VSS. 2002. Effects of human activities in the marine environment on seabirds along the coast of Rio Grande do Sul, Brazil. Ornitología Neotropical 13:137–42.

Petry MV, Fonseca VSS, Garcia LK, Piuco RC. 2008. Shearwater diet during migration along the coast of Rio Grande do Sul. Marine Biology 154:613–21.

Petry MV, Fonseca VSS, Scherer AL. 2007. Analysis of stomach contents from the black-browed albatross, *Thalassarche melanophris*, on the coast of Rio Grande do Sul, southern Brazil. Polar Biology 30:321–25.

Petry MV, Krüger L, Fonseca VSS, Brummelhause J, Piuco RC. 2009. Diet and ingestion of synthetics by Cory's Shearwater *Calonectris diomedea* off southern Brazil. Journal of Ornithology 150:601–06.

Petry MV, Petersen ES, Scherer JFM, Krüger L, Scherer AL. 2010. Levantamento e dieta de *Macronectes giganteus* ao longo da costa litorânea do Rio Grande do Sul, Brasil. Revista Brasileira de Ornitologia 18:237–39.

Pezzola A, Winschel C, Sánchez R. 2004. Estudio multitemporal de la degradación del monte nativo en el partido de Patagones – Buenos Aires. Boletín de Divulgación INTA EEA Hilario Ascasubi 12:1–11.

Phillips RA, Silk JRD, Croxall JP, Afanasyev V. 2006. Year-round distribution of white-chinned petrels from South Georgia: Relationships with oceanography and fisheries. Biological Conservation 129:336–47.

Pinto MBLC, Salvatore S, Di Beneditto APM. 2007. Stomach contents of the Magellanic penguin *Spheniscus magellanicus* from the northern distribution limit on the Atlantic coast of Brazil. Marine Ornithology 35:77–78.

Piola AR. 2008. Oceanografía física. In: Foro para la Conservación del Mar Patagónico y Áreas de Influencia, editor. Estado de conservación del Mar Patagónico y áreas de influencia. Puerto Madryn, Argentina: Edición del Foro, p 1–21.

Pütz K, Clausen AP, Huin N, Croxall JP. 2003. Re-evaluation of historical rockhopper penguin population data in the Falkland Islands. Waterbirds 26:169–75.

Quillfeldt P, Masello JF, McGill RAR, Adams M, Furness RW 2010a. Moving polewards in winter: A recent change in the migratory strategy of a pelagic seabird? Frontiers in Zoology 7:15, p 1–11.

Quillfeldt P, Michalik A, Veit-Köhler G, Strange IJ, Masello JF. 2010b. Inter-annual changes in diet and foraging trip lengths in a small pelagic seabird, the thin-billed prion *Pachyptila belcheri*. Marine Biology 157:2043–50.

Quillfeldt P, McGill RAR, Masello JF, Weiss F, Strange IJ, Brickle P, et al. 2008. Stable isotope analysis reveals sexual and environmental variability and individual consistency in foraging of thin-billed prions. Marine Ecology Progress Series 373:137–48.

Quillfeldt P, Strange IJ, Masello JF. 2007. Sea surface temperatures and behavioural buffering capacity in thin-billed prions *Pachyptila belcheri*: Breeding success, provisioning and chick begging. Journal of Avian Biology 38:298–308.

Raya-Rey A, Trathan P, Pütz K, Schiavini A. 2007. Effect of oceanographic conditions on the winter movements of rockhopper penguins *Eudyptes chrysocome chrysocome* from Staten Island, Argentina. Marine Ecology Progress Series 330:285–95.

Richardson AJ, Schoeman DS. 2004. Climate impact on plankton ecosystems in the northeast Atlantic. Science 305:1609–12.

Rignot E, Rivera A, Casassa G. 2003. Contribution of the Patagonia icefields of South America to sea level rise. Science 302:434–37.

Riou S, Gray CM, Brooke M, Quillfeldt P, Masello JF, Perrins C, et al. 2011. Recent impacts of anthropogenic climate change on a higher marine predator in western Britain. Marine Ecology Progress Series 422:105–12.

Rivalan P, Barbraud C, Inchausti P, Weimerskirch H. 2010. Combined impacts of longline fisheries and climate on the persistence of the Amsterdam Albatross *Diomedea amsterdamensis*. Ibis 152:6–18.

Rolland V, Weimerskirch H, Barbraud C. 2010. Relative influence of fisheries and climate on the demography of four albatross species. Global Change Biology 16:1919–22.

Ropelewski CF, Halpert MS. 1987. Global and regional scale precipitation patterns associated with the El Niño Southern Oscillation. Monthly Weather Review 115:1606–26.

Ropelewski CF, Halpert MS. 1989. Precipitation patterns associated with the high index phase of the Southern Oscillation. Journal of Climate 2:268–84.

Rosenberg DK, Harcourt SA. 1987. Population sizes and potential conservation problems of the endemic Galápagos penguin and flightless cormorant. Noticias de Galápagos 45:24–25.

Sabatini M, Martos P. 2002. Mesozooplankton features in a frontal area off northern Patagonia (Argentina). Scientia Marina 66:215–32.

Sabatini ME, Álvarez-Colombo GL. 2001. Seasonal pattern of zooplankton biomass in the Argentinian Shelf off Southern Patagonia (45–55°S). Scientia Marina 65:21–31.

Sandvik H, Erikstad KE. 2008. Seabird life histories and climatic fluctuations: A phylogenetic-comparative time series analysis of North Atlantic seabirds. Ecography 31:73–83.

Sandvik H, Erikstad KE, Barrett RT, Yoccoz NG. 2005. The effect of climate on adult survival in five species of North Atlantic seabirds. Journal of Animal Ecology 74:817–31.

Santos RA, Haimovici M. 2002. Cephalopods in the trophic relations of southern Brazil. Bulletin of Marine Science 71: 753–70.

Seeliger U, Odebrecht C, Castello JP (editors). 1997. Subtropical Convergence Environments: The Coast and Sea in the Southwestern Atlantic. Heidelberg: Springer-Verlag. 308 pages.

Sherman K. 1991. The Large Marine Ecosystem concept: Research and management strategy for living marine resources. Ecological Applications 1:349–60.

Sherman K, Hempel G (editors). 2009. The UNEP Large Marine Ecosystem Report: A Perspective on Changing Conditions in LMEs of the World's Regional Seas. Nairobi: UNEP. 852 pages.

Silvestri GE, Vera CS. 2003. Antarctic Oscillation signal on precipitation anomalies over southeastern South America. Geophysical Research Letters 30:2115, p 1–4.

Simeone A, Araya B, Bernal M, Diebold EN, Grzybowski K, Michaels M, et al. 2002. Oceanographic and climatic factors influencing breeding and colony attendance patterns of Humboldt penguins *Spheniscus humboldti* in central Chile. Marine Ecology Progress Series 227:43–50.

Simeone A, Luna-Jorquera G, Bernal M, Garthe S, Sepulveda F, Villablanca R, et al. 2003. Breeding distribution and abundance of seabirds on islands off north-central Chile. Revista Chilena de Historia Natural 76:323–33.

Simionato CG, Vera CS, Siegismund F. 2005. Surface wind variability on seasonal and interannual scales over Río de la Plata area. Journal of Coastal Research 21:770–83.

Skewgar E, Boersma PD, Harris G, Caille G. 2007. Anchovy fishery threat to Patagonian ecosystem. Science 315:45.

Southward AJ, Langmead O, Hardman-Mountford NJ, Aiken J, Boalch GT, Dando PR, et al. 2005. Long-term oceanographic and ecological research in the western English Channel. Advances in Marine Biology 47:1–105.

Spear LB, Ainley DG. 2008. The seabird community of the Peru Current, 1980–1995, with comparisons to other eastern boundary currents. Marine Ornithology 36:125–44.

Spinelli ML, Pájaro M, Martos P, Esnal GB, Sabatini M, Capitanio FL. 2012. Potential zooplankton preys (Copepoda and Appendicularia) for *Engraulis anchoita* in relation to early larval and spawning distributions in the Patagonian frontal system (SW Atlantic Ocean). Scientia Marina 76: 39–47.

Stramma L. 1989. The Brazil Current transport south of 23°S. Deep-Sea Research I 36:639–46.

Sydeman WJ, Thompson SA, Kitaysky A. 2012. Seabirds and climate change: Roadmap for the future. Marine Ecology Progress Series 454:107–17.

Timmermann A, Oberhuber J, Bacher A, Esch M, Latif M, Roeckner E. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. Nature 398: 694–97.

Tourinho PS, Ivar do Sul J, Fillmann G. 2010. Is marine debris ingestion still a problem for the coastal marine biota of southern Brazil? Marine Pollution Bulletin 60:396–401.

Valle CA, Cruz F, Cruz JB, Merlen G, Coulter MC. 1987. The impact of the 1982–83 El Niño–Southern Oscillation on seabirds in the Galapagos Islands, Ecuador. Journal of Geophysical Research 92:14437–44.

Vargas FH, Harrison S, Rea S, Macdonald DW. 2006. Biological effects of El Niño on the Galápagos penguin. Biological Conservation 127:107–14.

Veit RR, Pyle P, McGowan JA. 1996. Ocean warming and long-term change in pelagic bird abundance within the California Current system. Marine Ecology Progress Series 139:11–18.

Visser ME. 2008. Keeping up with a warming world; Assessing the rate of adaptation to climate change. Proceedings of the Royal Society of London B 275:649–59.

Waluda CM, Trathan PN, Rodhouse PG. 1999. Influence of oceanographic variability on recruitment in the *Illex argentinus* (Cephalopoda: Ommastrephidae) fishery in the South Atlantic. Marine Ecology Progress Series 183:159–67.

Waluda CM, Trathan PN, Rodhouse PG. 2004. Synchronicity in Southern Hemisphere squid stocks and the influence of the Southern Oscillation and Trans Polar Index. Fisheries Oceanography 13:255–66.

Watanuki Y, Ito M, Deguchi T, Minobe S. 2009. Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy. Marine Ecology Progress Series 393:259–71.

Weichler T, Garthe S, Luna-Jorquera G, Moraga J. 2004. Seabird distribution on the Humboldt Current in northern Chile in relation to hydrography, productivity, and fisheries. ICES Journal of Marine Science 61:148–54.

Weimerskirch H, Inchausti P, Guinet C, Barbraud C. 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. Antarctic Science 15: 249–56.

Weimerskirch H, Louzao M, de Grissac S, Delord K. 2012. Changes in wind pattern alter albatross distribution and life-history traits. Science 335:211–14.

Wentz FJ, Ricciardulli L, Hilburn K, Mears C. 2007. How much more rain will global warming bring? Science 317: 233–35.

Wilson RP, Grémillet D, Syder J, Kierspel MAM, Garthe S, Weimerskirch H, et al. 2002. Remote-sensing systems and seabirds: Their use, abuse and potential for measuring marine environmental variables. Marine Ecology Progress Series 228:241–61.

Wilson RP, Liebsch N, Davies IM, Quintana F, Weimerskirch H, Storch S, et al. 2007. All at sea with animal tracks; Methodological and analytical solutions for the resolution of movement. Deep Sea Research II 54:193–210.

Yeh S-W, Kug J-S, Dewitte B, Kwon M-H, Kirtman BP, Jin F-F. 2009. El Niño in a changing climate. Nature 461:511–14.

Yorio P. 2000. Breeding seabirds of Argentina: Conservation tools for a more integrated and regional approach. Emu 100:367–75.

Yorio P, Frere E, Gandini P, Conway W. 1999. Status and conservation of seabirds breeding in Argentina. Bird Conservation International 9:299–314.

Zavalaga CB, Halls JN, Mori GP, Taylor SA, Dell'Omo G. 2010. At-sea movement patterns and diving behavior of Peruvian boobies *Sula variegata* in northern Peru. Marine Ecology Progress Series 404:259–74.

Zavalaga CB, Plenge MA, Bertolero A. 2008. The breeding biology of the Peruvian tern (*Sternula lorata*) in Peru. Waterbirds 31:550–60.

Editorial responsibility: Leandro Bugoni