Effects of climate change and fisheries bycatch on Southern Ocean seabirds: a review

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ABSTRACT: Over the last century, major climate changes and intense human exploitation of natural living resources have occurred in the Southern Ocean, potentially affecting its ecosystems up to top marine predators. Fisheries may also directly affect seabirds through bycatch and additional food resources provided by discards. The past 20 yr of research has seen an increasing number of studies investigating the effects of climate change and fisheries activities on Southern Ocean seabirds. Here, we review these studies in order to identify patterns in changes in distribution, phenology, demography and population dynamics in response to changes in climate and fisheries bycatch. Shifts in distribution and breeding phenology were documented in parallel to increases in sea-surface temperatures and changes in sea-ice cover. Above all warm sea-surface temperatures negatively affected demographic parameters, although exceptions were found. Relationships suggest non-linear effects of sea-ice cover on demographic parameters and population dynamics, with optimum sea-ice cover conditions appearing to be the rule. Fishing efforts were mainly negatively related to survival rates, and only for a few species positively related to breeding success. A handful of studies found that chronic mortality of immature birds due to fisheries negatively affected populations. Climate factors and fisheries bycatch may simultaneously affect demographic parameters in a complex way, which can be integrated in population models to project population trajectories under future climate or fisheries scenarios. Needed are studies that integrate other environmental factors, trophic levels, foraging behaviour, climate–fisheries interactions, and the mechanisms underlying phenotypic plasticity, such as some pioneering studies conducted elsewhere.

KEY WORDS: Seabirds · Bycatch · Population dynamics · Demography · Distribution · Phenology · Sea ice · Sea-surface temperature

INTRODUCTION

Several studies have shown that recent climate change and variability have affected a wide range of species (Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003, Parmesan 2006), including seabirds (e.g. Montevecchi & Myers 1997, Kitaysky & Golubova 2000, Kitaysky et al. 2000, Sydeman et al. 2001,

Frederiksen et al. 2004). A major challenge in ecology and conservation is to predict the effect of future climate change on populations, species' distributions and ecosystems. In the Southern Ocean, there has been strong evidence for important climate changes over the last century. Among the most important changes that may have affected seabird distribution, phenology and populations are:

1. A large-scale change in the atmospheric circulation of the high southern latitudes, the major mode of variability being the southern annular mode (SAM). Since the late 1970s, the SAM has become more positive, resulting in a 15 to 20% increase of westerly winds around the Antarctic continent, an increase in temperature and a decrease in sea ice in the coastal region of West Antarctica, as well as changes in the frequency and intensity of cyclones south of 40° S. The change in SAM coincided with the development of the ozone hole (Marshall 2003, Turner et al. 2009).

2. An increase in atmospheric temperatures for the sub-Antarctic South Georgia, Macquarie, Kerguelen, Heard and Marion Islands and on the Antarctic Peninsula (British Antarctic Survey 1987, Adamson et al. 1988, Frenot et al. 1997, Budd 2000, Smith 2002, Meredith & King 2005, Solomon et al. 2007).

3. An increase in the frequency and intensity of El Niño events, with some El Niño signals being detected in the Antarctic (Solomon et al. 2007).

4. An increase of CO_2 concentration south of 20° S in the southern Indian Ocean (Solomon et al. 2007, Turner et al. 2009).

5. An increase in Antarctic air temperatures by about 0.2°C on average since the late-nineteenth century, with a particular increase in West Antarctica since the early 1950s (Masson-Delmotte et al. 2003, Vaughan et al. 2003, Turner et al. 2009).

6. A warming of the Antarctic Circumpolar Current waters by 0.06°C decade^{-1} at depths of 300 to 1000 m from the 1960s to 2000s, and by 0.09°C decade^{-1} since the 1980s (Levitus et al. 2000, Gille 2002). The warming is more intense on the southern side of the Antarctic Circumpolar Current than north of it.

7. An average increase of 2.3°C over the last 81 yr in the upper 150 m of the waters around South Georgia (Trathan et al. 2007).

8. An increase in sea-surface temperatures of the southern Indian Ocean over the period 1960 to 1999 (Alory et al. 2007).

9. A decrease in sea-ice extent in the Bellingshausen Sea and an increase in sea-ice extent in the Ross Sea from 1979 to 2006, and a decrease in sea-ice extent in East Antarctica from the 1950s to 1970s (Curran et al. 2003, de la Mare 2009, Ainley et al. 2010a).

10. A decrease of the sea-ice season duration (later advance and earlier retreat of sea ice) in the Bellingshausen Sea and an increase (earlier advance and later retreat of the sea ice) in the Ross Sea (Parkinson 2004).

These physical changes may have had profound effects on several components of the Southern Ocean ecosystems and across a range of trophic levels (Forcada et al. 2006, Murphy et al. 2007, Nicol et al. 2007, Trathan et al. 2007). For example, in the southern Atlantic Ocean, long-term surveys suggest a 38 to 81% decline in krill stocks since the mid-1970s (Atkinson et al. 2004). Although the causes (or predators) of this decline are still being debated (Hewitt et al. 2003, Ainley et al. 2007), a significant negative correlation between krill density and mean sea-surface temperature at South Georgia has been found for the period from 1928 to 2003, suggesting a large-scale response of krill and of the entire open-ocean ecosystem to climate change (Whitehouse et al. 2008). The length of the sea-ice season duration or the timing of sea-ice advance or retreat may have profound consequences on the structure of food webs and their productivity as recently shown in the Bering Sea (Hunt et al. 2011). In the Southern Ocean it has been established that ice-edge blooms have a productivity 4- to 8-fold that of open water (Smith & Nelson 1986), and have high densities of krill (Brierley et al. 2002, Nicol 2006).

Seabirds provide some of the best time series data for Southern Ocean animals because of their accessibility in land-based colonies where they can be studied. Although most seabird time series data may be too short to provide evidence for climate change effects on populations, several studies have found significant changes in demographic and behavioural parameters in relation to climate, such as sea-surface temperature or sea-ice extent (e.g. Fraser et al. 1992, Barbraud & Weimerskirch 2001a, Jenouvrier et al. 2003, Forcada et al. 2006, Trathan et al. 2006).

However, predicting population responses to projected climate change using population dynamics theory and models remains challenging because other environmental factors may affect individuals and population dynamics (Fig. 1). Among these, the accidental mortality of seabirds caused by fisheries has been recognised as a main factor potentially affecting seabird populations. Indeed, the high numbers of seabirds that are killed annually in fishing gear ('bycatch'; Perrin 1969, Weimerskirch & Jouventin 1987, Brothers 1991) have focused attention on the ecological effects of bycatch in industrial fisheries (Brothers et al. 1999, Sullivan et al. 2006, Watkins et al. 2008), and may act as a confounding factor when trying to predict the population dynamics under different scenarios of climate change. To date it remains unclear to what extent simultaneous changes in climate and bycatch have affected and will affect seabird populations. Recently, several studies have investigated the effects of climate change
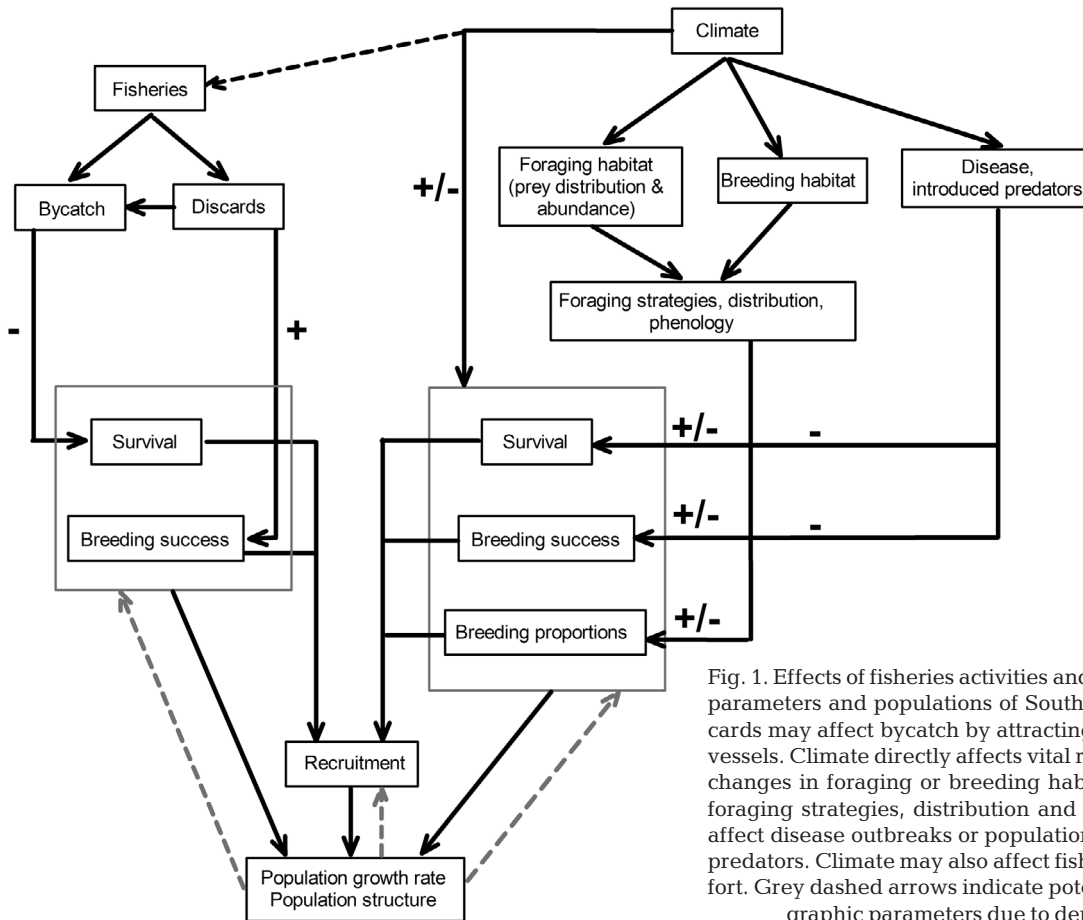
Fig. 1. Effects of fisheries activities and climate on demographic parameters and populations of Southern Ocean seabirds. Discards may affect bycatch by attracting seabirds behind fishing vessels. Climate directly affects vital rates or indirectly through changes in foraging or breeding habitat, which in turn affect foraging strategies, distribution and phenology. Climate may affect disease outbreaks or population dynamics of introduced predators. Climate may also affect fisheries distribution and effort. Grey dashed arrows indicate potential feedback on demographic parameters due to density dependence

(e.g. Peacock et al. 2000, Barbraud & Weimerskirch 2001b, Sydeman et al. 2001, Thompson & Ollason 2001, Ainley et al. 2005, Jenouvrier et al. 2005, Forcada et al. 2006, Le Bohec et al. 2008, Wolf et al. 2010) and bycatch (e.g. Oro et al. 1995, Tuck et al. 2003, Cuthbert et al. 2003, Votier et al. 2004, Lewison et al. 2004, Véran et al. 2007, Frederiksen et al. 2008) separately on seabirds worldwide, but few have addressed both issues simultaneously (Frederiksen et al. 2004, Rolland et al. 2009a). Here, we review the current research on the effects of climate and fisheries bycatch on Southern Ocean seabird demography and population dynamics.

In the Southern Ocean, the twentieth century was also characterised by intensive human exploitation of natural resources, particularly whales and fishes (Pauly et al. 1998, Myers & Worm 2003, Croxall & Nicol 2004, Ainley & Blight 2008, Ainley et al. 2010b). Although the relative importance of bottom-up or top-down processes on the effect of fish and whale harvesting on Southern Ocean top predators such as seabirds are highly debated (Ainley et al. 2007, Nicol et al. 2007, Ainley & Blight 2008, Barbraud & Cotté

2008, Ainley et al. 2010b), it is at present difficult to quantify the effects of either process given the lack of long-term data that incorporate both physical and biological drivers of ecosystem processes. Better documented are the direct interactions between seabirds and fisheries, and more particularly bycatch, which may have been implicated in population declines of several species of seabirds in the Southern Ocean (e.g. Weimerskirch et al. 1997, Tuck et al. 2001). However, the effect of bycatch on demographic parameters and population dynamics remains poorly known for several populations, and even less is known about the potential interactions between bycatch and climate on seabird population dynamics.

Recent technological developments in tracking devices (miniaturisation, memory capacity) have permitted the tracking of seabirds year round and the identification of foraging areas throughout the year (Wilson et al. 2002, Weimerskirch 2007, Burger & Schaffer 2008). This has allowed a better understanding of the spatial and temporal interactions between seabirds and fisheries, which was an important step in developing more realistic models to test the effects

of bycatch and climate on population dynamics (Rolland et al. 2008). Simultaneously, the application of the theory of exploited populations to seabird bycatch (Lebreton 2005, Véran et al. 2007) has permitted the development of a robust theoretical background to test for the effects of bycatch on seabird demographics.

In the present paper, we first review the effects of climate change on the distribution and phenology of Southern Ocean seabirds. We then review Southern Ocean studies on seabirds to determine how climate variability, fisheries bycatch and effort affect their demographic parameters and population dynamics. We were more specifically interested in attempting to determine whether general patterns are emerging in the effect of climate and fisheries bycatch on vital rates. In addition, we also consider how Southern Ocean seabird populations may respond to future climate change in light of the recent modelling efforts to tackle this question.

METHODS

This work is based on the analysis of contents from research articles published before September 2011. Research articles were selected with the ISI Web of Knowledge (Thomson Reuters) search engine, using the following search criteria:

Topic = (seabird* OR penguin* OR albatross* OR petrel* OR fulmar* OR shearwater*) AND (southern ocean OR Antarctic) AND (climate OR fisher* OR bycatch).

Timespan = All Years.

These search criteria returned 409 papers to which we added papers collected based on expert knowledge. From these, only papers reporting data on Southern Ocean seabird phenological, distributional, or demographic changes and at least 1 climate or fishery (effort or bycatch) associated variable were retained. Although the Southern Ocean is often defined as the ocean from the coast of Antarctica north to 60° S (www.scar.org/articles/southernocean.html), we here extended the northern limit of the Southern Ocean to 30°S. This allowed us to include in our review many studies that investigated the effects of climate and bycatch on seabird species that breed in the southern hemisphere and frequent the Southern Ocean and its vicinities. This yielded a total of 71 publications on which our review is based (Fig. 2). We recognize that some relevant publications may have been missed, but our review should be representative of research in the field.

The following questions were used to characterize the analyses presented in the reviewed manuscripts: (1) What was the demographic, phenological, or distribution parameter analyzed? (2) What was the climate or fishery (effort, bycatch) variable used? (3) What was the sign of the relationship between climate or fishery variables and seabird variables?

Responses to these questions were then summarized in order to quantify the type of climate or fishery variables affecting seabird variables and the sign of the relationships. Most studies that investigated statistical relationships between climate variables, fishing effort or bycatch, and Southern Ocean seabird demographic parameters (Appendix 1, Tables A1 & A2) focused on a handful of demographic parameters (mainly numbers of breeding pairs, breeding success or adult survival). Few studies focused on juvenile survival, recruitment, breeding proportions, or dispersal. However, these parameters were included in our review since we believe they will be more extensively studied in the future given the increasing number of long-term studies and the development of adequate statistical tools to estimate these parameters.

EFFECTS OF CLIMATE ON SOUTHERN OCEAN SEABIRD PHENOLOGY, DISTRIBUTION, DEMOGRAPHY AND POPULATION DYNAMICS

Distribution

Although, most observations worldwide of climate change responses have involved changes in species' phenology and distribution (Crick et al. 1997, Parmesan et al. 1999, Hüppop & Hüppop 2003), particularly for terrestrial species of the Northern Hemisphere (Parmesan & Yohe 2003, Root et al. 2003, Gaston et al. 2005), evidence remains scarce for Southern Ocean seabirds.

From a historical perspective, there is paleological evidence for major shifts in the distribution of Adélie penguin *Pygoscelis adeliae* populations in the Ross Sea during the Holocene, with 2 periods of large-scale abandonment at 5000 to 4000 and 2000 to 1100 calendar yr BP corresponding to cooling episodes that caused unfavourable marine conditions for breeding penguins (Emslie et al. 2007). There is also evidence for distributional changes in response to climate change for this species at other localities in East Antarctica (Emslie & Woehler 2005) and on the Antarctic Peninsula (Baroni & Orombelli 1994, Sun et al. 2000, Emslie 2001, Emslie & McDaniel 2002,
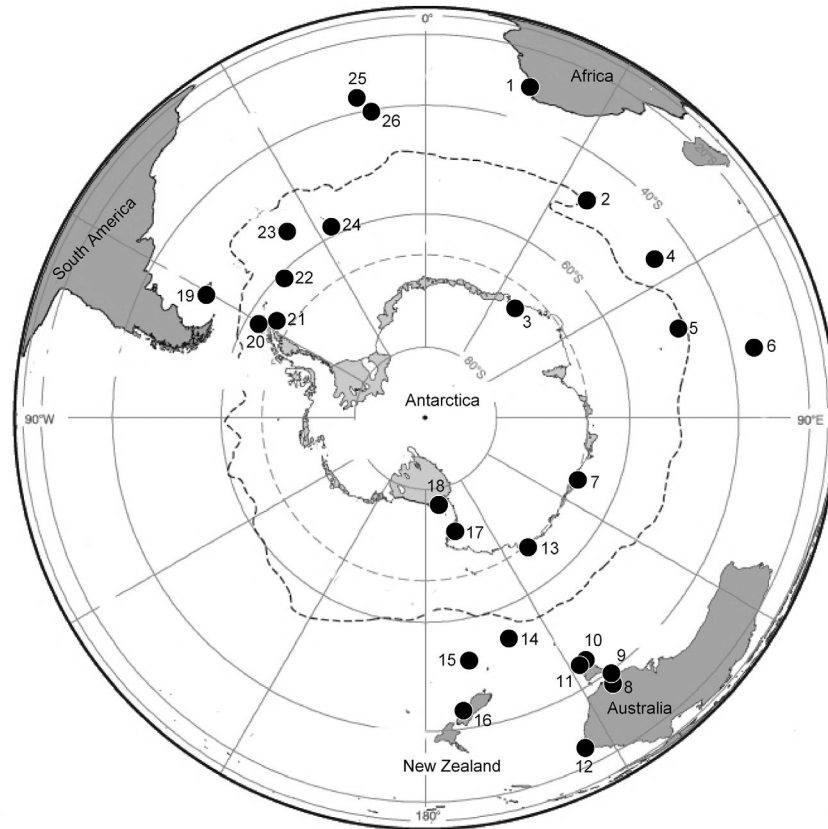
Fig. 2. Location of long-term monitoring studies where the effects of climate variability and fisheries bycatch on demography and population dynamics of Southern Ocean seabirds were investigated. Studied species in parentheses. 1: Malgas Island (cape gannet); 2: Marion & Prince Edward Islands (wandering albatross); 3: Showa (Adélie penguin); 4: Crozet Islands (king penguin, wandering albatross, sooty albatross, light-mantled sooty albatross, southern giant petrel, northern giant petrel, white-chinned petrel); 5: Kerguelen Islands (black-browed albatross, blue petrel, thin-billed prion, grey petrel); 6: Amsterdam Island (Amsterdam albatross, indian yellow-nosed albatross, sooty albatross); 7: Casey (snow petrel); 8: Philipp Island (little penguin); 9: Albatross Island (shy albatross); 10: Mewstone (shy albatross); 11: Pedra Branca (shy albatross); 12: Lord Howe (flesh footed-shearwater); 13: Dumont d'Urville (emperor penguin, Adélie penguin, Antarctic fulmar, snow petrel); 14: Macquarie Island (wandering albatross, grey-headed albatross, black-browed albatross); 15: Campbell Island (rockhopper penguin); 16: Otago Peninsula & Oamaru (yellow-eyed penguin, little penguin); 17: Coulman Island (Adélie penguin); 18: Ross Island (Adélie penguin); 19: Falkland Island/Islas Malvinas (thin-billed prion); 20: South Sandwich Islands (Adélie penguin, chinstrap penguin); 21: western Antarctic Peninsula (Adélie penguin, chinstrap penguin, gentoo penguin); 22: South Orkney Islands (Adélie penguin, chinstrap penguin, gentoo penguin); 23: South Georgia (king penguin, gentoo penguin, macaroni penguin, wandering albatross, black-browed albatross, grey-headed albatross); 24: South Shetland Islands (Adélie penguin, chinstrap penguin); 25: Tristan de Cunha (Atlantic yellow-nosed albatross); 26: Gough Island (Atlantic yellow-nosed albatross). Taxonomic names see Appendix 1

Emslie et al. 2003). Historical distributional changes in response to the advance or retreat of the Antarctic continental ice sheet are also documented for snow petrels *Pagodroma nivea* (Hiller et al. 1988, Verkulich & Hiller 1994, Steele & Hiller 1997). More recently, on centennial to decennial time scales, there is evidence that open-ocean feeding penguins, the chinstrap *P. antarctica* and the gentoo *P. papua*, spread southward between 20 and 50 yr ago along the Antarctic Peninsula, where the most rapid climate changes have been observed, with paleoevidence that gentoo had been absent from the Palmer region for 800 yr previously (Fraser et al. 1992, Emslie et al. 1998).

By contrast, colonies of the pagophilic (i.e. ice dependent) Adélie penguin situated at the northern part of the Antarctic Peninsula have declined dramatically during the past decades in response to a decrease in sea-ice extent and sea-ice season duration (Fraser et al. 1992, Ainley et al. 2005, Forcada et al. 2006, Hinke et al. 2007, but see Trivelpiece et al. 2011). On the other hand, gentoo populations are increasing, which has been interpreted in response to sea ice too because this species needs ice-free habitat around the colonies to breed (the sea-ice hypothesis; Fraser et al. 1992). However, populations of chinstrap penguins show contrasted responses, with some colonies declining while southernmost

colonies increase (Fraser et al. 1992, Hinke et al. 2007), which suggests much more complex mechanisms than the sea-ice hypothesis.

Long-term changes in at-sea distribution of Southern Ocean seabirds are still poorly documented due to the scarcity of long-term at-sea observations. In the Prydz Bay area, at-sea observations conducted between 1980 and 1992 by Woehler (1997) revealed a decrease in abundance of 5 non-resident sub-Antarctic species (wandering albatross *Diomedea exulans*, black-browed albatross *Thalassarche melanophrys*, light-mantled sooty albatross *Phoebetria palpebrata*, northern giant petrel *Macronectes halli*, white-chinned petrel *Procellaria aequinoctialis*). However, these changes were not analysed in the light of climate changes in the region during the period of the study. By contrast, in the southern Indian Ocean southward shifts in the distributions of wandering albatross and prions *Pachyptila* spp. between the early 1980s and 2000s could be ascribed to species redistribution or decrease in abundance due partly to the warming of subtropical waters (Péron et al. 2010). Surprisingly, the white-chinned petrel distribution shifted northward, suggesting more complex mechanisms, such as the expansion of fisheries activities in subtropical waters since the 1980s (Tuck et al. 2003). Péron et al. (2010) studied 12 seabird species and showed that the greatest warming of sea-surface waters was observed at 30 to 35°S. Their results suggest that the abundance at sea of the northernmost distributed species (those observed north of 38°S) tended to decline contrary to the southernmost species. Similar patterns and processes were documented elsewhere in other ocean basins (California Current System: Hyrenbach & Veit 2003; Bay of Biscay, North Atlantic: Hemery et al. 2008).

On shorter time scales, there is evidence that migratory movements of seabirds are affected by oceanographic conditions. Ballard et al. (2010) studied the migratory movement and wintering areas of Adélie penguins breeding on Ross Island (Ross Sea, Antarctica) during 3 consecutive years. They showed that the wintering areas were situated at the edge of the consolidated pack ice, well south of the large-scale ice edge itself, and that the wintering area shifted north in years of more extensive ice. Ballard et al. (2010) further suggested that this would move the penguins closer to the Antarctic Circumpolar Current Southern Boundary, where there is less food available. One can conjecture that this may increase winter mortality or breeding proportions in the following breeding season, although this remains to be quantified.

Phenology

Phenological changes were only recently documented for Southern Ocean seabirds. On a regional scale, data on first arrival and laying of first eggs over a 55 yr period for 9 species of Antarctic seabirds in East Antarctica revealed a clear tendency toward later arrival and laying (Barbraud & Weimerskirch 2006). On average, species now arrive at their colonies 9 d later and lay eggs 2 d later than in the early 1950s. This tendency was unexpected and inverse to most of those observed in the northern hemisphere for terrestrial species. Interestingly, these delays were partly linked to a decrease in sea-ice extent that has occurred in East Antarctica, and possibly to an increase in sea-ice season duration. Both factors may have contributed to reduce the quantity and accessibility of the food supplies available in early spring and may partly explain the delays observed, with seabirds needing more time to build up the reserves necessary for breeding. However, more detailed studies at an individual level are needed to understand the proximate and ultimate drivers of Southern Ocean seabirds breeding phenology and the effect of phenological changes on fitness. The fitness and population consequences of these phenological changes are currently unknown but could be serious for these top predators if they become less synchonized with the phenology of their food supplies. A brood that hatches later than expected may suffer from higher environmental deterioration, such as resource depletion, competition, or predation risk for the offspring (e.g. Lack 1968, Verhulst & Nilsson 2008). This could potentially affect reproductive success or juvenile survival. Although few studies have investigated the fitness consequences of a change in the timing of breeding in Southern Ocean seabirds, some observational and experimental studies suggest a decrease in reproductive success in individuals breeding late in the season (Barbraud et al. 2000a, Goutte et al. 2011).

Demography and population dynamics

The climate variables which were used for testing relationships with demographic parameters included large-scale climate indices (Southern Oscillation Index [SOI], Southern Annular Mode [SAM], Indian Ocean Dipole [IOD]) and local climate variables (sea-surface temperature [SST], sea-ice extent [SIE], sea-ice concentration [SIC], air temperature [T], sea-surface height [SSH]). SOI is related to wind stress,

sea-surface temperature and precipitation anomalies worldwide (Trenberth 1984). SAM is the leading mode of atmospheric circulation variability in the Southern Hemisphere (Gong & Wang 1998). IOD is related to wind stress, sea-surface temperature and precipitation anomalies over the Indian Ocean (Saji et al. 1999). Positive values of IOD are associated with a warm SST anomaly over the western Indian Ocean and a cold SST anomaly over the eastern tropical Indian Ocean. Although measured in the northern Indian Ocean, IOD also affects SST over the southern Indian Ocean <35° S. We found a total of 35 published studies concerning 22 species of seabirds.

The types of relationships between climate variables and demographic parameters are indicated in Table 1. Most relationships between demographic parameters and sea-surface temperature were negative (~50%). This is consistent with positive relationships between demographic parameters and SOI (~32% of the relationships were positive, whereas only ~16% were negative). Indeed, signals of El Niño–Southern Oscillation (ENSO) variability in the tropical Pacific are known to propagate to high latitudes through atmospheric teleconnections and oceanic processes (Kwok & Comiso 2002, White et al. 2002, Liu et al. 2004, Turner 2004). SOI and SST are inversely correlated in most parts of the Southern Ocean, with positive SOI globally corresponding to negative SST anomalies (Murphy et al. 2007).

Negative effects of warm sea-surface temperature anomalies on demographic parameters have also been found for a number of seabird species worldwide (e.g. North Atlantic Ocean: Kitayskiy & Golu-

bova 2000, Durant et al. 2003, Harris et al. 2005; Pacific Ocean: Veit et al. 1997, Bertram et al. 2005). In several coastal and oceanic ecosystems, and particularly in upwelling and frontal areas, warm sea-surface temperature anomalies are known to have negative effects on primary and secondary production (Wilson & Adamec 2002, Behrenfeld et al. 2006). Cooler temperatures and higher wind stress can produce deeper convective mixing and increased nutrient supply to support higher spring and summer chlorophyll concentrations, whereas warmer sea-surface temperatures and reduced wind stress can produce shallower mixed layers, leading to reduced nutrient entrainment, and reduced spring and summer chlorophyll (Daly & Smith 1993). Therefore, the negative relationships between demographic parameters and SST (positive for SOI) may reflect the effects of limited food resources on the demographic traits of seabirds. Although climatic fluctuations are often suspected to affect seabird populations through integration along the trophic web up to top predators, one may not exclude direct mechanisms. For example, snowfall or atmospheric temperatures may directly affect breeding success in some species (Murphy et al. 1991, Chastel et al. 1993). A small proportion of relationships between SST and demographic parameters were positive, as also detected in other oceanic ecosystems (Sandvik et al. 2008), suggesting the existence of local or regional oceanographic processes (e.g. see Blain et al. 2001, Park et al. 2008a,b for the Kerguelen plateau).

Although sample sizes were relatively small, the effect of sea ice (SIE and SIC) was contrasted between demographic parameters, probably because different mechanisms were involved (Table 1). About 44% of the relationships between SIE or SIC and breeding success were negative (~25% were positive), whereas ~37% of the relationships between SIE or SIC and adult survival were positive (~12% were negative), and ~54% of the relationships between SIE or SIC and breeding population size were positive (~38% were negative). An increase in SIE or SIC may reduce breeding success because it directly affects the foraging habitat of pagophilic species. When sea-ice extent is greater than normal or when sea-ice concentration is particularly high, Antarctic breeding species feeding within the pack ice or at the edges of the pack ice may have to cover greater distances between the nest and the foraging grounds because they are central place foragers during the breeding season. This would increase the amount of time spent travelling and therefore decrease the feeding frequency of chicks during the

Table 1. Numbers and percentages (in parentheses) of positive, negative and null relationships between climate variables and demographic parameters found in the literature review of Southern Ocean seabirds for all climate variables, and for sea-ice variables for 3 demographic parameters. See Appendix 1 for the definition of variables

	Positive	Effect Negative	Null
Climate variables			
SST	9 (20)	22 (50)	13 (30)
SOI	10 (32)	5 (16)	16 (52)
SIE or SIC	18 (37)	16 (33)	15 (30)
SAM	2 (22)	5 (56)	2 (22)
T	3 (25)	6 (50)	3 (25)
IOD	1 (33)	0 (0)	2 (67)
Effect of SIE or SIC on			
Adult survival	3 (37)	1 (12)	4 (50)
Breeding success	4 (25)	7 (44)	5 (31)
Breeding pairs	7 (54)	5 (38)	1 (8)

chick rearing period, or exceed the fasting capacity of the incubating partner during incubation. Overall this would lead to a decrease in breeding success. This is typically the case for penguins such as the emperor penguin *Aptenodytes forsteri* or the Adélie penguin *Pygoscelis adeliae* (Ainley & LeResche 1973, Ancel et al. 1992, Barbraud & Weimerskirch 2001a, Massom et al. 2009).

Conversely, an increase in SIE or SIC may increase (indirectly) adult survival because it positively affects the Antarctic food web, more particularly its productivity. Sea-ice conditions are known to affect Antarctic food webs, which may in turn affect demographic parameters such as survival and breeding proportions. Several studies suggest a positive relationship between winter SIE or SIC and the abundance of key species of the Antarctic ocean food web such as the Antarctic krill *Euphausia superba* (Loeb et al. 1997, Nicol et al. 2000). Therefore, we hypothesise that extensive sea ice in winter may correspond to higher levels of food resources for seabirds during spring and summer, which may affect their adult survival and their decision to breed (Barbraud & Weimerskirch 2001a, Jenouvrier et al. 2005). Indeed, it is well known that in seabirds the proportion of individuals engaging in reproduction depends in part on physical body condition, which might be directly affected by the amount of food resources available (Drent & Daan 1980, van Noordwijk de Jong 1986, Chastel et al. 1995).

Eventually, these contrasted effects of sea ice on different vital rates affect population size. Indeed, breeding population size in a given year is the outcome of the variations of lower level demographic parameters such as survival, breeding success, breeding proportions and recruitment. Therefore, the effect of SIE or SIC on breeding population size may be mediated through the effects of these climate variables on lower level demographic parameters. Table 1 shows that population size was often found to be positively linked to SIE or SIC. This is not surprising for long-lived species for which the population growth rate is extremely sensitive to adult survival. However, breeding success can also play an important role in population dynamics because it is more variable than adult survival (Gaillard & Yoccoz 2003). For example, the decrease in breeding success limits the population recovery of an emperor penguin population in East Antarctica (Jenouvrier et al. 2009). In addition, since population size in seabirds is often measured by the number of breeders at a colony, the amount of food available in a given year or the following winter may affect the number of birds attempt-ing to breed in the following year, although there may have been no actual change in the population size.

Recruitment and breeding proportions are also important parameters to take into account to understand population responses to sea ice. For example, in the Adélie penguin a negative effect of SIE on breeding population size with a 5 to 6 yr lag is suspected to result from negative effects of large SIE on juvenile survival, which has an effect on breeding population size when individuals recruit to the breeding population at ~6 yr of age (Wilson et al. 2001, Jenouvrier et al. 2006). Extensive sea ice may limit access of penguins to productive waters, with starvation or increased predation disproportionately affecting less-experienced birds.

The complex contrasted effects of sea ice (and to a lesser extent sea-surface temperature) on demographic rates strengthen the importance of considering the entire life cycle to understand the effects of climate on populations. The example of sea ice on seabirds is particularly interesting because it suggests the existence of optimal SIE or SIC conditions which may maximise demographic parameters and population growth rates of seabirds depending on a sea-ice habitat. Ballerini et al. (2009) found a quadratic relationship between Adélie penguin survival and winter SIE and hypothesised that high SIE may limit access to food resources, whereas low SIE may limit abundance of food resources. Interestingly, an increasing number of studies have found non-linear relationships between seabird demographic parameters and climate variables (Gjerdrum et al. 2003, Barbraud et al. 2011), suggesting the widespread existence of optimal environmental conditions for population growth rates. Such non-linear relationships have also been proposed to explain the contrasted population trends of Adélie penguins in Antarctica (Smith et al. 1999), with optimal population growth corresponding to intermediate frequencies of heavy sea-ice conditions (Fig. 3). This conceptual model of optimal environmental conditions may help explain the contrasted responses observed among different populations in the Southern Ocean and other ocean basins (Sandvik et al. 2008).

Mainly documented are relationships between climate variables and breeding success, adult survival and numbers of breeding pairs. The last 2 are the most easily and cost effectively obtained in the field, and statistical developments in capture-mark-recapture methods during the last 3 decades have allowed researchers to obtain robust estimates of adult survival (Williams et al. 2002). Very few studies have investigated the effects of climate on juvenile sur-

vival or recruitment (Appendix 1). However, these parameters may potentially be more sensitive to climate variability, since in such long-lived species, juvenile survival is predicted to be less environmentally canalised (canalisation here refers to a reduction in the variability of a trait) against temporal variability (and potentially environmental variability) than adult survival (Pfister 1998, Gaillard & Yoccoz 2003). In accordance with this prediction, some studies have found stronger relationships between survival of younger individuals and climate factors than with older individuals (Nevoux et al. 2007).

The effects of climate variability on breeding dispersal of Southern Ocean seabirds have only recently been investigated. Dugger et al. (2010) estimated breeding dispersal of Adélie penguins between 3 different colonies in the south-western Ross Sea and found that movement probabilities of breeding adults from one year to the next were higher in years with extensive sea ice or blockage to usual migration patterns (Fig. 4).
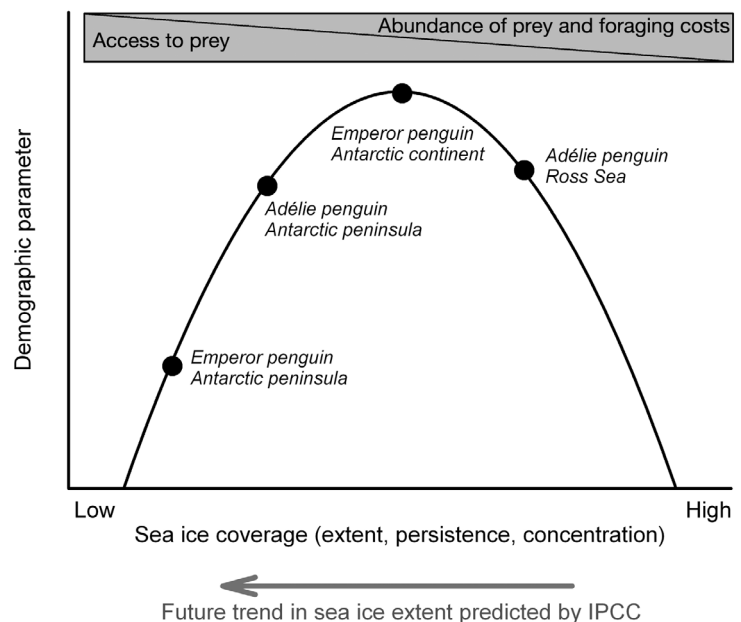
Part of the contrasted responses within species may be caused by the spatial variability in food webs of the Southern Ocean (Trathan et al. 2007). Different areas of the Southern Ocean are dominated by different food webs. For instance, the lower trophic levels of the Scotia Sea region are dominated by krill (Croxall et al. 1988, Murphy et al. 2007), whereas those of the southern Indian Ocean are dominated by myctophids (Pakhomov et al. 1996, Connan et al. 2008, Cherel et al. 2008). Given the variation of habitat preferences of the lower trophic levels we may thus expect different effects of climate change in different food webs and regions, and consequently contrasted upper trophic level responses (Trathan et al. 2007).

The interspecific variability in trophic niche and foraging strategies of seabirds (Weimerskirch 2007) may also partly explain the observed contrasted responses. For instance, at South Georgia, warm sea-surface temperature anomalies have positive effects on the breeding success of black-browed albatrosses *Thalassarche melanophrys* (Nevoux et al. 2010a) but negative effects on the breeding success of gentoo penguins *Pygoscelis papua* (Trathan et al. 2006).

Although several relationships between demographic parameters and climate variables were found for a number of seabird populations in the Southern Ocean, our understanding of the underlying ecological mechanisms remains extremely limited. This is mainly because long-term time series of abundance for prey species of Southern Ocean seabirds are scarce due to sampling difficulties and associated costs. This results in a poor understanding of how biological and physical processes interact across spatial and temporal scales. Perhaps best understood are the demographic and behavioural responses of seabirds breeding in the South Atlantic, where the food webs of this region have been studied since the beginning of the last century (Trathan et al. 2007). The food web of the South Atlantic and Scotia Sea is highly dominated by krill. Atmospheric teleconnections with ENSO generate anomalies in SST in the South Pacific sector of the Southern Ocean which are propagated eastward via the Antarctic Circumpolar Current and reach the South Atlantic with several months lag. Changes in the South Atlantic

Fig. 3. Conceptual model adapted from Smith et al. (1999) illustrating the consequences of sea-ice coverage variation on abundance and access to prey of Antarctic seabirds, and its potential effect on seabird demographic parameters. Dots show the hypothetical positions of populations of penguins. In the Antarctic Peninsula, 1 emperor penguin colony was recently reported as extinct probably as a consequence of sea-ice disappearance during the last decades (Barbrand & Weimerskirch 2001a). On the Antarctic continent colonies appear to be stable during the past 2 decades (Woehler & Croxall 1997, Kooyman et al. 2007, Jenouvrier et al. 2009, Barbraud et al. unpubl. data, Robertson et al. unpubl. data), although major declines were reported during the late 1970s at some colonies (Barbraud & Weimerskirch 2001). The future trend in sea-ice coverage as predicted by IPCC scenarios and models is indicated, and is expected to negatively affect the northernmost penguin colonies (Jenouvrier et al. 2009, Ainley et al. 2010a). Taxonomic names see Appendix 1

sector of SST and related fluctuations in SIE affect the recruitment and dispersal of krill, which, in turn, affects the breeding success and populations (Fig. 5) of seabirds that depend on this prey species (Reid et al. 2005, Forcada et al. 2006, Murphy et al. 2007). Similar processes seem to occur south of Kerguelen in the southern Indian Ocean. In this region SST anomalies are also linked to ENSO through atmospheric teleconnections and possibly eastward propagation of SST anomalies generated in the South Pacific (Guinet et al. 1998, Park et al. 2004, Murphy et al. 2007). During warm SST anomalies the diet of blue petrels *Halobaena caerulea* breeding at and foraging south of the Kerguelen Islands is highly skewed towards crustaceans (euphausiids and *Themisto gaudichaudii*), whereas fishes (mainly myctophids) constitute the main part of their diet during normal years (Connan et al. 2008). Interestingly the per capita energetic content of crustacean species consumed during warm SST anomalies is less important than the energetic value of fish species consumed, and body condition, breeding probability and success, and adult survival are all negatively affected by warm SST and positive SSH anomalies south of Kerguelen (Guinet et al. 1998, Barbraud & Weimerskirch 2003, 2005).
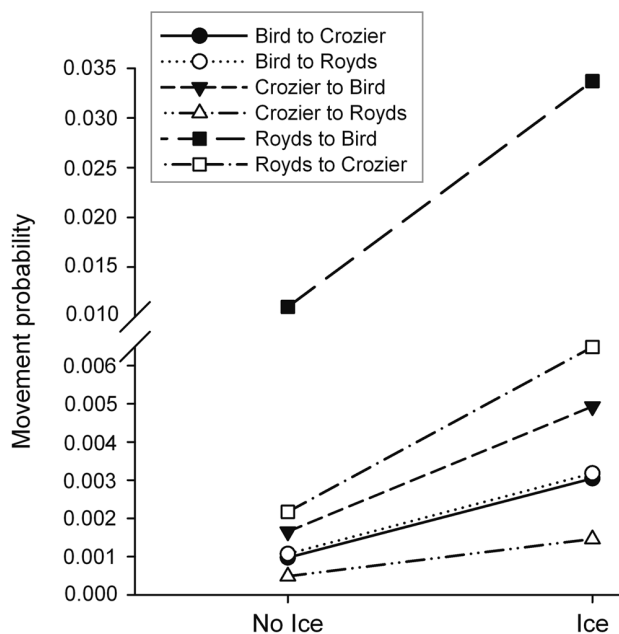

Fig. 4. *Pygoscelis adeliae.* Effect of sea-ice variability on annual breeding dispersal probability of adult Adélie penguins breeding in the south-western Ross Sea, from 1996 to 2007. Movement probabilities differed between colonies but were higher in years with extensive sea ice or when icebergs were present serving as physical barriers and altering the spring migration route of penguins. From Dugger et al. (2010)

EFFECTS OF FISHERIES BYCATCH ON DEMOGRAPHY AND POPULATION DYNAMICS OF SOUTHERN OCEAN SEABIRDS

Although accidental bycatch of seabirds in fishing gear has been an acknowledged problem for a relatively long time (e.g. Perrin 1969, Weimerskirch & Jouventin 1987, Brothers 1991), most studies examining the effects of fisheries bycatch on demographic parameters and population dynamics are relatively recent (Oro et al. 1995, Cuthbert et al. 2003, Tuck et al. 2003, Lewison et al. 2004, Votier et al. 2004, Véran et al. 2007, Barbraud et al. 2008, Frederiksen et al. 2008, Rolland et al. 2008, Véran & Lebreton 2008). The species reported most frequently caught in longlines worldwide include albatrosses, petrels and shearwaters (Brothers et al. 1999), most of which have highly unfavourable conservation status (Baker et al. 2002). In the Southern Ocean, accidental mortality in trawling fisheries may also be high (Sullivan et al. 2006, Croxall 2008, Watkins et al. 2008).

Table 2 summarizes the studies that investigated the effect of fisheries bycatch on 5 demographic parameters of Southern Ocean seabirds. Although some studies tested for explicit relationships and others inferred an effect of bycatch on population dynamics using population models including additive mortality effects, the majority of studies found negative effects of fishing effort or bycatch rates on demographic parameters (~64%). Despite positive effects of fisheries activities on breeding success of
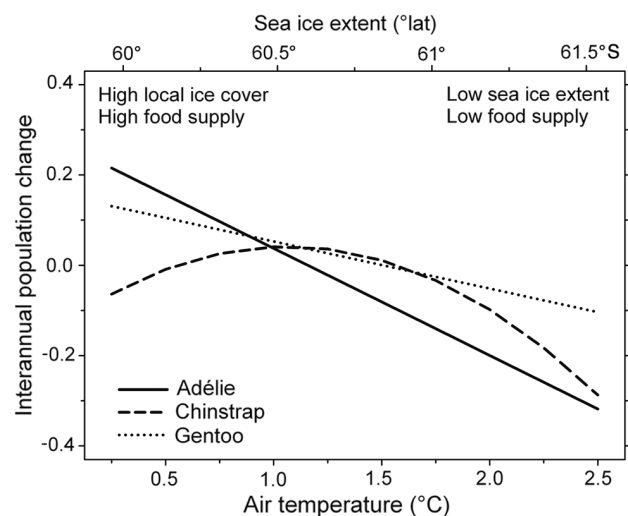

Fig. 5. *Pygoscelis* spp. Representation of the diversity of penguin population responses (interannual changes in numbers of breeding pairs) to the environment at Signy Island, South Orkney Islands. Responses may be linear or non-linear depending on the species' ecological requirements. From Forcada et al. (2006)

some species, probably due to additional food resources such as bait, offal, or discards (Northern Hemisphere: Garthe et al. 1996, Oro et al. 1996; Southern Hemisphere: Grémillet et al. 2008), most studies reported negative effects on adult survival. This may have severe consequences on populations of long-lived species, whose population growth rate is highly sensitive to small variations in adult mortality (Lebreton & Clobert 1991).

For methodological reasons, very few studies have investigated the effects of fisheries activities on juvenile survival or recruitment, and they also suggest negative effects. Even if population growth rate of seabirds is less sensitive to variations in these parameters, chronic mortality of the younger age classes may in the long term have detrimental effects on populations (Barbraud et al. 2008) as it would deplete the pool of future breeders. Higher vulnerability of younger individuals to fishing gear has been reported in several seabird species (Murray et al. 1993, Gales et al. 1998, Bregnballe & Frederiksen 2006). Younger birds may (1) spend more time in areas with high longline efforts than adult birds, (2) be less efficient foragers than adults and may therefore attempt to fish behind vessels more frequently, (3) be more hungry than adults and take more risks behind vessels, and (4) be less experienced than adults in foraging behind vessels without getting hooked. For a number of studies (~24%), no significant effect of fishing effort on demographic parameters was found. This may be due to a lack of statistical power or methodological problems, or the implementation of mitigation measures to limit bycatch. Indeed, mitigation measures (mainly within Exclusive Economic Zones and in the Convention on the Conservation of Antarctic Marine Living Resources area) have drastically reduced bycatch rates in some fisheries of the Southern Ocean during the last decades (Croxall & Nicol 2004, Robertson et al. 2006, SC-CCAMLR 2006, Delord et al. 2010), and it was generally assumed that the level of bycatch was proportional to the fishing effort (Véran et al. 2007) because very little information was available to directly estimate harvest rates. Further modelling is needed to take into account and specifically test whether the decrease in bycatch following mitigation measures can be detected on demographic parameters such as adult survival.

It is known that there are no detailed demographic data for several species of Southern Ocean seabirds affected by bycatch. This causes many difficulties in estimating the impact of bycatch on these species. The potential biological removal approach offers an interesting alternative way for assessing the poten-

Table 2. Numbers and percentages (in parentheses) of positive, negative and null relationships between fishing effort (trawl and longline) and demographic parameters found in the literature review of Southern Ocean seabirds

	Positive	Negative	Null
		Effect	
Adult survival	1 (5)	14 (64)	7 (31)
Juvenile survival	0 (0)	2 (67)	1 (33)
Recruitment	0 (0)	1 (100)	0 (0)
Breeding success	3 (100)	0 (0)	0 (0)
Breeding pairs	0 (0)	4 (100)	0 (0)

tial for populations to sustain additional mortalities (Wade 1998, Taylor et al. 2000, Niel & Lebreton 2005). This method has recently been further developed and used to assess the potential effects of bycatch on Southern Ocean seabirds (Hunter & Caswell 2005, Dillingham & Fletcher 2008).

The effect of fisheries on Southern Ocean seabird populations through the harvest of intermediate trophic level species remains largely unexplored (Wagner & Boersma 2011). Studies using predator–prey models or ecosystem models remain largely theoretical (May et al. 1979) and often suffer from a shortage of empirical data (Hill et al. 2006). Major fisheries have operated in the Southern Ocean since the early 1970s and have led to the overexploitation of several species such as marbled rock cod *Notothenia rossi* and icefish *Champsocephalus gunnari* (Croxall & Nicol 2004), but their potential effect on seabird population remains poorly known. However, correlations between predator populations and fish biomass in predator foraging areas suggest that several predator populations including seabirds (gentoo penguin, macaroni penguin, imperial shag *Phalacrocorax* spp.) that feed extensively on exploited fish species declined simultaneously during the 2 periods (early 1970s and mid-1980s) of heavy fishing (Ainley & Blight 2008).

The effect of the depletion of whale stocks during the 1950s to 1960s on Southern Ocean seabirds remains speculative, essentially because very few monitoring and trophic studies were underway during the whaling period (Ainley et al. 2010b). Given the major role of cetaceans in the structuring of Southern Ocean food webs (Balance et al. 2006), the demise of large whale species in the Southern Ocean may explain some changes in the population dynamics of several seabird species, through a release of trophic competition and the resulting krill surplus or an effect of upper level predators though top-down forcing (Ainley et al. 2010b).

Although the krill fishery has been the largest fishery in the Southern Ocean since the late 1970s, its impact on upper trophic levels, such as seabirds, is still poorly understood and remains to be quantified. There is evidence for ecosystem responses to the regional warming of the West Antarctic Peninsula that has occurred during the past 50 yr. In particular, decreased sea-ice extent and duration altered the phytoplankton and zooplankton communities and had negative effects on krill recruitment and on top predator populations such as Adélie and chinstrap penguins (Ducklow et al. 2007, Hinke et al. 2007, and references in Appendix 1). However, Trivelpiece et al. (2011) recently suggested that, in addition to climate, fisheries may have played an important role in shaping the population dynamics of penguins in the West Antarctic Peninsula and the Scotia Sea. According to their scenario (Fig. 6), favourable climate conditions and reduced competition for krill following the massive and large-scale harvesting of seals, whales, ice fishes and notothenioids from the early 1820s to the 1980s may have favoured Adélie and chinstrap penguins whose populations increased. Since the late 1970s climate changes (sea-ice loss), increased competition for krill following the recovery of marine mammal populations, and the expansion of the krill fishery resulted in poor environmental conditions for penguins (decrease in krill density), the populations of which declined.
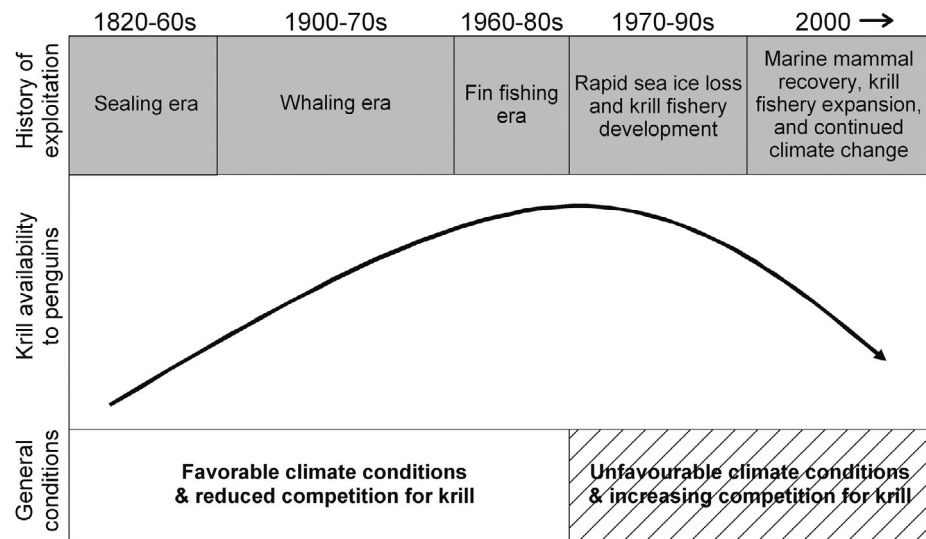
COMBINED EFFECTS OF CLIMATE AND FISHERIES BYCATCH ON POPULATION DYNAMICS

Comparing the relative effects of climate factors and bycatch levels on demographic parameters remains a difficult task at present due to the heterogeneity of the methods used to estimate their respective effects. To be comparable, both effects need to be tested within the same statistical and modelling framework and the variables need to be standardised (Grosbois et al. 2008). This was possible for a limited number of studies on 4 albatross species of the southern Indian Ocean (Rolland et al. 2010). The mean ± SE of the slopes of the relationships between adult survival (which was found to be the parameter affected by fishing effort) and the standardised fishing effort (assumed to be proportional to bycatch) was −0.237 ± 0.041. This mean was 0.162 ± 0.020 for the relationships between breeding success (which was found to be the parameter most frequently related to climate variables) and the standardised climate variables. Although these mean slopes are not

statistically different at the 0.05 level ($\chi^2 = 0.172$, p = 0.10), the mean effect of fishing effort is nevertheless 46.3% higher than the mean effect of climate variables. Because it mainly affects adult survival, one might conclude that for these 4 albatross species the population-level effect of fishing effort (and bycatch) is probably more important than the influence of climate variability.

The effects of climate variability on the one hand and of fisheries activities on the other were shown to be related to several demographic parameters in seabird populations in the Southern Ocean and other ocean basins (Appendix 1, Tables A1 & A2). However, very few studies have combined both effects into fully parameterized population models to understand past population changes and to predict population growth rates under several scenarios of climate and fishing effort. In the North Sea, Frederiksen et al. (2004) built a matrix population model integrating the effect of SST on adult survival and breeding success of the kittiwake *Rissa tridactyla*, which were also negatively affected by the lesser sandeel *Ammodytes marinus* fishery. Their model suggested that the observed changes in the demographic parameters related to changes in SST and fisheries activities could explain the observed change in population growth rate of the kittiwake population. Furthermore, stochastic modelling indicated that the population was unlikely to increase if the fishery was active or SST increased and that the population was almost certain to decline if both occurred. The same approach was used by Barbraud et al. (2008) on a population of the most frequently killed Southern Ocean seabird species by longline fisheries, the white-chinned petrel *Procellaria aequinoctialis*. The present study showed contrasted effects of fishing efforts, with a positive effect of toothfish *Dissostichus eleginoides* fishing effort on breeding success, and negative effects of toothfish and hake *Merluccius* spp. fishing effort on petrel recruitment. Climate (SOI) was found to mainly affect adult survival in this species. The population trajectory of a population matrix model explicitly integrating the relationships between environmental parameters and demographic parameters was very similar to the observed population growth rate estimated from independent survey data. Population modelling suggests that when fisheries are operating (and assuming a proportional level of bycatch), the population growth rate is more sensitive to a decrease in the mean or to an increase in the variance of SOI than to a change in the fishing effort. If the fisheries continue to operate at current levels of bycatch, it is likely that the population will probably

Fig. 6. *Pygoscelis adeliae*, *P. antarctica*. Diagram of ecosystem perturbations in the Scotia Sea. From the early 1820s to the 1980s climate conditions were favourable for Adélie and chinstrap penguins, and exploitation of seals, whales and fin fishes resulted in a reduced competition for krill. From the 1970s, climate conditions became progressively unfavourable, and recovery of marine mammal populations and the expansion of the krill fishery resulted in increased competition for krill. From Trivelpiece et al. (2011)

not recover from its past decline. However, due to the additive effects of SOI and fishing effort on adult survival, an increase in SOI (corresponding to a decrease in frequency and intensity of El Niño events) may compensate for the negative effects of fisheries bycatch.

For the black-browed albatross *Thalassarche melanophrys*, whose adult survival and breeding success are affected by SST and bycatch mortality, population modelling indicated that population equilibrium was precarious, resulting from multiple factors and complex relationships between demographic parameters and environmental conditions (Rolland et al. 2009a). If fishing effort (and bycatch) stops over the wintering area of the studied population, the population would increase at 3.5% yr^{-1}, suggesting that bycatch mortality probably currently limits the growth of the black-browed albatross population at Kerguelen (Fig. 7). These studies illustrate the importance of population models for quantifying the effects of climate and fisheries activities on populations and for projecting the possible trajectories of a population according to predicted climate change and possible modifications in human activities.

SUMMARY AND CONCLUSIONS

Overall, our review suggests that climate fluctuation mainly affected low elasticity demographic traits (fecundity, productivity), contrary to bycatch which mainly affects high elasticity traits (survival). Because seabirds are long-lived organisms, bycatch represents a serious threat to several seabird populations and mitigation strategies may be effective (decrease

fishing effort to preserve populations from the effect of climate change, e.g. Igual et al. 2009). Population models also suggest that climate can act synergistically with bycatch and accelerate population declines or may partially counteract additional mortality.
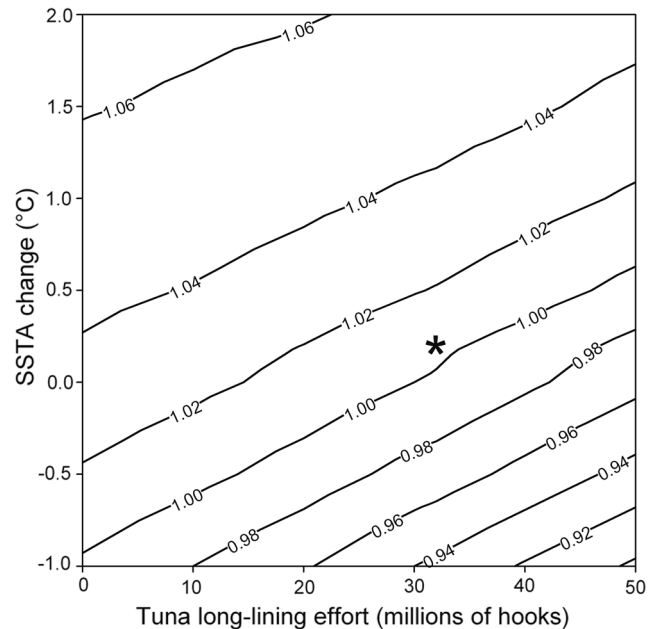

Fig. 7. *Thalassarche melanophrys*. Interaction between the effects of climate variability (sea-surface temperature anomalies [SSTA] in the foraging areas used during the breeding period) and fisheries bycatch (long-lining effort in the area used during the non-breeding period) on the population growth rate of a black-browed albatross population at Kerguelen Island. The star represents the conditions of fisheries and sea-surface temperature at the time the study was performed, and solid lines are isoclines where population growth rates are constant for different parameter values. From Rolland et al. (2009a)

Although climate factors that affect seabird demographic parameters are only to some extent within human control, any policy changes aimed at reversing the warming trend and decreasing trend in sea-ice extent in the Southern Ocean will be slow to take effects due to the inertia of the earth climate system. The microevolutionary responses of Southern Ocean seabirds to climate change are also limited due to the long generation time of these species and the fast environmental changes, although they probably can track some environmental changes through phenotypic plasticity. For example, life-history theory predicts that an increase in adult mortality should select for an earlier age at first reproduction and for an increase in reproductive effort (Gadgil & Bossert 1970, Schaffer 1974, Law 1979, Charlesworth 1994). Such responses have experimentally or empirically been reported for a number of fish species (e.g. Reznick et al. 1990, Rochet et al. 2000), and the decrease in age at first reproduction observed in a wandering albatross *Diomedea exulans* population during a period of high adult mortality caused by fisheries bycatch is consistent with this prediction (Weimerskirch & Jouventin 1987). The decrease in female age at sexual maturation in the crabeater seal *Lobodon carcinophagus* through time is also possibly linked to an increase in food availability following the decline of baleen whales due to whaling (Bengtson & Siniff 1981). However, evolutionary constraints specific to most Southern Ocean seabirds may limit their response capacity to an increase in mortality induced by fisheries bycatch. Clutch size is limited to 1 egg yr^{-1}, breeding frequency is highly constrained by the seasonality of the Southern Ocean, and size at maturity is constrained in those species with finite structural growth (Warham 1990).

Thus, it seems prudent and in accordance with the precautionary principle to evaluate and quantify the effect of fisheries bycatch and to apply mitigation measures when necessary for those fisheries known to interact with threatened populations. Population models can help identify the demographic parameters most affected by bycatch. The influence of other environmental factors on Southern Ocean seabird population dynamics also need to be assessed. For example, the population growth rate of Indian yellow nosed albatrosses *Thalassarche carteri* at Amsterdam Island is known to be limited by outbreaks of avian cholera causing high chick mortality rather than by climatic conditions or fishery-induced bycatch (Rolland et al. 2009a). Introduced predators are known to affect seabird demographic parameters and population dynamics too (Marion Island: Cooper et al. 1995;

Possession Island: Jouventin et al. 2003; Réunion Island: Dumont et al. 2010; cats: Nogales et al. 2004; rats: Jones et al. 2008), and several Southern Ocean islands host one or several species of introduced predators. Southern Ocean seabirds are also increasingly exposed to marine debris, pollutants and chemicals, which may also potentially affect their physiology, behaviour and demography (Burger & Gochfeld 2002). For example, in common guillemots *Uria aalge* breeding in the North Atlantic there was a doubling of adult mortality associated with major oil spills in the wintering areas of the birds, and recruitment was higher in years following oil spills than following non-oil-spill years, probably through reduced competition and compensatory recruitment at the breeding colony (Votier et al. 2008). Finally, increased freshwater input from melting glaciers and ice shelves acts to increase stratification along coastal margins, which, in turn, may affect phytoplankton blooms (Moline et al. 2008) and release persistent organic pollutants into the ecosystem where they may accumulate in higher trophic level predators (Geisz et al. 2008).

FUTURE CHANGE AND RESEARCH NEEDED

Predictions from climatologists in the 4th IPCC assessment can be used directly in population models to help determine the future of populations (Jenouvrier et al. 2009, Hare et al. 2010, Wolf et al. 2010, Barbraud et al. 2011). Future population models may eventually need to consider potentially important effects such as non-linear relationships between demographic parameters and climate or fishery variables (Mysterud et al. 2001, Gimenez & Barbraud 2009), density dependence (Frederiksen et al. 2001, Lima et al. 2002), synergistic effects with other environmental factors (Brook et al. 2008), or microevolutionary changes (Kinnison & Hairston 2007, Coulson et al. 2010, Ozgul et al. 2010). From a methodological point of view recent developments in capture-mark-recapture models permit robust estimates of juvenile survival, recruitment and dispersal (e.g. Lebreton et al. 2003). These methods are particularly appropriate for seabirds with delayed maturity, and we believe there will be an increasing use in the near future. Future studies aimed at testing the effects of climate factors on these demographic parameters (and others) should use robust and standardised statistical methods so that future results can be integrated into meta-analyses (Grosbois et al. 2008).

One additional uncertainty in the future concerning the combined effects of fisheries and climate on seabird populations is the effect of climate on fisheries. Longline fisheries are large-scale mobile fisheries the distribution and effort of which are influenced by environmental factors and especially large-scale climatic processes (Tuck et al. 2003, Lehodey et al. 1997, 2006). Thus, future climate change will undoubtedly affect target species of large migratory fishes such as tuna (Hobday 2010). Lacking are model-based projections of the spatio-temporal distribution of fisheries activities in the Southern Ocean that would help build more realistic scenarios for Southern Ocean seabirds.

Consequently, fisheries distribution and effort, and therefore future interactions, will be complex and more difficult to predict. Intensive land- and at-sea-based long-term studies remain the only source of consistent data allowing evaluation of population trends, dynamics and how they are affected by environmental factors, and engaging in such studies should be a high priority for research and management (Clutton-Brock & Sheldon 2010). Additional measurements on other trophic levels (abundance of prey), foraging behaviour, climate–fishery interactions, bycatch rates, and on the mechanisms underlying phenotypic plasticity will increase the comprehensive and predictive power of these long-term studies (Visser 2008).

Studies combining seabird demographic, trophic, behavioural (foraging) and physiological data will be most promising in order to understand the mechanistic responses of seabirds to climate change and to improve our ability to build sound scenarios for the effects of future climate changes. For example, in the Northern Hemisphere, pioneering studies have examined the links between food abundance, nutritional stress (hormone corticosterone), reproduction and survival of individuals of the kittiwake *Rissa tridactyla* (Kitaysky et al. 2010). When possible, future studies will also have to take into account potential ecological processes of trophic cascades, competition, predation and facilitation when attempting to address climate effects on Southern Ocean seabird populations (Ainley et al. 2010b).

LITERATURE CITED

Adamson DA, Whetton P, Selkirk PM (1988) An analysis of air temperature records for Macquarie Island: decadal warming, ENSO cooling and southern hemisphere circulation patterns. Pap Proc R Soc Tasman 122:107–112

Ainley DG, Blight LK (2008) Ecological repercussions of historical fish extraction from the Southern Ocean. Fish Fish 9:1–26

Ainley DG, LeResche RE (1973) The effects of weather and ice conditions on breeding Adélie penguins. Condor 75: 235–255

Ainley DG, Clarke ED, Arrigo K, Fraser WR, Kato A, Barton KJ, Wilson PR (2005) Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. Antarct Sci 17:171–182

Ainley DG, Ballard G, Ackley S, Blight LK and others (2007) Paradigm lost, or is top-down forcing no longer significant in the Antarctic marine ecosystem? Antarct Sci 19:283–290

Ainley D, Russell J, Jenouvrier S, Woehler E, Lyver PO'B, Fraser WR, Kooyman GL (2010a) Antarctic penguin response to habitat change as Earth's troposphere reaches 2°C above preindustrial levels. Ecol Monogr 80:49–66

Ainley DG, Ballard G, Blight LK, Ackley S and others (2010b) Impacts of cetaceans on the structure of Southern Ocean food webs. Mar Mamm Sci 26:482–498

Alory G, Wijffels S, Meyers G (2007) Observed temperature trends in the Indian Ocean over 1960–1999 and associated mechanisms. Geophys Res Lett 34. doi:10.1029/2006GL028044

Ancel A, Kooyman GL, Ponganis PJ, Gendner JP and others (1992) Emperor penguins foraging behaviour as a resource detector in winter and summer. Nature 360: 336–339

Arnold JM, Brault S, Croxall JP (2006) Albatross populations in peril: a population trajectory for black-browed albatrosses at South Georgia. Ecol Appl 16:419–432

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432:100–103

Baker GB, Wise BS (2005) The impact of pelagic longline fishing on the flesh-footed shearwater *Puffinus carneipes* in eastern Australia. Biol Conserv 126:306–316

Baker GB, Gales R, Hamilton S, Wilkinson V (2002) Albatrosses and petrels in Australia: a review of their conservation and management. Emu 102:71–97

Baker GB, Double MC, Gales R, Tuck GN and others (2007) A global assessment of the impact of fisheries-related mortality on shy and white-capped albatrosses: conservation implications. Biol Conserv 137:319–333

Balance L, Pitman RL, Hewitt RP, Siniff DB, Trivelpiece WZ, Clapham PJ, Brownell RL (2006) The removal of large whales from the Southern Ocean: Evidence for long-term ecosystem effects? In: Estes JA, Demaster DP, Doak DF, Williams TE, Brownell RL (eds) Whales, whaling and ocean ecosystems. University of California Press, Berkeley, CA, p 215–230

Ballard G, Toniolo V, Ainley DG, Parkinson CL, Arrigo KR, Trathan PN (2010) Responding to climate change: Adélie penguins confront astronomical and ocean boundaries. Ecology 91:2056–2069

Ballerini T, Tavecchia G, Olmastroni S, Pezzo F, Focardi S (2009) Nonlinear effects of winter sea ice on the survival

probabilities of Adélie penguins. Oecologia 161:253–265

Barbraud C, Cotté C (2008) Paradigms need hypothesis testing: no evidence for top-down forcing on Adélie and emperor penguin populations. Antarct Sci 20:391–392

Barbraud C, Weimerskirch H (2001a) Emperor penguins and climate change. Nature 411:183–186

Barbraud C, Weimerskirch H (2001b) Contrasted effects of the extent of sea-ice on the breeding performance of an Antarctic top predator, the snow petrel *Pagodroma nivea.* J Avian Biol 32:297–302

Barbraud C, Weimerskirch H (2003) Climate and density shape population dynamics of a marine top predator. Proc R Soc Lond B Biol Sci 270:2111–2116

Barbraud C, Weimerskirch H (2005) Environmental conditions and breeding experience affect costs of reproduction in blue petrels. Ecology 86:682–692

Barbraud C, Weimerskirch H (2006) Antarctic birds breed later in response to climate change. Proc Natl Acad Sci USA 103:6248–6251

Barbraud C, Lormée H, Le Nevé A (2000a) Body size and determinants of laying date variation in the snow petrel *Pagodroma nivea.* J Avian Biol 31:295–302

Barbraud C, Weimerskirch H, Guinet C, Jouventin P (2000b) Effect of sea-ice extent on adult survival of an Antarctic top predator: the snow petrel *Pagodroma nivea.* Oecologia 125:483–488

Barbraud C, Marteau C, Ridoux V, Delord K, Weimerskirch H (2008) Demographic response of a population of white-chinned petrels *Procellaria aequinoctialis* to climate and longline fishery bycatch. J Appl Ecol 45:1460–1467

Barbraud C, Rivalan P, Inchausti P, Nevoux M, Rolland V, Weimerskirch H (2011) Contrasted demographic responses facing future climate change in Southern Ocean seabirds. J Anim Ecol 80:89–100

Baroni C, Orombelli G (1994) Abandoned penguin rookeries as Holocene paleoclimatic indicators in Antarctica. Geology 22:23–26

Behrenfeld MJ, O'Malley RT, Siegel DA, McClain CR and others (2006) Climate-driven trends in contemporary ocean productivity. Nature 444:752–755

Bengtson JL, Siniff DB (1981) Reproductive aspects of female crabeater seals (*Lobodon carcinophagus*) along the Antarctic Peninsula. Can J Zool 59:92–102

Bertram DF, Harfenist A, Smith BD (2005) Ocean climate and El Niño impacts on survival of Cassin's auklets from upwelling and downwelling domains of British Columbia. Can J Fish Aquat Sci 62:2841–2853

Blain S, Tréguer P, Belviso S, Bucciarelli E and others (2001) A biogeochemical study of the island mass effect in the context of the iron hypothesis: Kerguelen Islands, Southern Ocean. Deep-Sea Res I 48:163–187

Bregnballe T, Frederiksen M (2006) Net-entrapment of great cormorants *Phalacrocorax carbo sinensis* in relation to individual age and population size. Wildl Biol 12:143–150

Brierley AS, Fernandes PG, Brandon MA, Armstrong F and others (2002) Antarctic krill under sea ice: elevated abundance in a narrow band just south of ice edge. Science 295:1890–1892

British Antarctic Survey (1987) British Antarctic Survey annual report for 1986/87. British Antarctic Survey, Cambridge

Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergies among extinction drivers under global change. Trends Ecol Evol 23:453–460

Brothers N (1991) Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. Biol Conserv 55:255–268

Brothers N, Cooper J, Lokkeborg S (1999) The incidental catch of seabirds by longline fisheries: worldwide review and technical guidelines for mitigation. FAO Fish Circ No 937

Budd GM (2000) Changes in Heard Island glaciers, king penguins and fur seals since 1947. Pap Proc R Soc Tasman 133:47–60

Burger J, Gochfeld M (2002) Effects of chemicals and pollution on seabirds. In: Schreiber EA, Burger J (eds) Biology of marine birds. CRC Press, Boca Raton, FL, p 485–526

Burger AE, Schaffer SA (2008) Application of tracking and data-logging technology in research and conservation of seabirds. Auk 125:253–264

Chambers LE (2004) The impact of climate on little penguin breeding success. Report 100, Bureau of Meteorology Research Center Research, Melbourne

Charlesworth B (1994) Evolution in age structured populations. Cambridge University Press, Cambridge

Chastel O, Weimerskirch H, Jouventin P (1993) High annual variability in reproductive success and survival of an Antarctic seabird, the snow petrel *Pagodroma nivea*: a 27-year study. Oecologia 94:278–285

Chastel O, Weimerskirch H, Jouventin P (1995) Body condition and seabird reproductive performance: a study of three petrel species. Ecology 76:2240–2246

Cherel Y, Ducatez S, Fontaine C, Richard P, Guinet C (2008) Stable isotopes reveal the trophic position and mesopelagic fish diet of female southern elephant seals breeding on the Kerguelen Islands. Mar Ecol Prog Ser 370: 239–247

Clutton-Brock T, Sheldon BC (2010) The seven ages of *Pan.* Science 327:1207–1208

Connan M, Mayzaud P, Trouvé C, Barbraud C, Cherel Y (2008) Interannual dietary changes and demographic consequences in breeding blue petrels from Kerguelen Islands. Mar Ecol Prog Ser 373:123–135

Cooper J, Marais AVN, Bloomer JP, Bester MN (1995) A success story: breeding of burrowing petrels (Procellariidae) before and after the eradication of feral cats *Felis catus* at subantarctic Marion Island. Mar Ornithol 23:33–37

Coulson T, Tuljapurkar S, Childs DZ (2010) Using evolutionary demography to link history theory, quantitative genetics and population ecology. J Anim Ecol 79: 1226–1240

Crick HQ, Dudley C, Glue DE (1997) UK birds are laying eggs earlier. Nature 388:526

Croxall JP (2008) Seabird mortality and trawl fisheries. Anim Conserv 11:255–256

Croxall JP, Nicol S (2004) Management of Southern Ocean fisheries: global forces and future sustainability. Antarct Sci 16:569–584

Croxall JP, McCann TS, Prince PA, Rothery P (1988) Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976–1987: implications for Southern Ocean monitoring studies. In: Sahrhage D (ed) Antarctic Ocean resource variability. Springer-Verlag, Berlin, p 261–285

Cunningham DM, Moors PJ (1994) The decline of rockhopper penguins *Eudyptes chrysocome* at Campbell Island, Southern Indian Ocean and the influence of rising sea temperatures. Emu 94:27–36

Curran MAJ, van Ommen TD, Morgan VI, Phillips KL,

Palmer AS (2003) Ice core evidence for Antarctic sea ice decline since the 1950s. Science 302:1203–1206

Cuthbert R, Ryan PG, Cooper J, Hilton G (2003) Demography and population trends of the Atlantic yellow-nosed albatross. Condor 105:439–452

Daly KL, Smith WO (1993) Physical–biological interactions influencing marine plankton production. Annu Rev Ecol Syst 24:555–585

de la Mare W (2009) Changes in Antarctic sea-ice extent from direct historical observations and whaling records. Clim Change 92:461–493

Delord K, Besson D, Barbraud C, Weimerskirch H (2008) Population trends in a community of large Procellariiforms of Indian Ocean: potential effects of environment and fisheries interactions. Biol Conserv 141:1840–1856

Delord K, Gasco N, Barbraud C, Weimerskirch H (2010) Multivariate effects on seabird bycatch in the legal Patagonian toothfish longline fishery around Crozet and Kerguelen Islands. Polar Biol 33:367–378

Dillingham PW, Fletcher D (2008) Estimating the ability of birds to sustain additional human-caused mortalities using a simple decision rule and allometric relationships. Biol Conserv 141:1783–1792

Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252

Ducklow HW, Baker K, Martinson DG, Quetin LB and others (2007) Marine pelagic ecosystems: the West Antarctic Peninsula. Philos Trans R Soc Lond B 362:67–94

Dugger KM, Ainley DG, Lyver POB, Barton K, Ballard G (2010) Survival differences and the effect of environmental instability on breeding dispersal in an Adélie penguin meta-population. Proc Natl Acad Sci USA 107: 12375–12380

Dumont Y, Russell JC, Lecomte V, Le Corre M (2010) Conservation of endangered endemic seabirds within a multi-predator context: the Barau's petrel in Réunion Island. Nat Resour Model 23:381–436

Durant JM, Anker-Nilssen T, Stenseth NC (2003) Trophic interactions under climate fluctuations: the Atlantic puffin as an example. Proc R Soc Lond B 270:1461–1466

Emmerson L, Southwell C (2008) Sea ice cover and its influence on Adélie penguin reproductive performance. Ecology 89:2096–2102

Emslie SD (2001) Radiocarbon dates from abandoned penguin colonies in the Antarctic Peninsula region. Antarct Sci 13:289–295

Emslie SD, McDaniel JD (2002) Adélie penguin diet and climate change during the middle to late Holocene in northern Marguerite Bay, Antarctic Peninsula. Polar Biol 25:222–229

Emslie SD, Woehler EJ (2005) A 9000-year record of Adélie penguin occupation and diet in the Windmill Islands, East Antarctica. Antarct Sci 17:57–66

Emslie SD, Fraser W, Smith RC, Walker W (1998) Abandoned penguin colonies and environmental change in the Palmer Station area, Anvers Islands, Antarctic Peninsula. Antarct Sci 10:257–268

Emslie SD, Berkman PA, Ainley DG, Coats L, Polito M (2003) Late-Holocene initiation of ice-free ecosystems in the southern Ross Sea, Antarctica. Mar Ecol Prog Ser 262: 19–25

Emslie SD, Coats L, Licht K (2007) A 45 000 yr record of Adélie penguins and climate change in the Ross Sea, Antarctica. Geology 35:61–64

Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean. Glob Change Biol 15: 1618–1630

Forcada J, Trathan PN, Reid K, Murphy EJ, Croxall JP (2006) Contrasting population changes in sympatric penguin species in association with climate warming. Glob Change Biol 12:411–423

Fraser WR, Ainley DG, Trivelpiece WZ, Trivelpiece SG (1992) Increases in Antarctic penguin populations: Reduced competition with whales or a loss of sea ice due to environmental warming? Polar Biol 11:525–531

Frederiksen M, Lebreton JD, Bregnballe T (2001) The interplay between culling and density-dependence in the great cormorant: a modelling approach. J Appl Ecol 38:617–627

Frederiksen M, Wanless S, Harris MP, Rothery P, Wilson LJ (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwake. J Appl Ecol 41:1129–1139

Frederiksen M, Daunt F, Harris MP, Wanless S (2008) The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. J Anim Ecol 77:1020–1029

Frenot Y, Gloaguen JC, van de Vijver B, Beyens L (1997) Datation de quelques sédiments tourbeux holocènes et oscillations glaciaires aux îles Kerguelen. CR Acad Sci Paris 320:567–573

Gadgil M, Bossert WH (1970) Life historical consequences of natural selection. Am Nat 104:1–24

Gaillard JM, Yoccoz NG (2003) Temporal variation in survival of mammals: A case of environmental canalization? Ecology 84:3294–3306

Gales R, Brothers N, Reid T (1998) Seabird mortality in the Japanese tuna longline fishery around Australia, 1988–1995. Biol Conserv 86:37–56

Garthe S, Camphuysen CJ, Furness RW (1996) Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. Mar Ecol Prog Ser 136:1–11

Gaston AJ, Gilchrist HG, Hipfner JM (2005) Climate change, ice conditions and reproduction in Arctic nesting marine birds: Brunnich's guillemot (*Uria lomvia* L.). J Anim Ecol 74:832–841

Geisz HN, Dickhut RM, Cochran MA, Fraser WR, Ducklow HW (2008) Melting glaciers: a probable source of DDT to the Antarctic Marine ecosystem. Environ Sci Technol 42: 3958–3962

Gille ST (2002) Warming of the Southern Ocean since the 1950s. Science 295:1275–1277

Gimenez O, Barbraud C (2009) The efficient semiparametric regression modeling of capture-recapture data: assessing the impact of climate on survival of two Antarctic seabird species. In: Thomson DL, Cooch EG, Conroy MJ (eds) Modeling demographic processes in marked populations. Springer-Verlag, Berlin, p 43–58

Gjerdrum C, Vallée AMJ, St Clair CC, Bertram DF, Ryder JL, Blackburn GS (2003) Tufted puffin reproduction reveals ocean climate variability. Proc Natl Acad Sci USA 100:9377–9382

Gong DY, Wang SW (1998) Antarctic oscillation: concept and applications. Chin Sci Bull 43:734–738

Goutte A, Antoine E, Chastel O (2011) Experimentally delayed hatching triggers a magnified response in a long-lived bird. Horm Behav 59:167–173

Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJM, Ryan PG (2008) A junk-food hypothesis

for gannets feeding on fishery waste. Proc R Soc Lond B 275:1149–1156

Grosbois V, Gimenez O, Gaillard JM, Pradel R and others (2008) Assessing the impact of climate variation on survival in vertebrate populations. Biol Rev Camb Philos Soc 83:357–399

Guinet C, Chastel O, Koudil M, Durbec JP, Jouventin P (1998) Effects of warm sea-surface anomalies on the blue petrel at the Kerguelen Islands. Proc R Soc Lond B 265:1001–1006

Hare JA, Alexander MA, Fogarty MJ, Williams EH, Scott JD (2010) Forecasting the dynamics of a coastal fishery species using a coupled climate–population model. Ecol Appl 20:452–464

Harris MP, Anker-Nilssen T, McCleery RH, Erikstad KE, Shaw DN, Grosbois V (2005) Effect of wintering area and climate on the survival of adult Atlantic puffins *Fratercula arctica* in the eastern Atlantic. Mar Ecol Prog Ser 297:283–296

Hemery G, D'Amico F, Castege I, Dupont B, D'Elbee J, Lalanne Y, Mouches C (2008) Detecting the impact of oceano-climatic changes on marine ecosystems using a multivariate index: the case of the Bay of Biscay (North Atlantic–European Ocean). Glob Change Biol 14:27–38

Hewitt RP, Dener DA, Emery JH (2003) An 8-year cycle in krill biomass density inferred from acoustic surveys conducted in the vicinity of the South Shetland Islands during the austral summers of 1991–1992 through 2001–2002. Aquat Living Resour 16:205–213

Hill SL, Murphy EJ, Reid K, Trathan PN, Constable AJ (2006) Modelling Southern Ocean ecosystems: krill, the food-web, and the impacts of harvesting. Biol Rev Camb Philos Soc 81:581–608

Hiller A, Wand U, Kämpf H, Stackebrandt W (1988) Occupation of the Antarctic continent by petrels during the past 35 000 years: inferences from a ^{14}C study of stomach oil deposits. Polar Biol 9:69–77

Hinke JT, Salwicka K, Trivelpiece SG, Watters GM, Trivelpiece WZ (2007) Divergent responses of *Pygoscelis* penguins reveal a common environmental driver. Oecologia 153:845–855

Hobday AJ (2010) Ensemble analysis of the future distribution of large pelagic fishes off Australia. Prog Oceanogr 86:291–301

Hunt GL, Coyle KO, Eisner LB, Farley EV and others (2011) Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES J Mar Sci 68:1230–1243

Hunter CM, Caswell H (2005) Selective harvest of sooty shearwater chicks: effects on population dynamics and sustainability. J Anim Ecol 74:589–600

Hüppop O, Hüppop K (2003) North Atlantic Oscillation and timing of spring migration in birds. Proc R Soc Lond B 270:233–240

Hyrenbach KD, Veit RR (2003) Ocean warming and seabird communities of the southern California Current System (1987–98): response at multiple temporal scales. Deep-Sea Res II 50:2537–2565

Igual JM, Tavecchia G, Jenouvrier S, Forero MG, Oro D (2009) Buying years to extinction: is compensatory mitigation for marine bycatch a sufficient conservation measure for long-lived seabirds. PLoS ONE 4:e4826

Inchausti P, Guinet C, Koudil M, Durbec JP and others (2003) Inter-annual variability in the breeding performance of seabirds in relation to oceanographic anom-

alies that affect the Crozet and the Kerguelen sectors of the Southern Ocean. J Avian Biol 34:170–176

Jenouvrier S, Barbraud C, Weimerskirch H (2003) Effects of climate variability on the temporal population dynamics of southern fulmars. J Anim Ecol 72:576–587

Jenouvrier S, Barbraud C, Weimerskirch H (2005) Long-term contrasted responses to climate of two Antarctic seabird species. Ecology 86:2889–2903

Jenouvrier S, Barbraud C, Weimerskirch H (2006) Sea ice affects the population dynamics of Adélie penguins in Terre Adélie. Polar Biol 29:413–423

Jenouvrier S, Caswell H, Barbraud C, Holland M, Stroeve J, Weimerskirch H (2009) Demographic models and IPCC climate projections predict the decline of an emperor penguin population. Proc Natl Acad Sci USA 106: 1844–1847

Jones HP, Tershy BR, Zavaleta ES, Croll DA, Keitt BS, Finkelstein ME, Howald GR (2008) Severity of the effects of invasive rats on seabirds: a global review. Conserv Biol 22:16–26

Jouventin P, Bried J, Micol T (2003) Insular bird populations can be saved from rats: a long-term experimental study of white-chinned petrels *Procellaria aequinoctialis* on Ile de la Possession (Crozet archipelago). Polar Biol 26: 371–378

Kinnison MT, Hairston NG (2007) Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. Funct Ecol 21:444–454

Kitaysky AS, Golubova EG (2000) Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. J Anim Ecol 69:248–262

Kitaysky AS, Hunt GL, Flint EN, Rubega MA, Decker MB (2000) Resource allocation in breeding seabirds: responses to fluctuations in their food supply. Mar Ecol Prog Ser 206:283–296

Kitaysky AS, Piatt JF, Hatch SA, Kitaiskaia EV and others (2010) Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. Funct Ecol 24:625–637

Kooyman GL, Ainley DG, Ballard G, Ponganis PJ (2007) Effects of giant icebergs on two emperor penguin colonies in the Ross Sea, Antarctica. Antarct Sci 19:31–38

Kwok R, Comiso JC (2002) Southern Ocean climate and sea ice anomalies associated with the Southern Oscillation. J Clim 15:487–501

Lack D (1968) Ecological adaptations for breeding in birds. Methuen, London

Law R (1979) Optimal life histories under age-specific predation. Am Nat 114:399–417

Le Bohec C, Durant J, Gauthier-Clerc M, Stenseth NC and others (2008) King penguin population threatened by Southern Ocean warming. Proc Natl Acad Sci USA 105: 2493–2497

Lebreton JD (2005) Dynamical and statistical models for exploited populations. Aust NZ J Stat 47:49–63

Lebreton JD, Clobert J (1991) Bird population dynamics, management, and conservation: the role of mathematical modelling. In: Perrins CM, Lebreton JD, Hirons GJM (eds) Bird population studies: relevance to conservation and management. Oxford University Press, Oxford, p 105–125

Lebreton JD, Hines JE, Pradel R, Nichols JD, Spendelow JA (2003) Estimation by capture-recapture of recruitment and dispersal over several sites. Oikos 101:253–264

Lehodey P, Bertignac M, Hampton J, Lewis A, Picaut J

(1997) El Niño Southern Oscillation and tuna in the western Pacific. Nature 389:715–718

Lehodey P, Alheit J, Barange M, Baumgartner T and others (2006) Climate variability, fish, and fisheries. J Clim 19:5009–5030

Lescroël A, Dugger KM, Ballard G, Ainley DG (2009) Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. J Anim Ecol 78:798–806

Levitus S, Antonov J, Boyer T (2000) Warming of the world ocean, 1955–2003. Geophys Res Lett 32:L02604. doi: 10.1029/2004GL021592

Lewison RL, Crowder LB, Read AJ, Freeman SA (2004) Understanding impacts of fisheries bycatch on marine megafauna. Trends Ecol Evol 19:598–604

Lima M, Merritt JF, Bozinovic F (2002) Numerical fluctuations in the northern short-tailed shrew: evidence of nonlinear feedback signatures on population dynamics and demography. J Anim Ecol 71:159–172

Liu J, Curry JA, Martinson DG (2004) Interpretation of recent Antarctic sea ice variability. Geophys Res Lett 31:L02205. doi:10.1029/2003GL018732

Loeb V, Siegel V, Holm-Hansen O, Hewitt R, Fraser W, Trivelpiece W, Trivelpiece S (1997) Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. Nature 387:897–900

Marshall GJ (2003) Trends in the Southern Annular Mode from observations and reanalyses. J Clim 16:4134–4143

Massom RA, Hill K, Barbraud C, Adams N, Ancel A, Emmerson L, Pook MJ (2009) Fast ice distribution in Adélie Land, East Antarctica: interannual variability and implications for emperor penguins *Aptenodytes forsteri.* Mar Ecol Prog Ser 374:243–257

Masson-Delmotte V, Delmotte V, Morgan V, Etheridge D, van Ommen T, Tartarin S, Hoffmann G (2003) Recent southern Indian Ocean climate variability inferred from a Law Dome ice core: new insights for the interpretation of coastal Antarctic isotopic records. Clim Dyn 21:153–166

May RM, Beddington JR, Clarck CW, Holt SJ, Laws RM (1979) Management of multispecies fisheries. Science 205:267–277

Meredith MP, King JC (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. Geophys Res Lett 32:L19604. doi:10.1029/2005GL024042

Moline MA, Karnovsky NJ, Brown Z, Divoky GJ and others (2008) High latitude changes in ice dynamics and their impact on polar marine ecosystems. Ann N Y Acad Sci 1134:267–319

Montevecchi WA, Myers RA (1997) Centurial and decadal oceanographic influences on changes in northern gannet populations and diets in the north-west Atlantic: implications for climate change. ICES J Mar Sci 54:608–614

Murphy EC, Springer AM, Roseneau DG (1991) High annual variability in reproductive success of kittiwakes (*Rissa tridactyla* L.) at a colony in western Alaska. J Anim Ecol 60:515–534

Murphy EJ, Watkins JL, Trathan PN, Reid K and others (2007) Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. Philos Trans R Soc Lond B 362:113–148

Murray TE, Bartle JA, Kalish SR, Taylor PR (1993) Incidental capture of seabirds by Japanese southern bluefin tuna longline vessels in New Zealand waters, 1988–1992. Bird Conserv Int 3:181–210

Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280–283

Mysterud A, Stenseth NC, Yoccoz NG, Langvatn R, Steinhem G (2001) Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. Nature 410:1096–1099

Nel DC, Taylor F, Ryan PG, Cooper J (2003) Population dynamics of the wandering albatross *Diomedea exulans* at Marion Island: longline fishing and environmental influences. Afr J Mar Sci 25:503–517

Nevoux M, Barbraud C (2005) Relationships between sea ice conditions, sea surface temperature and demographic traits of thin-billed prions. Polar Biol 29:445–453

Nevoux M, Weimerskirch H, Barbraud C (2007) Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. J Anim Ecol 76:159–167

Nevoux M, Forcada J, Barbraud C, Croxall JP, Weimerskirch H (2010a) Demographic response to environmental variability, an intra-specific comparison. Ecology 91: 2416–2427

Nevoux M, Weimerskirch H, Barbraud C (2010b) Long- and short-term influence of environment on recruitment in a species with highly delayed maturity. Oecologia 162: 383–392

Nicol S (2006) Krill, currents, and sea ice: *Euphausia superba* and its changing environment. Bioscience 56: 111–120

Nicol S, Pauly T, Bindoff NL, Wright SW and others (2000) Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. Nature 406:504–507

Nicol S, Croxall JP, Trathan P, Gales N, Murphy E (2007) Paradigm misplaced? Antarctic marine ecosystems are affected by climate change as well as biological processes and harvesting. Antarct Sci 19:291–295

Niel C, Lebreton JD (2005) Using demographic invariants to detect overharvested bird populations from incomplete data. Conserv Biol 19:826–835

Nogales M, Martin A, Tershy BR, Donlan CJ and others (2004) A review of feral cat eradication on islands. Conserv Biol 18:310–319

Olivier F, van Franeker JA, Creuwels JCS, Woehler EJ (2005) Variations of snow petrel breeding success in relation to sea-ice extent: Detecting local response to large-scale processes? Polar Biol 28:687–699

Olsson O, van der Jeugd HP (2002) Survival in king penguins *Aptenodytes patagonicus*: temporal and sex-specific effects of environmental variability. Oecologia 132:509–516

Oro D, Bosch M, Ruiz X (1995) Effects of a trawling moratorium on the breeding success of the yellow-legged gull *Larus cachinnans.* Ibis 137:547–549

Oro D, Jover L, Ruiz X (1996) Influence of trawling activity on the breeding ecology of a threatened seabird, Audouin's gull *Larus audouinii.* Mar Ecol Prog Ser 139: 19–29

Ozgul A, Childs DZ, Oli MK, Armitage KB and others (2010) Coupled dynamics of body mass and population growth in response to environmental change. Nature 466: 482–485

Pakhomov EA, Perissinotto R, McQuaid CD (1996) Prey composition and daily rations of myctophid fishes in the Southern Ocean. Mar Ecol Prog Ser 134:1–14

Park YH, Roquet F, Vivier F (2004) Quasi-stationary ENSO wave signals versus the Antarctic Circumpolar Wave

scenario. Geophys Res Lett 31:L09315. doi:10.1029/2004 GL019806

Park YH, Roquet F, Durand I, Fuda JL (2008a) Large-scale circulation over and around the northern Kerguelen Plateau. Deep-Sea Res II 55:566–581

Park YH, Fuda JL, Durand I, Naveira Garabato AC (2008b) Internal tides and vertical mixing over the Kerguelen Plateau. Deep-Sea Res II 55:582–593

Parkinson C (2004) Southern Ocean sea ice and its wider linkages: insights revealed from models and observations. Antarct Sci 16:387–400

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Syst 37:637–669

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Parmesan C, Ryrholm N, Stefanescu C, Hill JK and others (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing down marine food webs. Science 279: 860–863

Peacock L, Paulin M, Darby J (2000) Investigations into climate influence on population dynamics of yellow-eyed penguins *Megadyptes antipodes*. NZ J Zool 27:317–325

Péron C, Authier M, Barbraud C, Delord K, Besson D, Weimerskirch H (2010) Decadal changes in at-sea distribution and abundance of subantarctic seabird species along a latitudinal gradient in the southern Indian Ocean. Glob Change Biol 16:1895–1909

Perriman L, Houston D, Steen H, Johannesen E (2000) Climate fluctuation effects on breeding of blue penguins (*Eudyptula minor*). NZ J Zool 27:261–267

Perrin WF (1969) Using porpoise to catch tuna. World Fish 18:42–45

Pfister CA (1998) Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proc Natl Acad Sci USA 95:213–218

Pinaud D, Weimerskirch H (2002) Ultimate and proximate factors affecting the breeding performance of a marine top-predator. Oikos 99:141–150

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. J Avian Biol 38:298–308

Reid K, Croxall JP, Briggs DR, Murphy EJ (2005) Antarctic ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill. ICES J Mar Sci 62:366–373

Reznick DA, Bryga H, Endler JA (1990) Experimentally induced life-history evolution in a natural population. Nature 346:357–359

Rivalan P, Barbraud C, Inchausti P, Weimerskirch H (2010) Combined impact of longline fisheries and climate on the persistence of the Amsterdam albatross. Ibis 152:6–18

Robertson G, McNeill M, Smith N, Wienecke B, Candy S, Olivier F (2006) Fast sinking (integrated weight) longlines reduced mortality of white-chinned petrels (*Procellaria aequinoctialis*) and sooty shearwaters (*Puffinus griseus*) in demersal longline fisheries. Biol Conserv 132:458–471

Rochet MJ, Cornillon PA, Sabatier R, Pontier D (2000) Comparative analysis of phylogenetic and fishing effects in life history patterns of teleost fishes. Oikos 91:255–270

Rolland V, Barbraud C, Weimerskirch H (2008) Combined effects of fisheries and climate on a migratory long-lived marine predator. J Appl Ecol 45:4–13

Rolland V, Nevoux M, Barbraud C, Weimerskirch H (2009a) Respective impact of climate and fisheries on the growth of an albatross population. Ecol Appl 19:1336–1346

Rolland V, Barbraud C, Weimerskirch H (2009b) Assessing the impact of fisheries, climate and disease on the dynamics of the Indian yellow-nosed albatross. Biol Conserv 142:1084–1095

Rolland V, Weimerskirch H, Barbraud C (2010) Relative influence of fisheries and climate on the demography of four albatross species. Glob Change Biol 16:1910–1922

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60

Saji NH, Goswami BN, Vinayachandran PN, Yamagata T (1999) A dipole mode in the tropical Indian Ocean. Nature 401:360–363

Sandvik H, Coulson T, Saether BE (2008) A latitudinal gradient in climate effects on seabird demography: results from interspecific analyses. Glob Change Biol 14:703–713

Saraux C, Le Bohec C, Durant JM, Viblanc VA and others (2011) Reliability of flipper-banded penguins as indicators of climate change. Nature 469:203–206

SC-CCAMLR (Scientific Committees of the Commission for the Conservation of Antarctic Marine Living Resources) (2006) Report of the 24th meeting of the Scientific Committee. SC-CCAMLR, Hobart

Schaffer WM (1974) Selection for optimal life histories: the effects of age structure. Ecology 55:291–303

Smith VR (2002) Climate change in the sub-antarctic: an illustration from Marion Island. Clim Change 52:345–357

Smith WO, Nelson DM (1986) Importance of the ice edge phytoplankton production in the Southern Ocean. Bioscience 36:251–257

Smith RC, Ainley DG, Baker K, Domack E and others (1999) Marine ecosystem sensitivity to climate change. Bioscience 49:393–404

Solomon S, Qin D, Manning M, Chen Z and others (eds) (2007) Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Steele WK, Hiller A (1997) Radiocarbon dates of snow petrel nest-sites in central Dronning Maud Land, Antarctica. Polar Rec (Gr Brit) 33:29–38

Sullivan BJ, Reid TA, Bugoni L (2006) Seabird mortality on factory trawlers in the Falkland Islands and beyond. Biol Conserv 131:495–504

Sun L, Xie Z, Zhao J (2000) A 3000-year record of penguin populations. Nature 407:858

Sydeman WJ, Hester MM, Thayer JA, Gress F, Martin P, Buffa J (2001) Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969–1997. Prog Oceanogr 49:309–329

Taylor BL, Wade PR, DeMaster DP, Barlow J (2000) Incorporating uncertainty into management models for marine mammals. Conserv Biol 14:1243–1252

Terauds A, Gales R, Alderman R (2005) Trends in numbers and survival of black-browed (*Thalassarche melanophrys*) and grey-headed (*T. chrysostome*) albatrosses breeding on Macquarie Island. Emu 105:159–167

Terauds A, Gales R, Baker GB, Alderman R (2006) Popula-

tion and survival trends of wandering albatrosses (*Diomedea exulans*) breeding on Macquarie Island. Emu 106:211–218

Thompson PM, Ollason JC (2001) Lagged effects of ocean climate change on fulmar population dynamics. Nature 413:417–420

Trathan PN, Murphy EJ, Forcada J, Croxall JP, Reid K, Thorpe SE (2006) Physical forcing in the southwest Atlantic: ecosystem control. In: Boyd IL, Wanless S, Camphuysen CJ (eds) Top predators in marine ecosystems. Cambridge University Press, Cambridge, p 28–45

Trathan PN, Forcada J, Murphy EJ (2007) Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. Philos Trans R Soc Lond B 362:2351–2365

Trenberth K (1984) Signal versus noise in the Southern Oscillation. Mon Weather Rev 112:326–332

Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM (2011) Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. Proc Natl Acad Sci USA 108: 7625–7628

Tuck GN, Polacheck T, Croxall JP, Weimerskirch H (2001) Modelling the impact of fishery bycatches on albatross populations. J Appl Ecol 38:1182–1196

Tuck GN, Polacheck T, Bulman CM (2003) Spatio-temporal trends of longline fishing effort in the Southern Ocean and implications for seabird bycatch. Biol Conserv 114: 1–27

Turner J (2004) The El Niño–Southern Oscillation and Antarctica. Int J Climatol 24:1–31

Turner J, Summerhayes C, Gutt J, Bracegirdle T and others (2009) Antarctic climate change and the environment. SCAR & Scott Polar Res Inst, Cambridge

Van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life-history tactics. Am Nat 128:137–142

Vaughan DG, Marshall GJ, Connolley WM, Parkinson C and others (2003) Recent rapid regional climate warming on the Antarctic Peninsula. Clim Change 60:243–274

Veit RR, McGowan JA, Ainley DG, Wahls TR, Pyle P (1997) Apex marine top predator declines ninety percent in association with changing oceanic climate. Glob Change Biol 3:23–28

Véran S, Lebreton JD (2008) The potential of integrated modelling in conservation biology: a case study of the black-footed albatross (*Phoebastria nigripes*). Can J Stat 36:85–98

Véran S, Gimenez O, Flinte E, Kendall WL, Doherty J, Lebreton JD (2007) Quantifying the impact of longline fisheries on adult survival in the black-footed albatross. J Appl Ecol 44:942–952

Verhulst S, Nilsson JA (2008) The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. Philos Trans R Soc B 363:399–410

Verkulich SR, Hiller A (1994) Holocene deglaciation of the Bunger Hills revealed by ^{14}C measurements on stomach oil deposits in snow petrel colonies. Antarct Sci 6:395–399

Visser ME (2008) Keeping up with a warming world: assessing the rate of adaptation to climate change. Proc R Soc Lond B 275:649–659

Votier SC, Furness RW, Bearhop S, Crane JE and others (2004) Changes in fisheries discard rates and seabird

communities. Nature 427:727–730

Votier SC, Birkhead TR, Oro D, Trinder M and others (2008) Recruitment and survival of immature seabirds in relation to oil spills and climate variability. J Anim Ecol 77:974–983

Wade PR (1998) Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Mar Mamm Sci 14:1–37

Wagner EL, Boersma PD (2011) Effects of fisheries on seabird community ecology. Rev Fish Sci 19:157–169

Walther GR, Post E, Convey P, Menzel A and others (2002) Ecological responses to recent climate change. Nature 416:389–395

Warham J (1990) The petrels. Their ecology and breeding systems. Academic Press, London

Watkins BP, Petersen SL, Ryan PG (2008) Interactions between seabirds and deep-water hake trawl gear: an assessment of impacts in South African waters. Anim Conserv 11:247–254

Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? Deep-Sea Res I 54:211–223

Weimerskirch H, Jouventin P (1987) Population dynamics of the wandering albatross (*Diomedea exulans*) of the Crozet Islands: causes and consequences of the population decline. Oikos 49:315–322

Weimerskirch H, Brothers N, Jouventin P (1997) Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. Biol Conserv 79:257–270

White WB, Chen SC, Allan RJ (2002) Positive feedbacks between the Antarctic circumpolar wave and global El Niño–Southern Oscillation wave. J Clim 107:29–117

Whitehouse MJ, Meredith MP, Rothery P, Atkinson A, Ward P, Korb RE (2008) Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: forcings, characteristics and implications for lower trophic levels. Deep-Sea Res I 55:1218–1228

Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations. Academic Press, San Diego, CA

Wilson C, Adamec D (2002) A global view of bio-physical coupling from SeaWIFS and TOPEX satellite data, 1997–2001. Geophys Res Lett 29:98.1–98.2

Wilson PR, Ainley DG, Nur N, Jacobs SS, Barton KJ, Ballard G, Comiso JC (2001) Adélie penguin population change in the Pacific sector of Antarctica: relation to sea-ice extent and the Antarctic circumpolar current. Mar Ecol Prog Ser 213:301–309

Wilson RP, Grémillet D, Syder J, Kierspel MAM and others (2002) Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. Mar Ecol Prog Ser 228:241–261

Woehler EJ (1997) Seabird abundance, biomass and prey consumption within Prydz Bay, Antarctica, 1980/81–1992/93. Polar Biol 17:371–383

Woehler EJ, Croxall JP (1997) The status and trends of Antarctic and sub-Antarctic seabirds. Mar Ornithol 25: 43–66

Wolf SG, Snyder MA, Sydeman WJ, Doak DF, Croll DA (2010) Predicting population consequences of ocean climate change for an ecosystem sentinel, the seabird Cassin's auklet. Glob Change Biol 16:1923–1935

Appendix 1. Table A1. Studies that investigated the effects of climate factors on demographic parameters of Southern Ocean seabirds. ✓: demographic parameters investigated (Sa: adult survival; Sj: juvenile or immature survival; Re: recruitment; Pr: breeding proportions; Bs: breeding success; N: number of breeding pairs); SST: sea-surface temperature; SIE: sea-ice extent; SIC: sea-ice concentration; T: air temperature; SSH: sea-surface height; SOI: Southern Oscillation Index; SAM: Southern Annular Mode; IOD: Indian Ocean Dipole

Species	Sa	Sj	Re	Pr	Bs	N	Climate factor	Region	Reference
Emperor penguin *Aptenodytes forsteri*	✓	✓	✓		✓	✓	SST, SIE, SIC, SOI, T, SAM	Adélie Land	Barbraud & Weimerskirch (2001a), Ainley et al. (2005), Jenouvrier et al. (2005), Massom et al. (2009)
King penguin *Aptenodytes patagonicus*	✓						SST, SOI	South Georgia, Crozet Islands	Olsson & van der Jeugd (2002), Le Bohec et al. (2008), Saraux et al. (2011)
Adélie penguin *Pygoscelis adeliae*	✓				✓	✓	SST, SIE, SIC, T, SOI, SAM	Ross Sea, Adélie Land, Enderby Land, Antarctic Peninsula, Antarctica, Signy Islands	Fraser et al. (1992), Wilson et al. (2001), Ainley et al. (2005), Jenouvrier et al. (2006), Emmerson & Southwell (2008), Lescroël et al. (2009), Ballerini et al. (2009), Forcada & Trathan (2009)
Chinstrap penguin *Pygoscelis antarctica*					✓	✓	SIE, T, SAM	Antarctic Peninsula, Signy Islands	Forcada et al. (2006), Forcada & Trathan (2009)
Gentoo penguin *Pygoscelis papua*					✓	✓	SST, SIE, T, SAM	South Georgia, Antarctic Peninsula	Forcada et al. (2006), Trathan et al. (2006), Forcada & Trathan (2009)
Yellow-eyed penguin *Megadyptes antipodes*	✓						SST	New Zealand	Peacock et al. (2000)
Rockhopper penguin *Eudyptes chrysocome*	✓						SST	New Zealand	Cunningham & Moors (1994)
Macaroni penguin *Eudyptes chrysolophus*					✓		SAM	South Georgia	Forcada & Trathan (2009)
Little penguin *Eudyptula minor*					✓		SST, SOI	New Zealand, Australia	Perriman et al. (2000), Chambers (2004)
Wandering albatross *Diomedea exulans*	✓				✓		SST, SOI	Crozet Islands	Inchausti et al. (2003), Delord et al. (2008), Rolland et al. (2010)
Amsterdam albatross *Diomedea amsterdamensis*	✓	✓	✓		✓	✓	SST, IOD	Amsterdam Island	Rivalan et al. (2010), Barbraud et al. (2011)
Black-browed albatross *Thalassarche melanophrys*	✓	✓	✓		✓		SST, SOI	Kerguelen Islands, South Africa, South Georgia, South Australia	Pinaud & Weimerskirch (2002), Inchausti et al. (2003), Nevoux et al. (2007, 2010a,b), Rolland et al. (2008, 2009a), Barbraud et al. (2011)
Atlantic yellow-nosed albatross *Thalassarche chlororhynchos*	✓				✓	✓	SOI	Tristan da Cunha, Gough	Cuthbert et al. (2003)
Indian yellow-nosed albatross *Thalassarche carteri*	✓				✓	✓	SST, SOI	Amsterdam Island	Rolland et al. (2009b), Inchausti et al. (2003), Delord et al. (2008)
Sooty albatross *Phoebetria fusca*	✓				✓	✓	SST, SOI	Crozet Islands, Amsterdam Island	Rolland et al. (2010)
Light-mantled sooty albatross *Phoebetria palpebrata*	✓				✓		SST, SOI	Crozet Islands	Inchausti et al. (2003), Delord et al. (2008)
Southern giant petrel *Macronectes giganteus*					✓		SOI	Crozet Islands	Delord et al. (2008)
Northern giant petrel *Macronectes halli*					✓		SOI	Crozet Islands	Delord et al. (2008), Jenouvrier et al. (2003)
Antarctic fulmar *Fulmarus glacialoides*	✓		✓	✓	✓		SIC, SST	Adélie Land	Barbraud et al. (2000b), Barbraud & Weimerskirch (2001b), Jenouvrier et al. (2005), Olivier et al. (2005), Barbraud et al. (2011)
Snow petrel *Pagodroma nivea*	✓	✓	✓	✓	✓	✓	SIE, SIC, T	Adélie Land, Wilkes Land	Guinet et al. (1998), Inchausti et al. (2003), Barbraud & Weimerskirch (2003), Barbraud & Weimerskirch (2005)
Blue petrel *Halobaena caerulea*	✓						SST, SSH, SOI	Kerguelen Islands	Nevoux & Barbraud (2005), Quillfeldt et al. (2007)
Thin-billed prion *Pachyptila belcheri*					✓		SST, SIC	Kerguelen Islands, Falkland Islands	Nevoux & Barbraud (2005), Quillfeldt et al. (2007)
White-chinned petrel *Procellaria aequinoctialis*	✓	✓					SST, SOI	Crozet Islands	Barbraud et al. (2008)
Grey petrel *Procellaria cinerea*	✓	✓					SST, SOI	Kerguelen Islands	Barbraud et al. (unpubl. data)

Table A2. Studies that investigated the effects of fisheries activities (mainly fishing effort) on demographic parameters of Southern Ocean seabirds. ✓: demographic parameters investigated (Sa: adult survival; Sj: juvenile/immature survival; Re: recruitment; Bs: breeding success; N: number of breeding pairs)

Species	Sa	Sj	Re	Bs	N	Type of fishery	Region	Reference
Wandering albatross *Diomedea exulans*	✓	✓			✓	Longline	Southern Ocean, South Atlantic, South Indian	Weimerskirch et al. (1997), Tuck et al. (2001), Nel et al. (2003), Terauds et al. (2006), Delord et al. (2008), Rolland et al. (2010)
Amsterdam albatross *Diomedea amsterdamensis*	✓					Longline	South Indian	Rivalan et al. (2010)
Black-browed albatross *Thalassarche melanophrys*	✓			✓		Longline, trawl	South Pacific, Tasman Sea, Kerguelen Islands, South Atlantic	Terauds et al. (2005), Arnold et al. (2006), Sullivan et al. (2006), Rolland et al. (2008, 2009a)
White-capped albatross *Thalassarche steadi*	✓	✓				Longline	South Pacific, South Atlantic	Baker et al. (2007)
Shy albatross *Thalassarche cauta*	✓	✓				Longline	South Pacific, South Atlantic	Baker et al. (2007)
Grey-headed albatross *Thalassarche chrysostoma*	✓					Longline	South Pacific	Terauds et al. (2005)
Atlantic yellow-nosed albatross *Thalassarche chlororhynchos*	✓					Longline	South Atlantic	Cuthbert et al. (2003)
Indian yellow-nosed albatross *Thalassarche carteri*	✓					Longline	South Indian	Rolland et al. (2009b)
Sooty albatross *Phoebetria fusca*					✓	Longline	South Indian	Delord et al. (2008), Rolland et al. (2010)
Light-mantled sooty albatross *Phoebetria palpebrata*					✓	Longline	South Indian	Delord et al. (2008)
Southern giant petrel *Macronectes giganteus*					✓	Longline	South Indian	Delord et al. (2008)
Northern giant petrel *Macronectes halli*					✓	Longline	South Indian	Delord et al. (2008)
White-chinned petrel *Procellaria aequinoctialis*	✓					Longline, trawl	South Indian	Barbraud et al. (2008)
Grey petrel *Procellaria cinerea*	✓		✓	✓		Longline, trawl	South Indian	Barbraud et al. (unpubl. data)
Flesh-footed shearwater *Puffinus carneipes*	✓		✓			Longline	Australia	Baker & Wise (2005)
Cap gannet *Morus capensis*				✓		Trawl	South Atlantic	Grémillet et al. (2008)