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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

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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:

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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 CO₂ 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

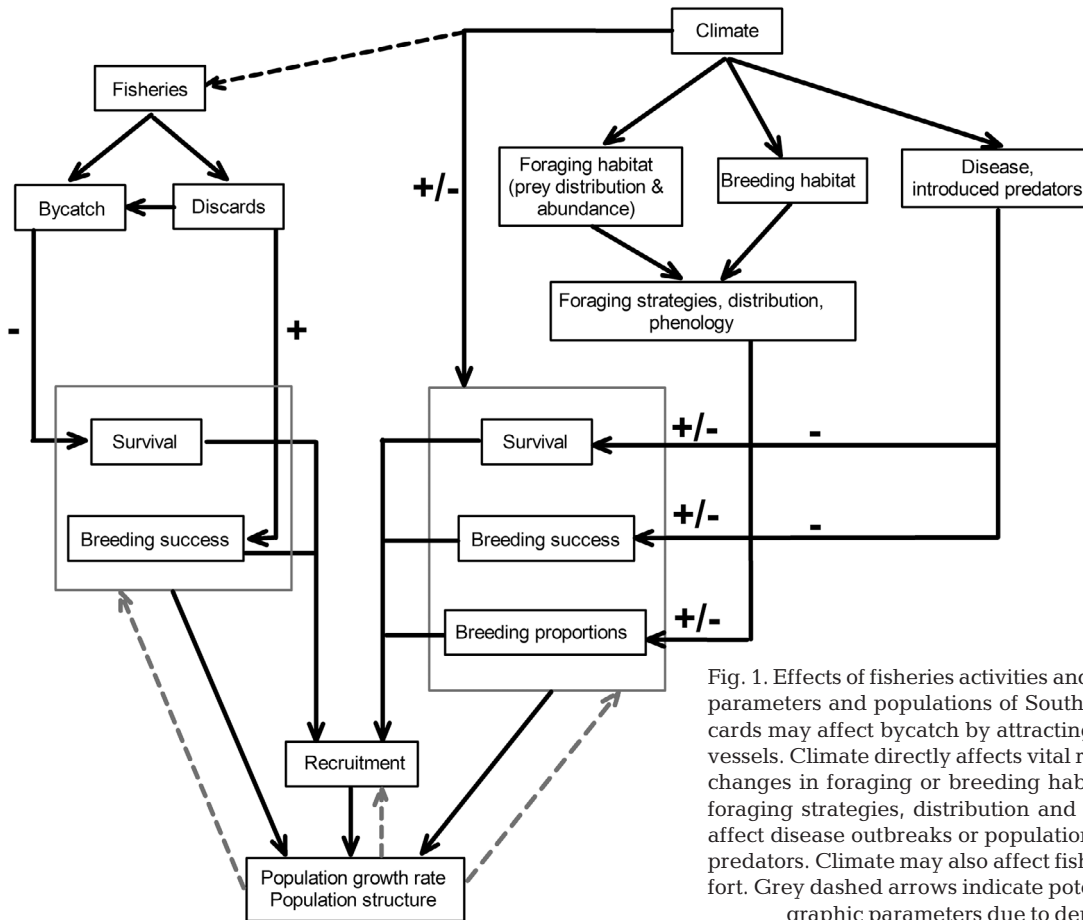


Fig. 1. Effects of fisheries activities and climate on demographic parameters and populations of Southern Ocean seabirds. Discards may affect bycatch by attracting seabirds behind fishing vessels. Climate directly affects vital rates or indirectly through changes in foraging or breeding habitat, which 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 (Roland 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,

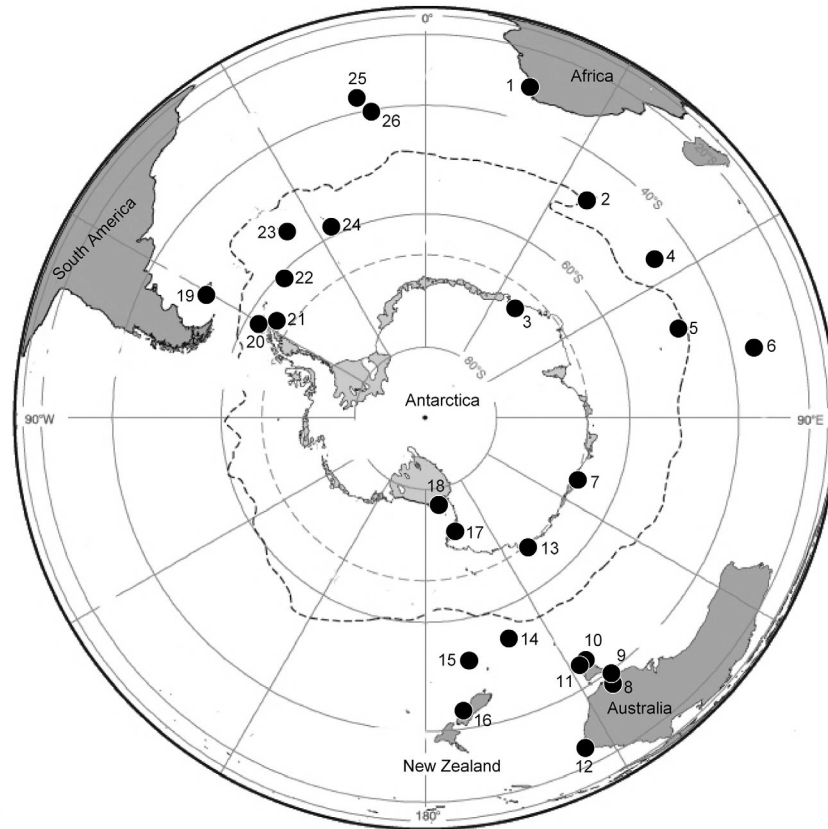


Fig. 2. Location of long-term monitoring studies where the effects of climate variability and fisheries bycatch on demography and population dynamics of Southern Ocean seabirds were investigated. Studied species in parentheses. 1: Malgas Island (cape gannet); 2: Marion & Prince Edward Islands (wandering 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 *Phoebastria 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 synchronized 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

	Effect		
	Positive	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).

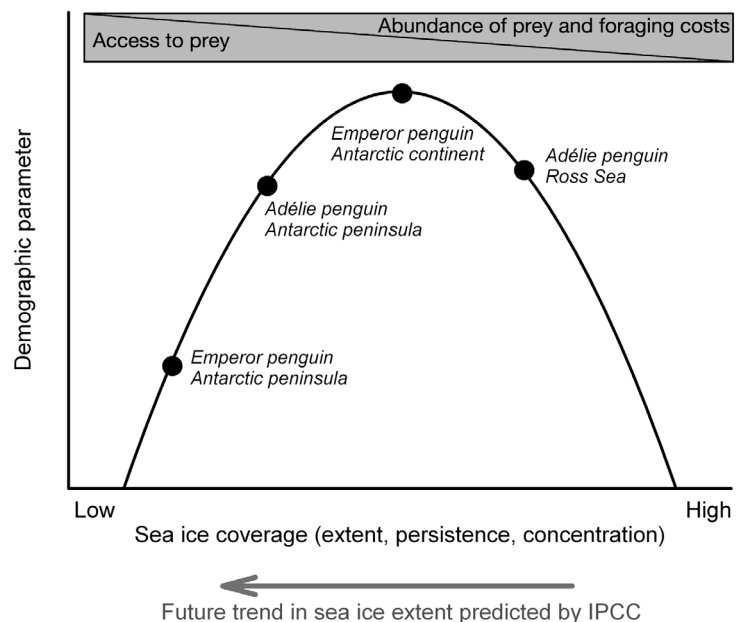
Part of the contrasted responses within species may be caused by the spatial variability in food webs of the Southern Ocean (Trathan et al. 2007). Different areas of the Southern Ocean are dominated by different food webs. For instance, the lower trophic levels of the Scotia Sea region are dominated 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 (Barbraud & 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).

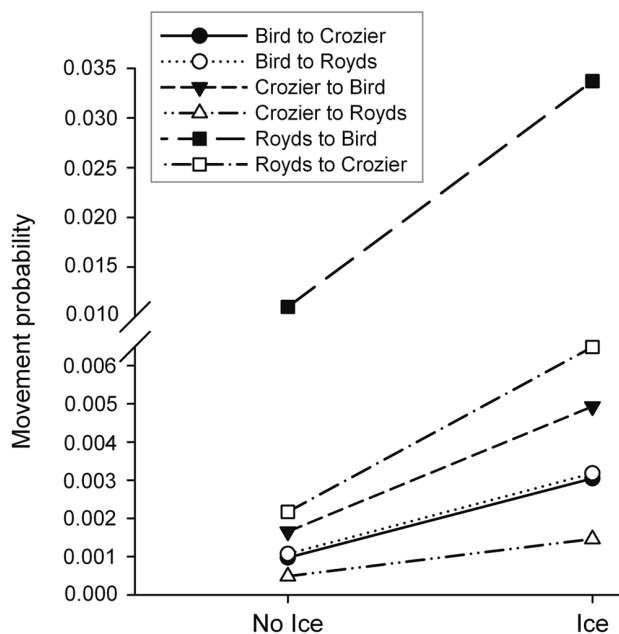


Fig. 4. *Pygoscelis adeliae*. Effect of sea-ice variability on annual breeding dispersal probability of adult Adélie penguins breeding in the south-western Ross Sea, from 1996 to 2007. Movement probabilities differed between colonies but were higher in years with extensive sea ice or when icebergs were 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 long-lines 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

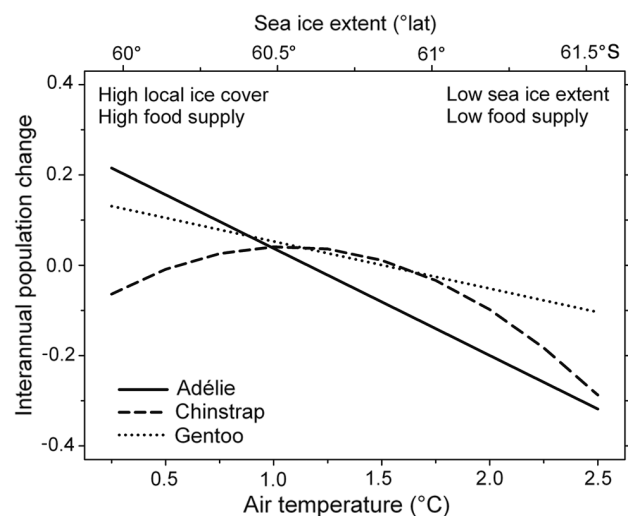


Fig. 5. *Pygoscelis* spp. Representation of the diversity of penguin population responses (interannual changes in numbers of breeding pairs) to the environment at Signy Island, South Orkney Islands. Responses may be linear or non-linear depending on the species' ecological requirements. From Forcada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

	Effect		
	Positive	Negative	Null
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 *Champscephalus 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 through 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.

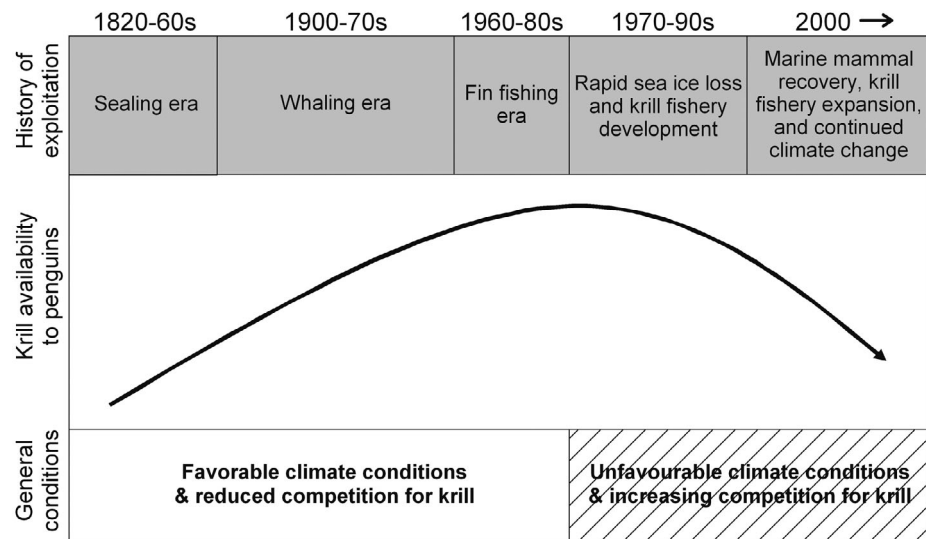
COMBINED EFFECTS OF CLIMATE AND FISHERIES BYCATCH ON POPULATION DYNAMICS

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 \pm 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 chin-strap 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 $3.5\% \text{ yr}^{-1}$, 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.

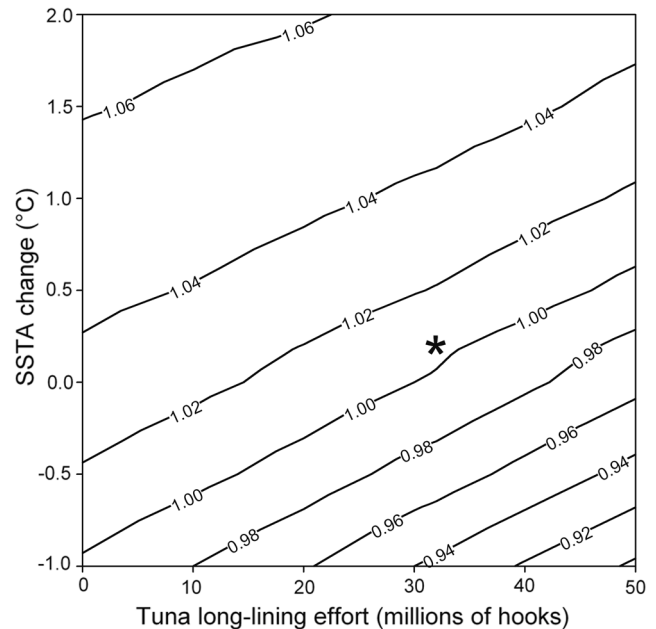


Fig. 7. *Thalassarche melanophrys*. Interaction between the effects of climate variability (sea-surface temperature anomalies [SSTA] in the foraging areas used during the breeding period) and fisheries bycatch (long-lining effort in the area used during the non-breeding period) on the population growth 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 (Roland 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 (Myrsetrud 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).

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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 <i>Aptenodytes forsteri</i>	✓		✓	✓	✓	✓	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 <i>Aptenodytes patagonicus</i>	✓			✓			SST, SOI	South Georgia, Crozet Islands	Olsson & van der Jeugd (2002), Le Bohec et al. (2008), Saraux et al. (2011)
Adélie penguin <i>Pygoscelis adeliae</i>	✓		✓	✓			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)
Chinstrap penguin <i>Pygoscelis antarctica</i>				✓	✓		SIE, T, SAM	Antarctic Peninsula, Signy Islands	Lescoëri et al. (2009), Ballerini et al. (2009), Forcada & Trathan (2009)
Gentoo penguin <i>Pygoscelis papua</i>				✓	✓		SST, SIE, T, SAM	South Georgia, Antarctic Peninsula	Forcada & Trathan (2006), Forcada & Trathan (2009), Trathan et al. (2006), Forcada & Trathan (2009)
Yellow-eyed penguin <i>Megadyptes antipodes</i>	✓			✓	✓		SST	New Zealand	Peacock et al. (2000)
Rockhopper penguin <i>Eudyptes chrysocome</i>				✓	✓		SST	New Zealand	Cunningham & Moors (1994)
Macaroni penguin <i>Eudyptes chrysolophus</i>				✓	✓		SAM	South Georgia	Forcada & Trathan (2009)
Little penguin <i>Eudyptula minor</i>				✓	✓		SST, SOI	New Zealand, Australia	Perriam et al. (2006), Chambers (2004)
Wandering albatross <i>Diomedea exulans</i>	✓			✓	✓		SST, SOI	Crozet Islands	Inchausti et al. (2003), Delord et al. (2008), Rolland et al. (2010)
Amsterdam albatross <i>Diomedea amsterdamensis</i>	✓	✓		✓	✓		SST, IOD	Amsterdam Island	Rivallan et al. (2010), Barbraud et al. (2011)
Black-browed albatross <i>Thalassarche melanophrys</i>	✓	✓		✓	✓		SST, SOI	Kerguelen Islands, South Africa, South Georgia, South Australia	Pinaud & Weimerskirch (2002), Inchausti et al. (2003)
Atlantic yellow-nosed albatross <i>Thalassarche chlororhynchos</i>	✓			✓	✓		SOI	Tristan da Cunha, Gough	Nevoux et al. (2007, 2010a,b), Rolland et al. (2008, 2009a), Cuthbert et al. (2003)
Indian yellow-nosed albatross <i>Thalassarche carteri</i>	✓			✓	✓		SST, SOI	Amsterdam Island	Rolland et al. (2009b)
Sooty albatross <i>Phoebastria fusca</i>	✓			✓	✓		SST, SOI	Crozet Islands, Amsterdam Island	Inchausti et al. (2003), Delord et al. (2008), Rolland et al. (2010)
Light-mantled sooty albatross <i>Phoebastria palpebrata</i>				✓	✓		SST, SOI	Crozet Islands	Inchausti et al. (2003), Delord et al. (2008)
Southern giant petrel <i>Macronectes giganteus</i>				✓	✓		SOI	Crozet Islands	Delord et al. (2008)
Northern giant petrel <i>Macronectes halli</i>				✓	✓		SOI	Crozet Islands	Delord et al. (2008)
Antarctic fulmar <i>Fulmarus glacialisoides</i>	✓	✓		✓	✓		SIC, SST	Adélie Land	Jenouvrier et al. (2003)
Snow petrel <i>Pagodroma nivea</i>	✓	✓		✓	✓		SIE, SIC, T	Adélie Land, Wilkes Land	Barbraud et al. (2000b), Barbraud & Weimerskirch (2001b), Jenouvrier et al. (2005), Olivier et al. (2005), Barbraud et al. (2011)
Blue petrel <i>Halobaena caerulea</i>	✓						SST, SSH, SOI	Kerguelen Islands	Guinet et al. (1998), Inchausti et al. (2003), Barbraud & Weimerskirch (2003), Barbraud & Weimerskirch (2005)
Thin-billed prion <i>Pachyptila belcheri</i>	✓			✓			SST, SIC	Kerguelen Islands, Falkland Islands	Nevoux & Barbraud (2005), Quillfeldt et al. (2007)
White-chinned petrel <i>Procellaria aequinoctialis</i>	✓			✓	✓		SST, SOI	Crozet Islands	Barbraud et al. (2008)
Grey petrel <i>Procellaria cinerea</i>	✓			✓	✓		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 <i>Diomedea exulans</i>	✓	✓			✓	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 <i>Diomedea amsterdamensis</i>	✓					Longline	South Indian	Rivalan et al. (2010)
Black-browed albatross <i>Thalassarche melanophrys</i>	✓		✓			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 <i>Thalassarche steadi</i>	✓	✓				Longline	South Pacific, South Atlantic	Baker et al. (2007)
Shy albatross <i>Thalassarche cauta</i>	✓	✓				Longline	South Pacific, South Atlantic	Baker et al. (2007)
Grey-headed albatross <i>Thalassarche chrysoloma</i>	✓					Longline	South Pacific	Terauds et al. (2005)
Atlantic yellow-nosed albatross <i>Thalassarche chlororhynchos</i>	✓					Longline	South Atlantic	Cuthbert et al. (2003)
Indian yellow-nosed albatross <i>Thalassarche carteri</i>	✓					Longline	South Indian	Rolland et al. (2009b)
Sooty albatross <i>Phoebastria fusca</i>	✓			✓		Longline	South Indian	Delord et al. (2008), Rolland et al. (2010)
Light-mantled sooty albatross <i>Phoebastria palpebrata</i>	✓			✓		Longline	South Indian	Delord et al. (2008)
Southern giant petrel <i>Macronectes giganteus</i>	✓			✓		Longline	South Indian	Delord et al. (2008)
Northern giant petrel <i>Macronectes halli</i>	✓			✓		Longline	South Indian	Delord et al. (2008)
White-chinned petrel <i>Procellaria aequinoctialis</i>	✓		✓	✓		Longline, trawl	South Indian	Barbraud et al. (2008)
Grey petrel <i>Procellaria cinerea</i>	✓		✓	✓		Longline, trawl	South Indian	Barbraud et al. (unpubl. data)
Flesh-footed shearwater <i>Puffinus carneipes</i>	✓					Longline	Australia	Baker & Wise (2005)
Cap gannet <i>Morus capensis</i>	✓				✓	Trawl	South Atlantic	Grémillet et al. (2008)