

Trends in bird and seal populations as indicators of a system shift in the Southern Ocean

HENRI WEIMERSKIRCH^{1*}, PABLO INCHAUSTI², CHRISTOPHE GUINET¹ and CHRISTOPHE BARBRAUD¹

¹Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, F-79360 Villiers en Bois, France,

²Laboratoire d'Ecologie, Ecole Normale Supérieure, 17 rue d'Ulm, F-75005 Paris, France

*henriw@cebc.cnrs.fr

Abstract: Although world oceans have been warming over the past 50 years, the impact on biotic components is poorly understood because of the difficulty of obtaining long-term datasets on marine organisms. The Southern Ocean plays a critical role in global climate and there is growing evidence of climate warming. We show that air temperatures measured by meteorological stations have steadily increased over the past 50 years in the southern Indian Ocean, the increase starting in mid 1960s and stabilizing in mid 1980s, being particularly important in the sub-Antarctic sector. At the same time, with a time lag of 2–9 years with temperatures, the population size of most seabirds and seals monitored on several breeding sites have decreased severely, whilst two species have increased at the same time. These changes, together with indications of a simultaneous decrease in secondary production in sub-Antarctic waters and the reduction of sea-ice extent further south, indicate that a major system shift has occurred in the Indian Ocean part of the Southern Ocean. This shift illustrates the high sensitivity of marine ecosystems, and especially upper trophic level predators, to climatic changes.

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Introduction

There is growing evidence that climate warming is occurring and long-term monitoring studies suggest that the recent trends in climate are probably already affecting the species distribution or phenology (Hughes 2000). However, interactions between biotic and abiotic components are both complex and subtle, and analyses of long-term data on both biotic and abiotic components are crucial to understanding these interactions (Harrington *et al.* 1999, Smith *et al.* 1999). World oceans have warmed over the past 50 years (Levitus *et al.* 2000) but the impact of this warming on biotic components is less well documented than for the increase in temperatures affecting terrestrial habitats because of the difficulty of obtaining long-term datasets on marine organisms.

The Southern Ocean plays a critical role in global climate and there is growing evidence of the occurrence of important changes in climate over the past 50 years (King 1994, Smith *et al.* 1999, Levitus *et al.* 2000, Reid & Croxall 2001, Gille 2002). The availability of climatic information obtained through satellites that started to operate in the late 1970s has made it possible to study and model the changes and interactions occurring in the ocean-atmosphere systems (or ocean-sea ice-atmosphere systems in polar regions). Apart from data gathered at scattered stations, there is much less meteorological information before the late 1970s that would allow direct documentation of the occurrence of climate change. Therefore the ecological and meteorological information that is available before the

1970s is particularly valuable since these data can be used to examine possible climate changes and, at the same time, they are long enough to allow a better understanding of the ecological effects of climate change in the open oceans.

In marine ecosystems top predators, such as seabirds and seals, are the only components of the marine ecosystems that can be easily monitored and for which long-term datasets on breeding populations exist. They are top predators whose demography and population abundances are directly influenced by the availability of their prey such as krill, fish or squid (Croxall *et al.* 1999) which are themselves directly influenced by abiotic components (Loeb *et al.* 1997, Nicol *et al.* 2000). Changes in the population sizes or demographic parameters of several seabird species have already been related to large-scale climatic changes occurring in marine ecosystems worldwide (Aebischer *et al.* 1990, Ainley & Divoky in press) and more specifically to abiotic components such as sea-ice extent, sea-surface temperatures or air temperature anomalies (e.g. Guinet *et al.* 1998, Barbraud & Weimerskirch 2001, Thompson & Ollason 2001, Inchausti *et al.* in press, Croxall *et al.* 2002 for a review).

In the Southern Ocean, the Antarctic Peninsula and the south-western part of the Atlantic sector of the Southern Ocean have been the foci of most studies. Comparatively much less is known for the Indian Ocean part of the Southern Ocean. The aim of this paper is to compare long-term population data of top marine predators (seabirds and seals) with climatic data extending back to before the era of

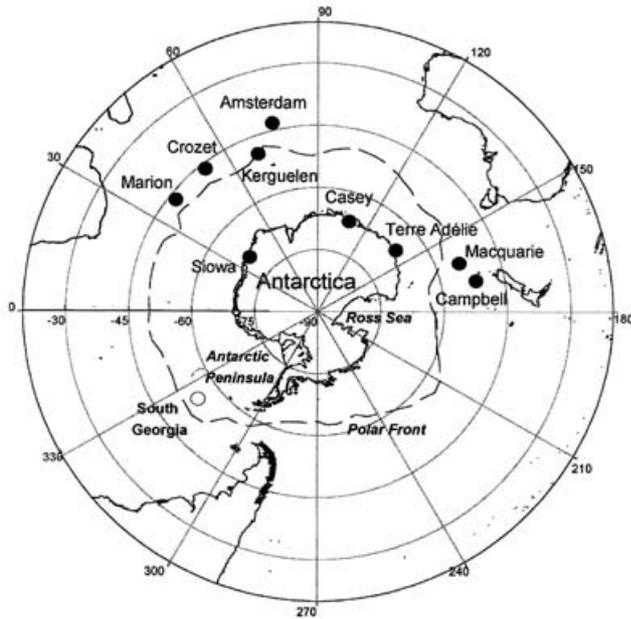


Fig. 1. Map of the Southern Ocean showing the places names mentioned in the text (circles). Black circles indicate sites where data were used in this study.

satellites in order to examine the occurrence of climate change in the Indian Ocean and their proximate ecological consequences during the past 50 years.

Methods

We collated population abundance data for nine top predator species in seven locations in the extended Southern Indian Ocean between 30 and 160°E (Fig. 1). These species have been followed for at least 25 years and have censuses started before 1970. We used data on the breeding population sizes of seabirds and seals available in our long-term datasets (CEB Chizé, CNRS) for the French Antarctic Territories (Amsterdam, Kerguelen, Crozet, Terre Adélie). The species are Amsterdam fur seals *Arctocephalus tropicalis* (Guinet *et al.* 1994) and rockhopper penguins *Eudyptes chrysochome* from Amsterdam Island (Guinard *et al.* 1998), wandering albatrosses *Diomedea exulans* (Weimerskirch *et al.* 1997), king penguins *Aptenodytes patagonicus* (Weimerskirch *et al.* 1992, Guinet *et al.* 1996) and elephant seals *Mirounga leonina* (Guinet *et al.* 1999) from the Îles Crozet. For Kerguelen, the species considered are wandering albatrosses, southern elephant seals and king penguins (Weimerskirch *et al.* 1992, 1997, Guinet *et al.* 1996, 1999) and for Terre Adélie, emperor penguins *Aptenodytes forsteri* and southern fulmars *Fulmarus glacialis* (Barbraud & Weimerskirch 2001, Micol & Jouventin 2001). For other sites, we used published data on black-browed albatrosses *Diomedea melanophris* from Campbell Island (Waugh *et al.* 1999), wandering

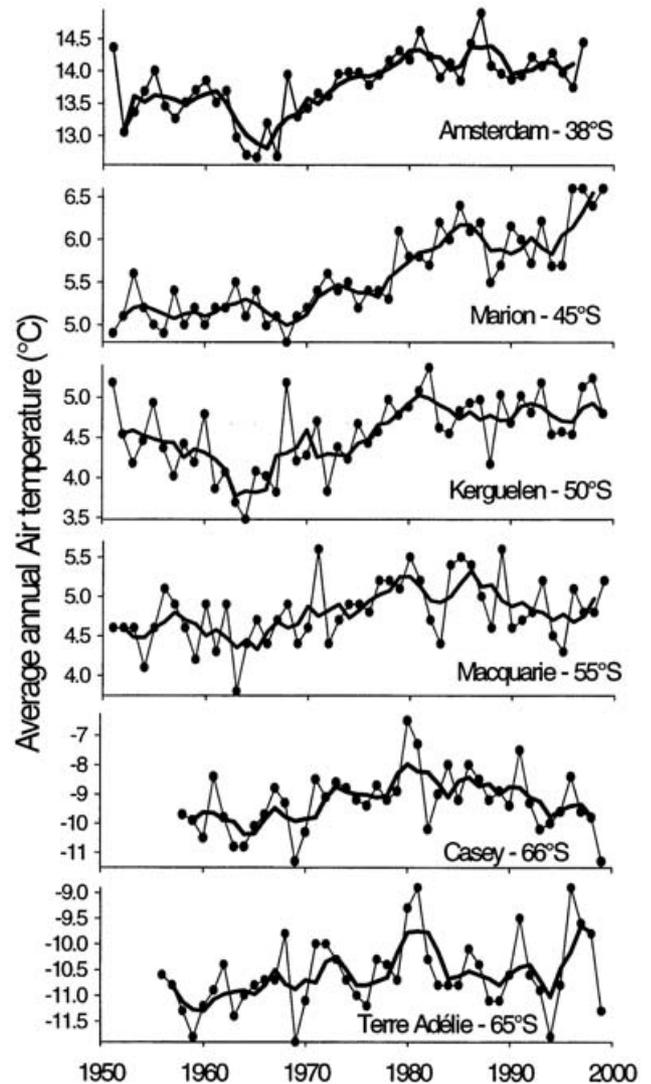


Fig. 2. Changes in average annual air temperature at seven sites of the Southern Indian Ocean. The points and thin line indicate the average values, and the solid line is the moving average (average over three years).

albatrosses from Macquarie Island (de la Mare & Kerry 1994) and Adélie penguins *Pygoscelis adeliae* from Syowa, Antarctica (Kato *et al.* 2002).

Although ocean temperature is more relevant to marine organisms than air temperature, air temperature is easier to measure and is a useful proxy for sea surface temperature as it is strongly influenced by the ocean surface. Furthermore sea surface temperatures are available from remote sensing only since the early 1980s. The annual average temperatures were calculated for the meteorological stations of the extended Indian Ocean (Fig. 1) whose records cover at least 40 years (Fig. 1). The data were obtained from Météo France, Toulouse, for the French stations and for other sites from the Mean Monthly Surface Air Temperature of the

Table I. Cross-correlations of air temperatures of different locations in the Indian Ocean. Data in the table show the time lag corresponding to the largest correlation and its standard error (s.e.). Temperature data were linearly detrended prior to the analysis. For each site in columns (first series in the correlation), the lags correspond to the number of years with respect to those in rows (second series in the correlation), i.e. Marion island temperatures have a lag of 3 years with respect to Amsterdam.

	Marion	Kerguelen	Crozet	Macquarie	Casey	Terre Adélie
Amsterdam	Lag = 3 0.585 (s.e. = 0.154)	Lag = 1 0.791 (s.e. = 0.151)	Lag = 1 0.486 (s.e. = 0.151)	Lag = 0 0.640 (s.e. = 0.149)	Lag = 0 0.701 (s.e. = 0.162)	Lag = 4 0.663 (s.e. = 0.152)
Marion	—	Lag = 4 0.684 (s.e. = 0.153)	Lag = 1 0.347 (s.e. = 0.147)	Lag = 6 0.357 (s.e. = 0.156)	Lag = 5 0.437 (s.e. = 0.169)	Lag = 4 -0.490 (s.e. = 0.162)
Kerguelen		—	Lag = 0 0.426 (s.e. = 0.144)	Lag = 0 0.553 (s.e. = 0.146)	Lag = 0 0.542 (s.e. = 0.158)	Lag = 8 0.494 (s.e. = 0.175)
Crozet			—	Lag = 0 0.347 (s.e. = 0.147)	None significant	Lag = 0 0.377 (s.e. = 0.154)
Macquarie				—	Lag = 0 0.852 (s.e. = 0.158)	Lag = 6 0.574 (s.e. = 0.167)
Casey					—	Lag = 8 0.396 (s.e. = 0.171)

Antarctic CRC and Australian Antarctic Division Climate datasets (<http://www.antcrc.utas.edu.au/~jacka/climate.html>). Surface air temperatures anomalies for the Southern Ocean at 45°S were obtained from the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA (<http://www.cdc.noaa.gov>). We used NCEP/NCAR Reanalysis data based on analysis/forecast system performing data assimilation using past data from 1948 to the present (Kalnay *et al.* 1996) to calculate monthly means of surface air temperature anomalies.

We used cross-correlations to examine the relationships between temperatures at various sites and to identify phase relations between two time series (SYSTAT 10, Wilkinson 2000) with the correlation at lag 0 corresponding to the Pearson correlation. Before the analyses, we log-transformed population data and we linearly detrended both population and temperature data to meet the assumptions of the cross-correlation test. The significance of the CCF at different lags is done by comparing the ratio correlation (lag)/standard error (lag) with a normal variate (similar to what is done with the Pearson coefficient) (see Diggle 1990).

Results

There was a clear increase in the average annual air temperature of all locations from their minimum value during the 1960s until mid 1980s at rates ranging from 0.07 to 0.30°C per decade (Fig. 2). The increase in the 1970s is particularly clear for the sub-tropical and sub-Antarctic sites, Amsterdam, Marion and Kerguelen. The increase in temperature was simultaneous or with a one-year lag for Amsterdam, Crozet, Kerguelen and Macquarie, whereas

temperatures increase was delayed at Marion and in Terre Adélie (Fig. 2, Table I). The average annual temperature appeared to stabilize or even decrease again at some sites after the mid 1980s (Fig. 2).

Population abundance of most top predators, except two species, king penguins and Amsterdam fur seals, started to decrease at the end of the 1960s (Fig. 3). The decreases took place for all species during the 1970s, with some species decreasing still during the early 1980s. For several species, the decreases during the 1970s were followed by a large (Adélie penguins, southern fulmar) or a partial (wandering albatrosses on Crozet and Kerguelen, black-browed

Table II. Cross-correlations between population abundance and average annual temperature for top marine predators in the Indian Ocean. Results show the correlation between population abundance and temperature for the shortest time lag that was statistically significant at $P = 0.05$ (as indicated by an asterisk) and its associated standard error. Prior to the analyses, population data were log-transformed and both population and temperature data linearly detrended.

	Time lag	Correlation	s.e.
Crozet			
elephant seal	9	-0.492*	0.229
wandering albatross	4	-0.412*	0.167
king penguin	5	0.347	0.192
Kerguelen			
elephant seal	10	-0.380*	0.167
wandering albatross	9	-0.462*	0.243
Macquarie			
wandering albatross	3	-0.574*	0.189
Marion			
wandering albatross	4	-0.473*	0.236
Terre Adélie			
southern fulmar	2	-0.396*	0.172
emperor penguin	2	-0.380*	0.174

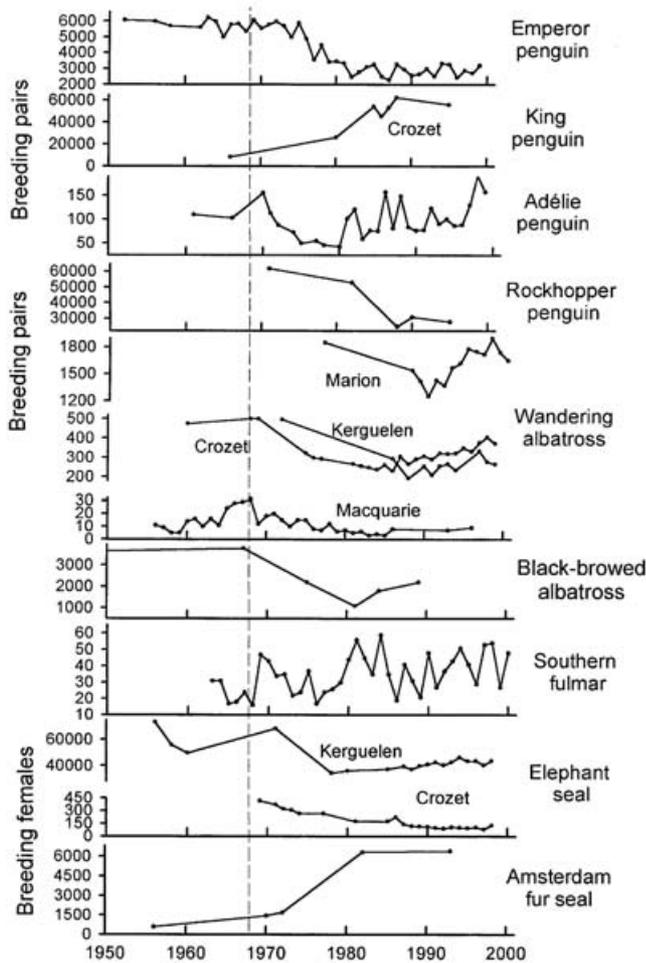


Fig. 3. Changes in the size of populations of nine species of seabird and seals breeding in the southern Indian Ocean. The dashed vertical line indicates the approximate time when population changes started to occur.

albatross at Campbell) recovery of the populations, while other species (emperor penguins, elephant seals) did not recover and remained at lower levels. Two species, king penguins at Crozet and Kerguelen, as well as Amsterdam fur seals showed increases in their numbers at the same time.

For species with long regular records, i.e. wandering albatrosses and southern elephant seals, decreases in population occurred with a lag after the increase in temperature, varying according to the species and locality (Table II). Wandering albatrosses decreased simultaneously at Crozet, Kerguelen and Macquarie, but at Marion Island (Nel *et al.* 2001) the decrease and subsequent increase was delayed by four years compared to the three other sites (Fig. 3).

The sea surface temperature anomalies at 45°S between 1948 and 2000, estimated by NCEP models, clearly showed that surface temperatures have increased in the Indian Ocean to 120°E with negative values to the mid 1970s to

early 1980s, and then positive values after (Fig. 4). In the Pacific and Atlantic part of the Southern Ocean, there was no significant long-term trend for the same time period. These data also showed that a large and relatively localised anomaly, leading to an increase of 0.7°C, occurred in the south Indian Ocean during the 1960s.

Discussion

The increase in air temperatures during the 1970s documented at the meteorological stations in the Indian Ocean suggest that this part of the Southern Ocean, and especially the sub-Antarctic sector, has been affected by a large-scale change (regional to ecosystem) in surface air temperatures between the mid 1960s and the mid 1980s. It has affected terrestrial habitats of some islands (Marion Island: Smith & Steenkamp 1990; Îles Kerguelen: Frenot & Gloagen 1993). The increase in air temperatures during the 1970s was simultaneous with the increase in the ocean temperatures estimated for the Southern Ocean (Levitus *et al.* 2000, Gille 2002). South of the sub-tropical front the general circulation in the Southern Ocean is from west to east because of the Antarctic Circumpolar Current (White & Peterson 1996). However, the time lags reported between the different sub-Antarctic sites are not all totally coherent with such a circulation. In particular, temperature increases at Marion take place after Kerguelen or Amsterdam, indicating that the warming event was not diffusing simply from the west (as indicated by the absence of a similar event in the south Atlantic), but may rather have come from tropical waters of the Indian Ocean (Marsac & Leblanc 1998, unpublished data).

The changes in environmental conditions have probably produced profound functional consequences in the ecosystem of the western Indian Ocean, as illustrated by the decline in chlorophyll *a* and zooplankton concentrations after the late 1970s (Hunt *et al.* 2001). This suggests that decreases in food availability at lower trophic levels may underlie the general decrease of top predator populations that we have documented here. In addition to the species studied here, decreases of other species or populations in the extended Indian Ocean have been documented. Although derived from less regular datasets clear decreases have been shown between the 1960s and 1980s for rockhopper penguins (*Eudyptes chrysocome*) and grey-headed albatrosses (*Diomedea chrysostoma*) from Campbell Island (Cunningham & Moors 1994, Waugh *et al.* 1999) and albatrosses and petrels in Antarctic waters of the central Indian Ocean (Woehler 1996). However, the exact timing of the decrease of these species or populations has never been accurately documented.

The decrease in the population of top predators monitored in the Indian Ocean occurred with a lag compared to the increase in temperatures. Seabird and sea mammals are long-lived and consequently factors affecting demographic

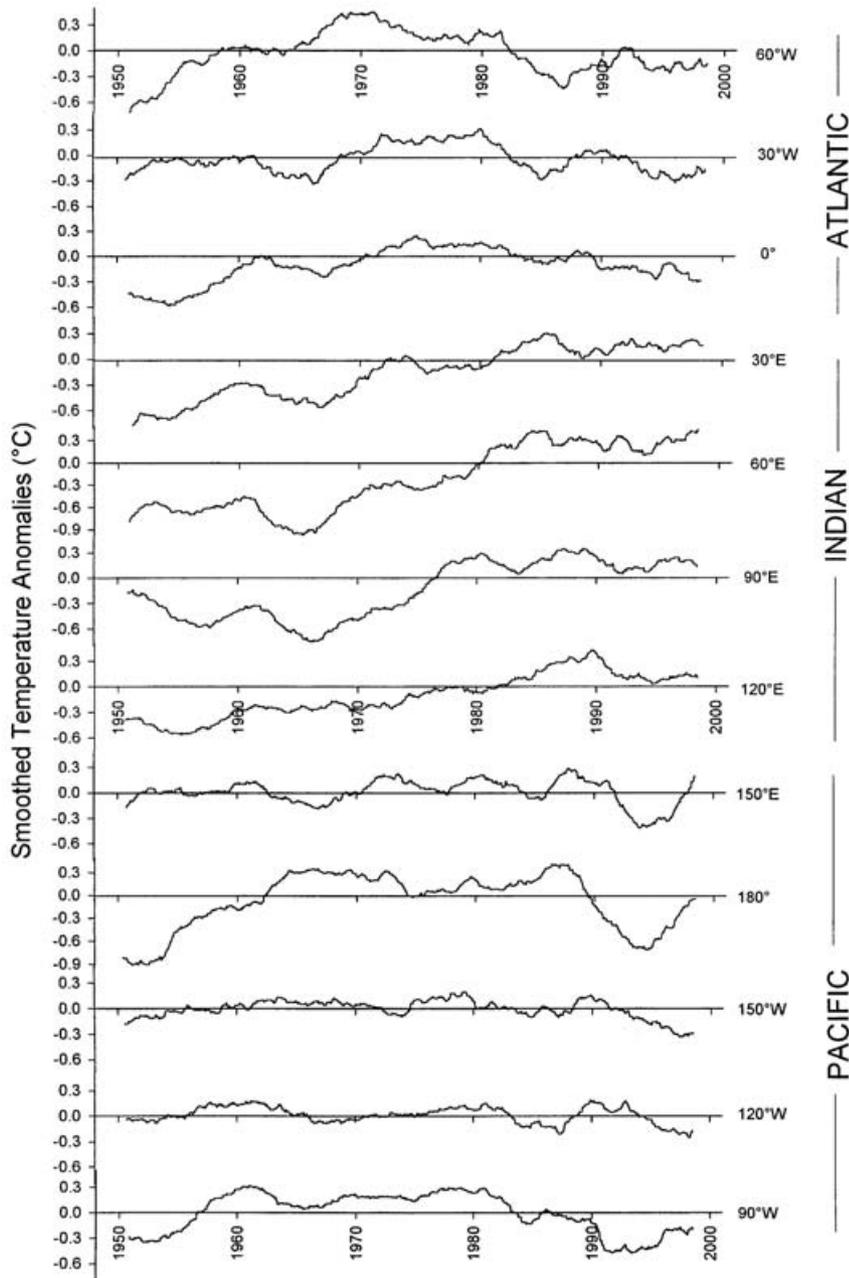


Fig. 4. Changes over the past 50 years in the monthly temperature anomalies at 45°S throughout the Southern Ocean (NCEP model). Values are moving average averaged over 48 months.

parameters, such as reproduction or recruitment, could be expected to have a delayed effect on population size (Wooller *et al.* 1992, Thompson & Ollason 2001). These delays were, however, variable according to the species and localities, probably because each species has a different demography and is preying at different trophic levels, and environmental changes may affect different demographic parameters. For example, a decrease in adult survival would have an immediate effect on the breeding population, whereas a decrease in fecundity or immature survival would have a lagged effect on population size (see Weimerskirch *et al.* 1997 for a simulation). This suggests that in the Indian Ocean, where a lag between temperature increase and

population decrease occurs, the environmental changes could have affected fecundity or recruitment rather than adult survival (Hindell 1991).

Because air and sea temperatures have reached a plateau since the mid 1980s and have not returned to original values, the pattern that occurred in the Indian Ocean is likely to be a 'regime shift', i.e. a jump from one stable state to another (Scheffer *et al.* 2001). We cannot exclude the possibility that the change may be also part of a very long-term cycle (several decades). Regime shifts have been observed in other marine environments (Hare & Mantua 2000, Reid *et al.* 1998). A regime shift occurred at the same time in the North Pacific and had profound effects at all

levels of the trophic web, especially on seabirds (Hare & Mantua 2000). The changes in numbers of emperor penguins and elephant seals at Îles Kerguelen are typical of a regime shift, an abrupt decrease from one steady state to another, whereas in other species (e.g. wandering albatrosses) the conjunction of regime shift and of other processes may have allowed the partial recovery of the population. Some species of albatrosses in the Indian Ocean were incidentally killed in long line fishing operations (Brothers 1991, Weimerskirch *et al.* 2000) which has been shown to have impacted, at least in part, on wandering albatrosses (Weimerskirch *et al.* 1997, Tuck *et al.* 2001), but may not be the only reason for their observed decreases. Wandering albatrosses from Îles Crozet, Îles Kerguelen (this study) and Marion Island (Nel *et al.* 2001) have followed very similar trends during the past 40 years, suggesting that a common suite of broad scale environmental and/or anthropogenic factors has affected these populations. However, fishing effort of tuna long liners in the 1970s were different between the foraging areas of the different populations (Weimerskirch *et al.* 1997, Nel *et al.* 2001) suggesting that other factors such as a regime shift operating at a more regional scale has probably affected these populations.

Only two species (king penguins and Amsterdam fur seals) increased during the period of general decrease in top-predators and of increase in temperatures. While the species that have decreased are mainly squid eaters, and to a lesser extent crustacean or fish predators (Cherel & Klages 1998, Guinet *et al.* 1996), king penguins and Amsterdam fur seals specialise in feeding on myctophid fishes (Cherel & Ridoux 1992, Guinet *et al.* 1996). These species may have been favoured by the regime shift because they rely on a particular component of the trophic web, but other factors may be implicated. Since they have increased throughout the Southern Ocean, their increase may be the result of an environmental change at ecosystem scale, in contrast to the more limited regional scale changes for the other species. The increase may also be part of the recovery of populations that have been exploited to very low levels during the past two centuries (Weimerskirch *et al.* 1992, Guinet *et al.* 1994).

Ocean warming is also likely to have affected sea ice conditions in Antarctica. A regional decrease in sea ice extent in Antarctica has been suggested from whaling records at the same time as the regime shift documented here (de la Mare 1997, but see Vaughan 2000), and more precisely during the late 1970s off Terre Adélie (Barbraud & Weimerskirch 2001). Such a decrease in sea ice extent that generally affects negatively krill survival and recruitment (Loeb *et al.* 1997) is likely to be responsible for the decrease of Antarctic top predators in the 1970s such as Adélie or emperor penguins (Croxall *et al.* 2002). Barbraud & Weimerskirch (2001) have shown that emperor penguins in Terre Adélie decreased because of an increase in adult

mortality related to an increase in temperatures and a decrease in sea ice extent. The decrease in sea ice extent documented during the late 1970s for the Adélie Land area could be related to the regional increase in temperatures in the Indian Ocean. An additional indication of the large scale and long lasting anomaly that occurred in the Indian Ocean during the 1970s is the significant variability in sea surface (White & Cayan 1998) and the unusual turbulence (wind speed) in tropical waters of the Indian Ocean (Marsac & Leblanc 1998) occurring at the same time.

The average temperatures recorded in Antarctic stations (Casey, Terre Adélie, Fig. 2) and the NCEP temperature anomalies modelled at 45°S (Fig. 4) indicate that multi-annual cycles in temperature occurred superimposed over the temperature shift, probably related to cyclic events such as the Antarctic Circumpolar Wave (White & Peterson 1996). Moreover, it is interesting to note that the sharp increase in air temperature anomalies through the 1970s was particularly rapid only in the southern Indian Ocean, compared to the other parts of the Southern Ocean (Fig. 4). The limited available data for the same top predators over a similar time scale in the South Atlantic or in the Ross Sea sectors (elephant seals at South Georgia: Boyd *et al.* 1996, Adélie penguins in the Ross Sea: Smith *et al.* 1999, Wilson *et al.* 2001) suggest that the latter ones did not experience decreases during the 1970s similar to those in the Indian Ocean. Some populations (wandering albatrosses at South Georgia: Croxall *et al.* 1998; Adélie penguins on the Antarctic Peninsula: Smith *et al.* 1999) did decrease but at much lower rates and at a different time to those of the same species in the Indian Ocean. Increases in ocean temperatures also occurred in the Atlantic and Pacific Oceans sectors but at different times than those reported for the Indian Ocean, and with a lower extent, suggesting that there are large geographic differences in the climatic changes occurring in different part of the Southern Ocean (see also Fig. 4 for air temperatures).

Upper trophic level predators such as seabirds and seals are the only elements of the trophic web that are readily accessible and able to be monitored, and for this reason are often considered to be convenient bio-indicators of marine ecosystems (Croxall 1992, Furness & Greenwood 1993). Several long-term monitoring studies of population size, complemented by demographic parameters, are available in the Southern Ocean and provide valuable signals to changes occurring in the marine environment. The results of this study clearly show that climate change and ocean warming can have profound effect on the biotic components of marine ecosystems.

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