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Inter-annual variability in the breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the Kerguelen sectors of the Southern Ocean

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Global warming is expected to increase the frequency and intensity of inter-annual variation in Sea-Surface Temperatures (SST) associated with a latitudinal shift of frontal structures in the Southern Ocean. However, the long-term consequences of these major climatic events on the biotic environment remain poorly understood. We studied the effect of SST anomalies in the southern Indian Ocean on the breeding success of eight seabird species, and found these temperature anomalies to have different effects depending on the foraging habitat of the species. The breeding success of four seabird species foraging mainly south of the Polar Front in Antarctic waters was significantly depressed by warm SST occurring mainly in winter and spring, prior to breeding. Conversely, warm SST anomalies were associated with a higher breeding success for species foraging mainly north of the Polar Front, while no significant effect was found for two species that forage on the Kerguelen plateau. These different responses to changes in the SST were also observed for two closely related species (sooty albatross *Phoebetria fusca* and light-mantled sooty albatross *P. palpebrata*) breeding at Kerguelen. These observations highlight the importance of multi-species long-term monitoring programs for understanding the ecological consequences of environmental variability. Our results suggest that the predicted southward shift of the Polar Front caused by oceanic warming could lead to an important decrease in the breeding performance of top predator seabirds depending on the location and changes of their foraging habitat in relation the Polar Front.

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Inter-annual variability is a characteristic feature of the Southern Ocean, yet the consequences of this variability for the biological processes are poorly understood (SCAR 1992, De La Mare 1997). The warming trend observed in this ocean after the 1950s (Jacka et al. 1984, Smith et al. 1999) would increase the frequency and/or the intensity of extreme events of inter-annual variation in Sea-Surface Temperature (SST) in association with latitudinal shifts of frontal structures (Moore et al. 1999, SCAR 1992). The SST has been related to the inter-annual variation in the depth of the oceanic mixed winter layer (Waluda et al. 1999) which determines the replenishment of surface waters with nutrients originating from deeper waters, thereby partly controlling the primary and secondary production in pelagic waters (Lévy et al. 1998). In the short term, the foraging success of avian marine predators has been associated with variations in oceanographic conditions (Abrams 1985, Hunt et al. 1992, Veit et al. 1996, 1997, Montevecchi and Myers 1997, Baduini et al. 2001), in some cases leading to total breeding failure (Croxall 1992, Chastel et al. 1993, Guinet et al. 1998). However, the long-term consequences of oceanographic anomalies on the breeding success of avian predator populations are poorly known and it is unclear whether species with different foraging strategies and diets would react similarly to the variation in oceanographic conditions.

The study of the inter-annual fluctuations in the breeding performance of these top predators in relation to the inter-annual variability in oceanographic conditions can provide an insight into the possible long-term biological consequences of climatic change in the Southern Ocean ecosystem. This paper has two main goals. First, to assess how inter-annual variability in SST – used as a proxy for food availability – is related to the reproductive success of eight species of seabirds breeding on the Crozet and Kerguelen islands in the Indian Ocean. Second, to explore the temporal scale at which the SST anomalies are significantly related to breeding success as a means to investigate the possible mechanisms by which environmental variability affects the demography of these seabird species.

Methods

Long-term monitoring of population size and seabirds demography has been carried out since the late sixties at the Crozet and Kerguelen Islands (Fig. 1) in the southern Indian Ocean (Weimerskirch and Jouventin 1998). Annual breeding success of eight species was estimated as the ratio between the number of chicks fledged and the number of eggs laid in each colony. These eight species chosen are those for which we have the longest series of data on breeding success for the Crozet and Kerguelen islands. Table 1 summarises the available information on the breeding locality, monitoring period, number of breeding pairs monitored, diet and foraging distribution at sea, obtained either from satellite telemetry studies (Jouventin and Weimerskirch 1990, Weimerskirch et al. 1993), by programs of observation at sea, or from diet studies (Stahl et al. 1985, Cherel and Klages 1998) for the eight species (Fig. 1 and Table 1).

SST is the only oceanographic parameter measured continuously during breeding in the different foraging zones of the studied seabird species since 1982. Monthly averages of SST were calculated from January 1982 until December 1998 using *in situ* and satellite radiometer measurements obtained on a 1° scale. Satellite observations were obtained from the Lamont-Doherty Earth Observatory at Columbia University and the Integrated Global Ocean Service System (Reynolds and Marsico 1993). Given that the relationship between environmental factors and seabird distribution often depends on the spatial scale being considered (e.g. Hunt and Schneider 1987, Jacquet et al. 1996), we divided the study area around Crozet and Kerguelen into two sub-sectors located north and south of each island (Fig. 1). This subdivision should account for the interspecific differences in the foraging ranges of the studied seabirds around each island during their breeding seasons (Table 1). Accordingly, we defined the study areas at Crozet as rectangles centred at Ile de la Possession, delimited by 38°30′S–54°30′S, 42°E–62°E and at Kerguelen, delimited by 35°S–57°S, 60°30′E–80°30′E,

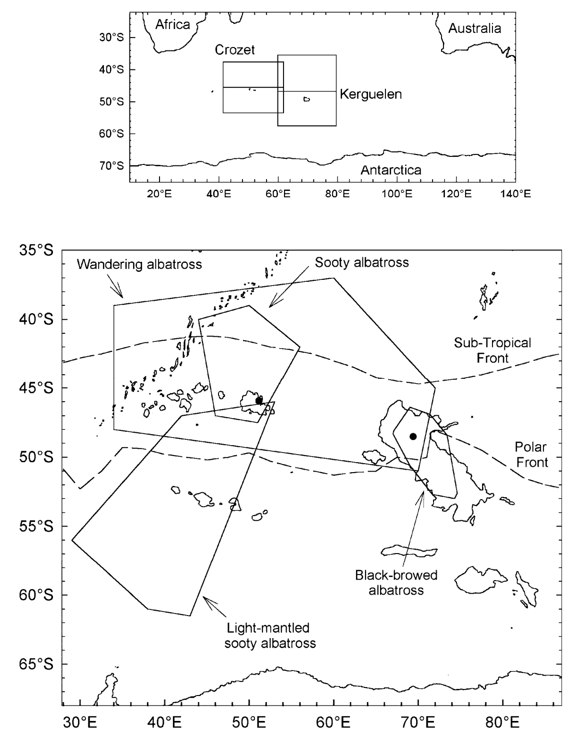

Fig. 1. Physical oceanographic studies on this sector of the Southern Ocean have established the general distribution of water masses (Park et al. 1993). The areas where Sea Surface Temperature anomalies were calculated for the Crozet and Kerguelen sectors are shown by continuous lines in the upper panel; each sector was further subdivided into a northern and a southern sub-sector. The sub-Antarctic waters are delimited to the north by the Sub-Tropical Front and to the south by the Polar Front, and the Antarctic waters are situated south of the Polar Front. (lower panel) The foraging ranges of sooty and wandering albatross at Crozet, and of black-browed and light-mantled sooty albatross at Kerguelen were assessed by using either satellite tracking data, or by an at-sea observation program during the breeding periods of these species. The foraging range of each species is represented by maximum convex polygons including all the core areas that regroup a minimum of 2% of the locations.

Table 1. Breeding locality, study period, diet composition, and main foraging habitat of the eight seabird species considered in this paper.

Species	Breeding locality	Monitoring period	Study period	Breeding pairs during study period	Diet composition (items comprising > 10% of diet mass)	Main breeding and foraging habitat
Wandering albatross *Diomedea exulans*	Crozet	1966–1997	1982–1997	250–300	squid 77%, fish 15% a	Sub-Antarctic waters b
Sooty albatross *Phoebetria fusca*	Crozet	1971–1997	1982–1997	70–100	carrion 51%, squid 41% a	Sub-Antarctic waters b
Light-mantled sooty albatross *Phoebetria palpebrata*	Crozet	1981–1993	1982–1992	30–50	squid 56%, carrion 17%, crustacean 16%, fish 11% a	Antarctic waters b
Black-browed albatross *Thalassarche melanophrys*	Kerguelen	1979–1997	1982–1997	100–150	Fish 73%, carrion 14%, squid 10% f	Kerguelen Plateau b, c
Blue petrel *Halobaena caerulea*	Kerguelen	1986–1997	1986–1997	100–150	crustacean 59%, fish 37% g	Antarctic waters d
Thin-billed prion *Pachyptila belcheri*	Kerguelen	1986–1997	1986–1997	100–150	crustacean 97% g	Antarctic waters d
White-headed petrel *Pterodroma lessoni*	Kerguelen	1986–1997	1986–1997	20–40	squid > fish > crustacean e	Antarctic waters d
Grey petrel *Procellaria cinerea*	Kerguelen	1986–1997	1986–1997	40–60	squid 70%, fish 28% a	Antarctic waters of Kerguelen Plateau d

a. Ridoux 1994.
b. Weimerskirch 1998.
c. Cherel and Weimerskirch 1995.
d. Woehler et al. 1991.
e. Zotier 1990.
f. Cherel and Weimerskirch unpubl. data.
g. Cherel and Bocher unpubl. data.

respectively (Fig. 1). We calculated the monthly anomalies in SST at each sub-sector of each island as the difference between the mean observed SST over the study zones for a given month and the long term mean SST observed for that month, calculated over the whole study period (January 1982–May 1998).

We used correlations to investigate the critical period of the year when environmental anomalies affect the annual breeding success of each of the eight seabird species. We used the Spearman coefficient to compute correlations between annual breeding success of each species and monthly values of SST anomalies from February (preceding reproduction) until May the following year (when chicks of most species are fledged) for all seabird species starting to breed in the Austral spring or summer. The only exception was the grey petrel *Procellaria cinerea* that breeds in the Austral winter and for which we used the monthly SST anomalies between the month of November preceding reproduction until the month of December the following year. Because SST anomaly and breeding success were measured with different temporal resolutions (monthly and yearly, respectively), one could compute as many correlation coefficients for each species as the number of months considered, with each of these coefficients being based on sixteen pairs of monthly SST and breeding success for the years 1982–1998. Care must be taken when computing numerous correlation coefficients from the same data since chance alone may result in spuriously significant correlations. To avoid this we used a bootstrap procedure (Gleason 1988) to generate sampling distributions of the correlation coefficients for each species by randomly assigning 10,000 times the annual breeding success to the SST values. This procedure allowed calculating approximate 95% confidence intervals of the observed correlation coefficients for all months considered (Gleason 1988). The bootstrap method used allowed creating pseudo-data sets that explicitly incorporated all sources of correlation of the original data, from both the multiple contrasts and the multivariate structure, and thus their p-values and confidence intervals incorporate all correlations and distributional characteristics, thereby tending to be more conservative than other methods (Westfall and Young 1993). These confidence intervals were used to decide the statistical significance of the correlation for different time lags whenever the value of zero was not included in the 95% confidence interval (i.e. a two-tailed test at significance level 0.05) indicating a statistically significant shift towards a positive or a negative correlation between SST anomaly and breeding success in a given month.

Results

The time series of monthly SST anomalies from 1982 until 1998 showed that the range of temperature anoma-

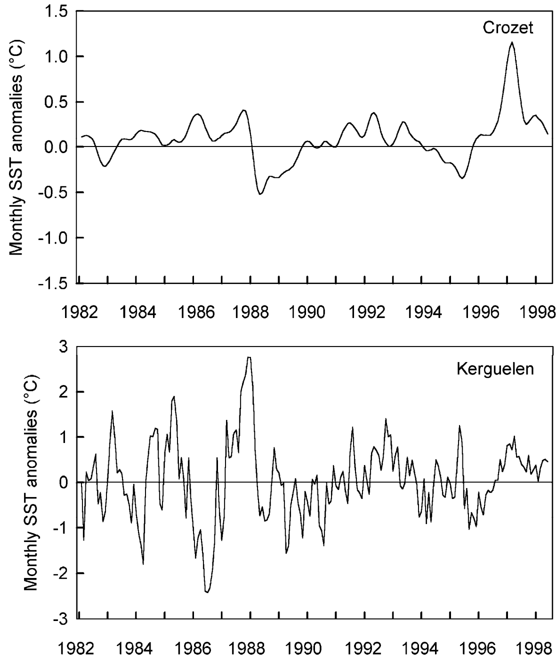

Fig. 2. Time series of monthly Sea Surface Temperatures anomalies in the Crozet (top) and Kerguelen (bottom) Island sector from January 1982 until May 1998. The zero line separates positive above and negative underneath SST anomalies.

lies was nearly three times greater at Kerguelen compared to Crozet (Fig. 2) and major warm SST anomalies occurred during different years at Kerguelen (1987–1988) and Crozet (1997–1998). Since seabird species from the Crozet Islands were foraging both in the northern and southern sectors, we used the SST anomalies calculated over the whole study zone to calculate the Spearman correlation coefficient between SST anomalies and breeding success (similar results were obtained using the SST anomalies for either sector). At the Kerguelen Islands, significant relationships between breeding success and SST anomalies were found in the southern sector which is consistent with the southern foraging distribution of the seabirds species in this area (Table 1).

Three kinds of demographic responses to SST anomalies were observed depending on the seabirds preferred foraging area during the breeding season (Fig. 3). First, the breeding success of the light-mantled sooty albatross *Phoebetria palpebrata*, blue petrel *Halobaena carulea*, thin-billed prion *Pachyptilla belcheri*, and white-headed petrel *Pterodroma lessoni*, all species that forage in Antarctic waters south of the Polar Front, were negatively associated with SST anomalies. Most correlation coefficients for these four species were negative and significant negative correlations between sea surface temperature anomalies and breeding success were found in the winter and spring preceding reproduction, suggesting that these species were negatively affected by warm sea surface anomalies. Second, wandering albatross *Diomedea exulans* and sooty albatross *Phoebetria fusca* that forage mostly in subtropical waters north of the Polar Front had an opposite response to that of the first group of species, their breeding success tended to be enhanced by warm SST episodes (Fig. 3). Most correlation coefficients for wandering and sooty albatross were positive and significant positive relationships were found between SST anomalies and the breeding success of these two species. Thirdly, black-browed albatross *Thalassarche melanophrys* and grey petrel showed no significant relationship between SST anomalies and breeding success at any time scale (Fig. 3).

Discussion

The breeding success of several top predator seabirds of the southern Indian Ocean was related to warm SST anomalies occurring in their foraging zone during the austral winter and in spring, before breeding. The SST anomalies occurring during the rest of the year (and especially during the breeding season) showed little or no effect on the breeding performance of any of the seabirds studied (Fig. 3). The influence of winter and spring SST on food availability, and thus, on the breeding performance could be related to the inter-annual variation of the depth of the oceanic winter mixed layer (Waluda et al. 1999) that determines primary and secondary production by controlling the nutrient replenishment of surface waters (Lévy et al. 1998). Although the seabird species considered here forage in different geographic areas during the breeding and the non-breeding periods, they arrive at breeding colonies several weeks before the start of the egg-laying. The winter SST anomalies would co-determine food availability in the foraging zones used before and during the breeding period, and consequently, could affect breeding success through its effects on body condition in the critical months of egg-laying and early chick growth. Our results suggest that the winter climatic and oceanographic conditions determine food availability during the breeding season for species that forage in Antarctic waters. Major shifts in trophic structure associated with warm SST conditions near the Marion and Kerguelen Islands in the southern Indian Ocean led to an increase in the biomass of zooplankton from sub-Antarctic/subtropical waters at both localities (Semelkina 1993, Pakhomov and Froneman 1999). The breeding performance of seabird species foraging south of the Polar Front suggests that warm SST episodes may have reduced food availability in Antarctic waters located south of the Crozet and Kerguelen Islands. A southward shift in the location of the Polar Front increases the distance between the breeding colonies on

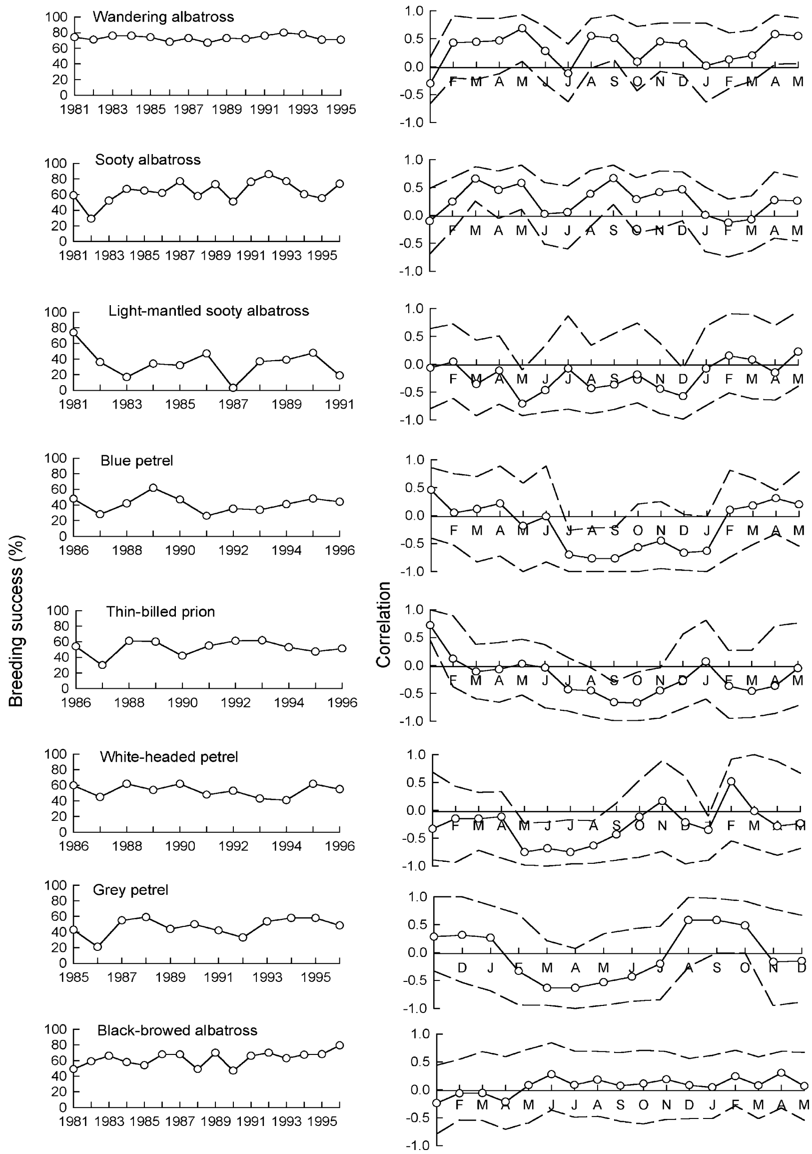

Fig. 3. Inter-annual variation in breeding success for eight seabird species breeding at the Crozet and Kerguelen Islands from 1982 to 1998 left panels. Spearman correlation coefficient values calculated between the Sea-Surface Temperatures SST anomalies over the period ranging from February (preceding the reproduction period) until May the following year, and the breeding success for the eight seabird species studied, are shown in the right panels. The broken lines show the 95% confidence intervals bootstrap calculations of the correlation coefficients for each species; their statistical significance at different time lags was determined whenever the value of zero was included in the 95% confidence interval.

sub-Antarctic islands and the feeding zones in Antarctic waters. A shift of 3° (i.e. 330 km) of latitude in the position of the Polar Front is observed in the Kerguelen region (Moore et al. 1999), thus reducing the accessibility of food resources and ultimately affecting the breeding performance of seabirds species feeding in Antarctic waters. In contrast, warm SST conditions appear to enhance the breeding success of seabird species whose foraging areas are located mostly north of the Polar Front.

The absence of a relationship between SST anomalies and breeding success in the black-browed albatross and the grey petrel suggests that the breeding success of these species was not directly affected by SST anomalies. The grey petrel is the only winter-breeding species considered here and is also known to forage in waters above the continental shelf. Similarly, the black-browed albatross only occurs across the Kerguelen plateau during the breeding period (Cherel and Weimerskirch 1995, Weimerskirch 1998). These results suggest that shelf areas may have been affected in a different way by oceanographic anomalies and that the same environmental anomaly might have different effects on the breeding performance of different marine predators. These differences appear to be related to the different foraging zones exploited by the seabird species studied here and may reflect major differences in the trophic structure of the oceanic waters north and south of the Polar Front (Pakhomov and McQuaid 1996). In this regard, it is remarkable that the breeding success of two closely related species such as the sooty and the light-mantled sooty albatross that forage north and south to the Polar Front, respectively (Fig. 1), showed opposite relationships with SST anomalies (Fig. 3).

The larger range of temperature anomalies in the Kerguelen region compared to the Crozet region may result from the influence of the Polar Front that reaches areas just south of the Kerguelen Island (Fig. 1) and the important inter-annual shift observed in the location of the Polar Front (Moore et al. 1999). Thus, a southern shift in the location of the Polar Front would induce an input of warmer sub-Antarctic and subtropical water within the Kerguelen region (Moore et al. 1999). In contrast, the Crozet Islands are located within the inter-frontal zone and only a major shift in the location of the Polar Front zone could induce a substantial change in sea surface temperatures. The Polar Front exhibited the highest inter-annual variability between 1987 to 1993 in the Crozet-Kerguelen region, reaching its southernmost positions in the summer of 1987–1988 precisely when the warm SST anomalies were observed (Moore et al. 1999). The major warm 1987–1988 SST anomalies and to a lesser extent, the 1991–1992 warm event, occurred at the same time as a restricted sea-ice extension in the sector south to the Crozet and Kerguelen Islands, associated with the recently described Antarctic Circumpolar Wave (White and Peterson 1996).

We have shown that there is a large-scale temporal consistency in the pattern of inter-annual variability in climatic, physical and biological processes within the Crozet-Kerguelen region that is reflected in the demography of several top marine predators breeding in this region. Hence, climate change is likely to induce different responses in different marine ecosystem processes and consequently in top marine predators. We predict that a southward shift of the Polar Front due to oceanic warming would induce a similar shift in the foraging areas of seabirds that forage in Antarctic waters which in turn would lead to a decline in breeding performance and population size at the Crozet and Kerguelen Islands. The reverse situation would be predicted for species that breed on sub-Antarctic islands and forage in sub-Antarctic and subtropical waters.

This study highlights the importance of long-term monitoring programs of marine predators that have a large foraging range and consume a large diversity of prey since they may provide an integrated view of the consequences of oceanographic anomalies on both high and low trophic levels. The combination of such monitoring programs and studies simulating the effect of climate change on oceanographic parameters are essential for forecasting the potential effects of global climatic change on marine Antarctic ecosystems over the next few decades.

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References

Abrams, R. 1985. Environmental determinant of pelagic seabird distribution in the African sector of the Southern Ocean. – J. Biogeogr. 12: 466–472.

Baduini, C., Hyerenbach, K., Coyle, K., Pinchuk, A., Mendenhall, V. and Hunt, G. 2001. Mass mortality of short-tailed shearwaters in the south-eastern Berin sea during summmer 1997. – Fisheries and Ocean. 10: 117–130.

Chastel, O, Weimerskirch, H. and Jouventin, P 1993. High annual variability in reproductive success and survival of an Antarctic seabird, the snow petrel *Pagodroma nivea*: a 27-year study. – Oecologia 94: 736–751.

Cherel, Y. and Klages, N. 1998. A review of the food of albatross. – In: Roberston, G. and Gales, R. (eds). Albatross biology and conservation. Surrey Beatty and Sons, Chipping Norton, pp. 113–136.

Cherel, Y. and Weimerskirch, H. 1995. Seabirds as indicators of marine resources: black-browed albatrosses feeding on ommastrephids squids in Kerguelen waters. – Mar. Ecol. Prog. Ser. 129: 295–300.

Croxall, J. 1992. Southern Ocean environmental changes: effect on seabirds, seal and whale populations. – Philos. Trans. R. Soc. Lond. B 339: 319–328.

De La Mare, W. 1997. Abrupt mid-twentieth-century decline in Antarctic sea-ice extent from whaling records. – Nature 389: 57–60.

Gleason, J. 1988. Algorithms for balanced bootstrap simulation. – Am. Statist. 42: 263–266.

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

Hunt, G. and Schneider, D. 1987. Scale-dependent processes in the physical and biological environment of marine birds. – In: Croxall, J. (ed.). Seabirds: feeding biology and role in marine ecosystem. Cambridge University Press, Cambridge, pp. 7–41.

Hunt, G., Priddle, J., Whitehouse, M., Veit, R. and Heywood, R. 1992. Changes in the seabird species abundance near South Georgia during a period of rapid change in sea surface temperature. – Antarct. Sci. 4: 15–22.

Jacka, T., Christou, L and Cook, B. 1984. A data bank of mean monthly and annual surface temperatures for Antarctica, the Southern Ocean and South Pacific Ocean. – ANARE Research Notes 22: 1–97.

Jacquet, N., Whitehead, H. and Lewis, M. 1996. Coherence between 19th century sperm whale distributions and satellite-derived layer pigments in tropical Pacific. – Mar. Ecol. Prog. Ser. 145: 1–10.

Jouventin, P. and Weimerskirch, H. 1990. Satellite tracking of the wandering albatross. – Nature 343: 746–748.

Lévy, M., Memery, L. and André, J. 1998. Simulation of primary production and export fluxes in the north-west Mediterranean Sea. – J. Mar. Res. 56: 197–238.

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

Moore, J., Abbott, M. and Richman, J. 1999. Location and dynamics of the Antarctic Polar Front from satellite sea surface temperature data. – J. Geophys. Res. 104: 3059–3073.
Pakhomov, E. and Froneman, P. 1999. The Prince Edward Islands pelagic ecosystem, south Indian Ocean: a review of achievements, 1976–1990. – J. Marine Syst. 18: 355–367.
Pakhomov, E. and McQuaid, C. 1996. Distribution of surface zooplankton and seabirds across the Southern Ocean. – Polar Biol. 16: 271–286.
Park, Y., Gambéroni, L. and Charriaud, E. 1993. Frontal structures, water masses, and circulation in the Crozet basin. – Geophy. Res. 98: 12361–12385.
Reynolds, R. and Marsico, D. 1993. An improved real time global sea surface temperature analysis. – J. Climate 6: 114–119.
Ridoux, V. 1994. The diet and dietary segregation of seabirds at the sub-Antarctic Crozet Island. – Marine Orn. 22: 1–183.
SCAR. 1992. Scientific priorities for the IGBP. – ICSU Press, Miami.
Semelkina, A. 1993. Development of the zooplankton in the Kerguelen region in the year 1987–1988. – In: In: Les rapports des campagnes à la mer: campagnes SKALP 1987 et 1988 aux Iles Kerguelen à bord des navires SKIFF et Kalper. Terres Australes et Antarctiques Françaises, Paris.
Smith, R., Ainley, D., Baker, K., Domack, E., Emslie, S., Fraser, B., Kennett, J., Leventer, A., Mosley-Thompson, E., Stammerjohn, S. and Vernet, M. 1999. Marine ecosystem sensitivity to climate change. – Bioscience 49: 393–404.
Stahl, J., Jouventin, P., Mougin, J., Roux, J. and Weimerskirch, H. 1985. The foraging zones of seabirds in the Crozet Islands sector of the Southern Ocean. – In: Siegfried, W., Condy, R. and Laws, R. (eds). Antarctic nutrients cycles and food webs. Springer-Verlag, Berlin, pp. 478–486.
Veit, R., Pyle, P. and McGowan, J. 1996. Ocean warming and long-term change in pelagic bird abundance within the California current system. – Mar. Ecol. Prog. Ser. 139: 11–18.
Veit, R., McGowan, J., Ainley, D., Wahls, T. and Pyle, P. 1997. Apex predator declines ninety per cent in association with changing oceanic climate. – Global Change Biol. 3: 23–28.
Waluda, C., Trathan, P. and Rodhouse, P. 1999. Influence of oceanographic variability on recruitment in the *Ilex argentinus* Cephalopoda: Ommastrephidae fishery in the South Atlantic. – Mar. Ecol- Prog. Ser. 183: 159–167.
Weimerskirch, H 1998. Foraging strategies of Indian Ocean albatrosses and their relationships with fisheries. – In: Robertson, G and Gales, R. (eds). Albatross biology and conservation. Surrey Beatty and Sons, Chipping Norton, pp. 168–179.
Weimerskirch, H. and Jouventin, P. 1998. Changes in population sizes and demographic parameters of six albatross species breeding on the French sub-Antarctic islands. – In: Robertson, G. and Gales, R. (eds). Albatross biology and conservation. Surrey Beatty and Sons, Chipping Norton, pp. 84–91.
Weimerskirch, H, Salamolard, M., Sarrazin, F. and Jouventin, P. 1993. Foraging strategy of wandering albatross through the breeding season: a study using satellite telemetry. – Auk 110: 325–342.
Westfall, P.H. and Young, S.S. 1993. Resampling-based multiple testing: examples and methods for p-value adjustment. – John Wiley and Sons, Inc, New York.
White, W. and Peterson, R 1996. An Antarctic circumpolar wave in surface pressure, wind, temperature and sea-ice extent. – Nature 380: 699–702.
Woehler, E., Hodges, C. and Watts, D. 1991. An atlas of the pelagic distribution and abundance of seabirds in the southern Indian Ocean. – ANARE Res. Notes 77: 1–406.
Zotier, R. 1990. Breeding ecology of the white-headed petrel *Pterodroma lessoni* on the Kerguelen Island. – Ibis 132: 525–534.

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