



Effects of warm sea-surface temperature anomalies on the blue petrel at the Kerguelen Islands

Christophe Guinet¹, Olivier Chastel¹, Malik Koudil², Jean Pierre Durbec² and Pierre Jouventin¹

¹Centres d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, F-79360 Beauvoir sur Niort, France

²Centre d'Océanologie de Marseille, Campus de Luminy, Case 901, F-13288 Marseille Cedex 9, France

Several long-term studies on Southern Ocean seabirds and seals have suggested a possible link between major declines in breeding performance and El Niño Southern Oscillation events. We report that the breeding performances and body condition of the blue petrel (*Halobaena carulea*) on the Kerguelen Islands is depressed by episodic, warm sea-surface temperatures (SSTs) in the winter before breeding. Lagged cross-correlations between SSTs in the Kerguelen sector and the Southern Oscillation Index indicate that warm SSTs were found south of the Kerguelen Islands within a year of, and between 4.2 and 5.4 years after an El Niño event took place. These results can be discussed with respect to the recently described Antarctic Circumpolar Wave that drives climatic anomalies eastward around the Southern Ocean.

Keywords: sea-surface temperatures; *Halobaena carulea*; blue petrel; breeding success; bio-indicators; Kerguelen Islands

1. INTRODUCTION

Studies of the at-sea distribution of seabirds in the Southern Ocean have shown that each water mass can be characterized by distinct assemblages of seabird species (Croxall 1984; Stahl *et al.* 1985, Pakhomov & McQuaid 1996). Seabird species abundances and assemblages are also influenced by short- and long-term changes in sea-surface temperatures (SSTs) (Hunt *et al.* 1981, 1992; Stahl *et al.* 1985; Veit *et al.* 1996, 1997). Parallel long-term trends were described across weather, abundance of prey and breeding performance of the kittiwake gull (*Rissa tridactyla*) over the North Sea (Aebischer *et al.* 1990). Major seabird breeding failures are associated with warm events occurring in the upwelling systems along the Peruvian coast in relation to El Niño. Breeding success of Galapagos penguins (*Spheniscus mendiculus*) on the Galapagos Islands was seriously depressed by the occurrence of warm SSTs (Boersma 1978), and other studies have related the disastrous effect of the 1982–1983 El Niño Southern Oscillation (ENSO) on seabirds (Schreiber & Schreiber 1984; Hays 1986).

Several long-term surveys on seabirds and seals breeding on subantarctic and Antarctic localities have shown periodic fluctuations in breeding performances possibly in relation to El Niño events (Croxall 1992; Chastel *et al.* 1993; Boyd 1993; Guinet *et al.* 1994). In this study we investigate (i) the effect of episodic, warm SSTs prior to and during the breeding season on adult body condition and reproductive success of the blue petrel (*Halobaena caerulea*), an oceanic seabird breeding at the Kerguelen Islands; and (ii) the time-scale relationship

between these episodic warm events and the Southern Oscillation Index (SOI).

2. MATERIALS AND METHODS

Blue petrels are small, burrow-nesting seabirds (190 g) that forage over oceanic waters and prey mainly on small crustaceans (Ridoux 1994). Data on breeding performances of blue petrels were obtained from a long-term study (1986–1995) on Mayes Island, in the Kerguelen Archipelago, located in the southern Indian Ocean (48° 38'S, 68° 38'E). A number of measures of the overall breeding performance were made during each breeding season: (i) breeding success was calculated as the number of chicks fledged from the number of eggs laid; (ii) hatching success as the number of eggs hatched from eggs laid; and (iii) fledging success as the number of chicks fledged from eggs hatched. To investigate relationships between SST and adult body condition, blue petrels were weighed during the prebreeding visits (September). During the prebreeding visit, birds stay in their nest and fast for 7–8 d before going back to sea (Chastel *et al.* 1995a). In this study, body condition indices were calculated using individual mass at arrival at the colony from the sea. To make these calculations, empty burrows were checked every 2 d until they were occupied, to record the date of return and the mass of each bird coming from the sea prior to laying (late October). Before laying, adult blue petrels undergo a prelaying exodus (early October to late October; Weimerskirch *et al.* 1989). For each year, an average body condition index was calculated by scaling body mass to body size (Chastel *et al.* 1995b).

We used SST obtained through satellite remote sensing. Monthly averages of SST were calculated from *in situ* and satellite radiometer measurements obtained on a 1° scale from January

1982 until December 1995. Satellite observations were obtained from the Lamont–Doherty Earth Observatory (LDO) at Columbia University and the Integrated Global Ocean Service System (IFOSS), a joint working committee between the Intergovernmental Oceanographic Commission (IOC) and the World Meteorological Organization (WMO). Satellite data were adjusted for biases (Reynolds 1988; Reynolds & Marsico 1993).

Spatial scale is of crucial importance in analysing the relationship between environmental factors and seabirds and cetacean distributions (Hunt & Schneider 1987; Jaquet *et al.* 1996). At the Kerguelen Islands, blue petrels alternate short and long foraging trips during breeding (Chaurand & Weimerskirch 1994a). Antarctic krill (*Euphausia superba*) has been found in samples coming from long trips (Y. Cherel, unpublished data), suggesting that blue petrels can reach Antarctic waters where SSTs normally range from -1.8 to 1.5 °C (Lomakina 1996). These Antarctic waters are found within a range of 1000 km south of Kerguelen (Reynolds & Marsico 1993), which is consistent with the at-sea distribution of the blue petrel within the Kerguelen sector of the southern Indian Ocean (Woehler *et al.* 1991). For our analyses, monthly SSTs were obtained on a 1° scale and averaged over a 1000 km semicircle radius surrounding Southern Kerguelen Island (from latitude $48^{\circ} 38'S$).

Time-series of monthly anomalies in SSTs were determined relative to the monthly mean values for the applicable record length calculated over the study zone, thus removing the average seasonal cycles. A lagged cross-correlation was used to investigate possible relationships between SST anomalies recorded from March preceding the breeding season until the following February (end of the breeding season) in the Kerguelen sector and the breeding performances of blue petrels. However, the occurrence of ENSOs, using the SOI (Rasmusson & Wallace 1983) time-series from 1975 to 1995, also lagged m months from the SSTs observed on the Kerguelen sector. Correlations were run on a data set of SST anomalies and SOI obtained between January 1982 and December 1995 ($n=156$), and were calculated for m in a range of 0 to -70 months.

Correlations between numerous variables must always be interpreted cautiously, as chance alone may have resulted in a number of significant correlations. We used a randomization procedure to evaluate the statistical significance of correlation coefficients within our cross-correlation analyses. We calculated a 95% confidence interval on the correlation coefficient using a bootstrap estimation method (Hall 1992). Breeding performance parameters were randomly rearranged to SST values 10 000 times, and the SST anomalies found south of the Kerguelen Islands were randomly rearranged 5000 times for each lag to the SOI. The resulting set of coefficients provides an approximate sampling distribution of the correlation coefficient (Gleason 1988) and, consequently, 95% approximate confidence intervals of the observed value of the correlation coefficient. This procedure allowed us to detect when the correlation coefficient differed significantly from 0 at the 0.05 level (indicating a significant shift toward a positive or negative relationship) out of the 10 000 and 5000 random rearrangements of the data. Results were found to be significant when the correlation coefficient was significant at the 0.05 level (two-tail test), and when a correlation coefficient value of 0 was not included within the 95% confidence intervals.

3. RESULTS

Body condition, breeding success, hatching success and fledging success of blue petrels showed significant

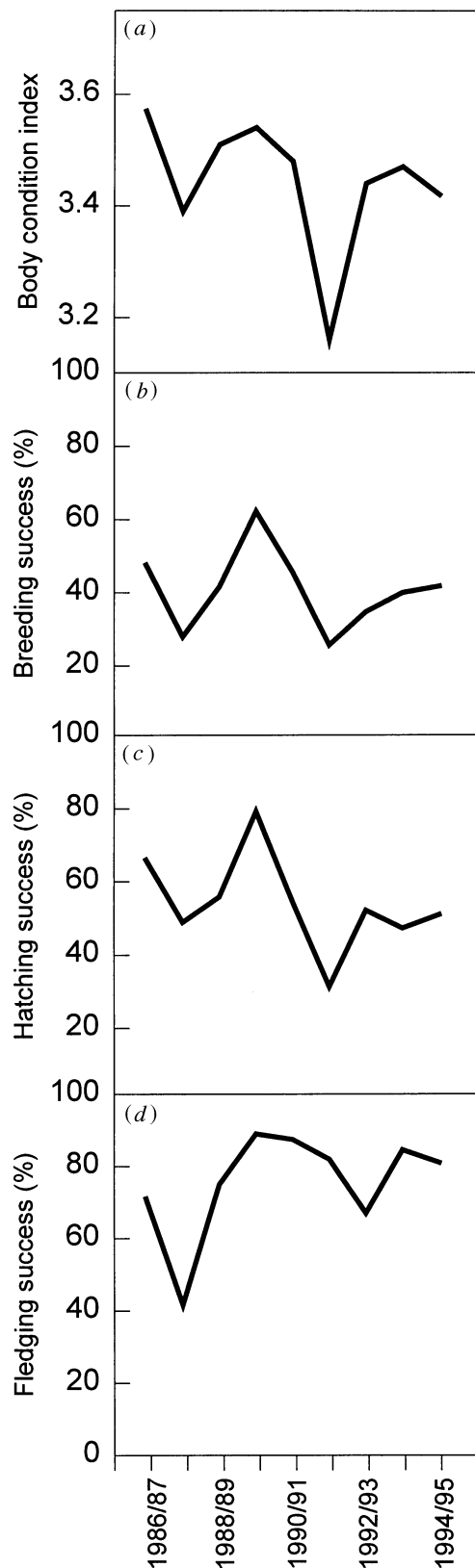


Figure 1. Annual variations (1986–1987 to 1994–1995) in adult condition, breeding success (%), hatching success (%) and fledging success of blue petrels on Mayes Island (Kerguelen Archipelago). Sample size for adult condition varied from 18 (1986) to 192 (1991) with an average of 80. Sample size for reproductive performances (breeding success, hatching success and fledging success) varied from 21 (1986) to 138 (1993) with an average of 110. Statistics indicate significant year-to-year variations. (a) $F_{8,1036} = 19.45$, $p < 0.001$; (b) $\chi^2_8 = 28.99$, $p < 0.001$; (c) $\chi^2_8 = 35.95$, $p < 0.001$; (d) $\chi^2_8 = 19.25$, $p < 0.001$.

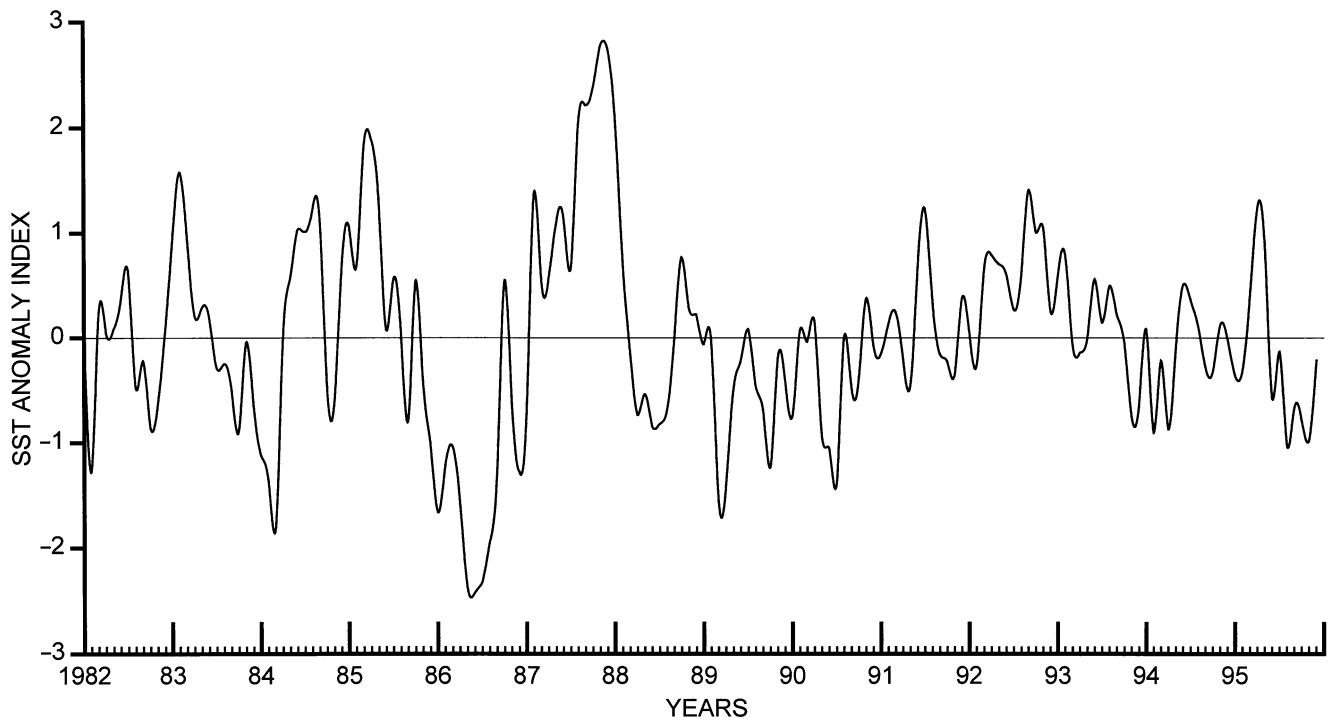


Figure 2. Monthly SST anomaly index for the southern Kerguelen Islands sector from January 1982 to December 1995.

year-to-year variations (figure 1). Body condition was low in 1987–1988 and in 1991–1992. Blue petrels also experienced poor breeding performances during these years, with the 1991–1992 season being the poorest when 74% of the eggs laid failed to produce a fledgling. Body condition was positively correlated with breeding success and hatching success (Spearman rank correlations, $r_s=0.850$, $p=0.004$ and $r_s=0.883$, $p=0.002$, respectively, for $n=9$ years). Although the overall breeding success was directly related with hatching success ($r_s=0.850$, $p<0.004$ for $n=9$ years), no significant relationships were found with fledging success. Fledging success was not correlated with any other parameters. The SST anomalies observed south of Kerguelen from 1982 to 1995 are shown in figure 2, with warm anomalies occurring during the 1983–1985 and 1991–1993 periods and particularly in 1987. In contrast, cold anomalies were detected in 1986 and between 1988 and 1990. Annual changes in body condition, breeding success and hatching success (figure 1) were negatively correlated with year-to-year variation in SSTs observed in each of July, August and September (figure 3). A negative relationship was found between fledging success and SST in both October (egg formation period) and January (chick rearing period, figure 3). No correlations were found between SST anomalies recorded from March to June preceding the breeding season and any of the breeding parameters recorded (figure 3).

The lagged cross-correlation between SST anomalies south of the Kerguelen Islands and the SOI were negatively related for two periods during the study. The first period corresponded with a lag of 0 to –10 months, indicating that warm waters were found south of Kerguelen within ten months of a warm event taking place in the south subtropical Pacific Ocean. The second period corresponded with a lag of –50 to –65 months, indicating that warm waters were found south of Kerguelen 4.2–5.4 years after the occurrence of an El Niño event (figure 4). The

window of positive correlation indicated that warm waters were observed at Kerguelen 32–48 months after cold water events (La Niña) in the south subtropical Pacific Ocean (figure 4).

4. DISCUSSION

This study indicates that warm episodes before the onset of the breeding cycle (July, August and September) can affect the body condition and the breeding performances of blue petrels, with hatching success being particularly affected (figure 3). The depressed breeding performance of blue petrels in association with warm water events off the Kerguelen Islands can be interpreted in light of their at-sea distribution and foraging ecology. Breeding blue petrels forage mainly over Antarctic waters (Ryan & Cooper 1989) where the distribution of zooplankton communities can be related to SSTs (Deacon 1982; Pakhomov & McQuaid 1996). Our study suggests that when high SSTs occur south of the Kerguelen Islands, either (i) planktonic crustaceans, whose distribution is also related to meso-macro scale SSTs (Deacon 1982; Pakhomov & McQuaid 1996), remained beyond the range of breeding blue petrels, in waters too deep for these surface feeders, or (ii) that prey population levels were low under these environmental conditions. Near Kerguelen, the warmest SST event took place in 1987. Interestingly, sampling of physical and biological oceanographic data conducted that year showed (i) that beside the subantarctic and Antarctic zooplankton community typical of the region, fauna typical of tropical latitudes were also present (Ivanchenko *et al.* 1989; Semelinka 1993), and (ii) that the Polar Front was located 1–2 degrees further south than its multiannual average position (Nagata *et al.* 1988; Semelinka 1993).

Breeding oceanic seabirds are energetically limited during the reproduction by the cost of travelling to and

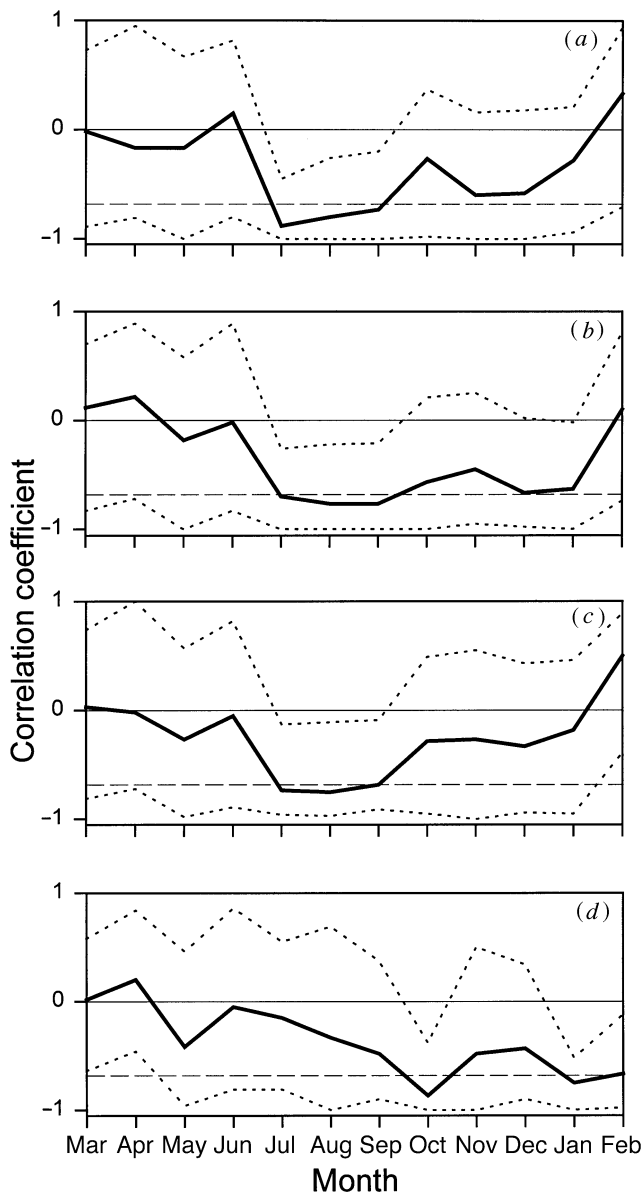


Figure 3. Variation in the Spearman correlation coefficient calculated between SST observed from March (previous to the breeding season) until February (at the end of the breeding season) and (a) body condition, (b) overall breeding success, (c) hatching success and (d) fledging success of blue petrel over the nine study years. Limits of the 95% confidence interval are indicated by the short, dashed lines. Statistical significance of the Spearman correlation coefficient at $p=0.05$ is indicated by a long, dashed line on the figure.

from distant feeding areas. In poor years, when warm surface waters occurred, the preferred foraging grounds of the blue petrel, in terms of energy acquisition, were probably located too far from their breeding grounds. The blue petrel appears to be a 'capital breeder' that needs to accumulate extra reserves to engage in or to persevere a breeding attempt (Chastel *et al.* 1995a,b). Depletion of the 'capital' (i.e. low body condition) very early in the breeding season (July–September, more than one month before laying) results mainly in egg desertion (Chastel *et al.* 1995a). The overall breeding success is directly related to hatching success but not fledging success, which indicates that in blue petrels most breeding failure takes place

at an early stage of reproduction in relation to the body condition of the birds, whereas the fledging success is probably more related to food availability during the chick-rearing period. Nearly half of the total hatching failure occurred during the first incubation shift (Chastel *et al.* 1995a). Incubating blue petrels have a threshold mass at which they spontaneously desert their eggs (Chaurand & Weimerskirch 1994b), and birds of a poorer body condition reach this mass more rapidly, and are thus more likely to abandon their eggs (Chastel *et al.* 1995a).

Unlike the July–September situation, where there is a broadly consistent pattern across breeding performance and body condition of the blue petrels and SST anomalies, the correlations in October and January may be more suspect. However, calculation of the 95% confidence intervals on the Spearman correlation coefficients indicate that the correlations observed in October and January are unlikely to have resulted from chance alone (figure 3). The negative correlation between SST in January and February and the fledging success probably reflects the difficulties experienced by adults provisioning chicks. Furthermore, adult body condition during the chick-rearing period plays an important role in regulating allocation decisions and, therefore, parental effort (Chaurand & Weimerskirch 1994b). However, the relationship found between SST in October and fledging success remains unclear.

We might also expect the observed SST fluctuations to be found on an even broader scale. Blue petrels breeding on the Kerguelen Islands experienced poor breeding performances both in 1987–1988 and in 1991–1992, the latter being the poorest observed. When we compare these observations to the time–longitude diagrams of interannual anomalies in SST and sea-ice extent (White & Peterson 1996), these two seasons coincide with large-scale positive SSTs and restricted sea-ice extent for the Kerguelen Islands sector (70° E).

Our study suggests that the oceanographic conditions of the Kerguelen Islands sector seem to vary in relation to El Niño activity, and that the breeding performances of seabirds such as the blue petrel are affected when warm anomalies reach their foraging grounds. The lagged cross-correlation between SSTs observed in the Kerguelen Islands sector and the SOI showed a negative correlation with periodicity of 4–5 years and with an interfering cold event between the two. This can be interpreted with respect to an eastward propagation of climatic anomalies called the Antarctic Circumpolar Wave (White & Peterson 1996), which takes 8–10 years to encircle the pole. In this system, SST anomalies generated in the south Pacific Ocean follow the hemispheric course of the Antarctic Circumpolar Current, with portions of the anomalies moving north to the southern Peru Current (Humbolt), and the remainder passing through Drake's Passage, spreading towards the equator in the south Atlantic and Indian Oceans. Indeed, poor breeding performances of the blue petrels occurred in years of warm anomalies, associated with the Antarctic Circumpolar Wave reaching Kerguelen (White & Peterson 1996), and our results suggest that these warm SST anomalies should be expected in the southern part of Kerguelen within a year of, and between 4.2 and 5.4 years after, the occurrence of an ENSO event.

In relation to global climate warming, we should expect a change of the at-sea distribution of the blue petrel in

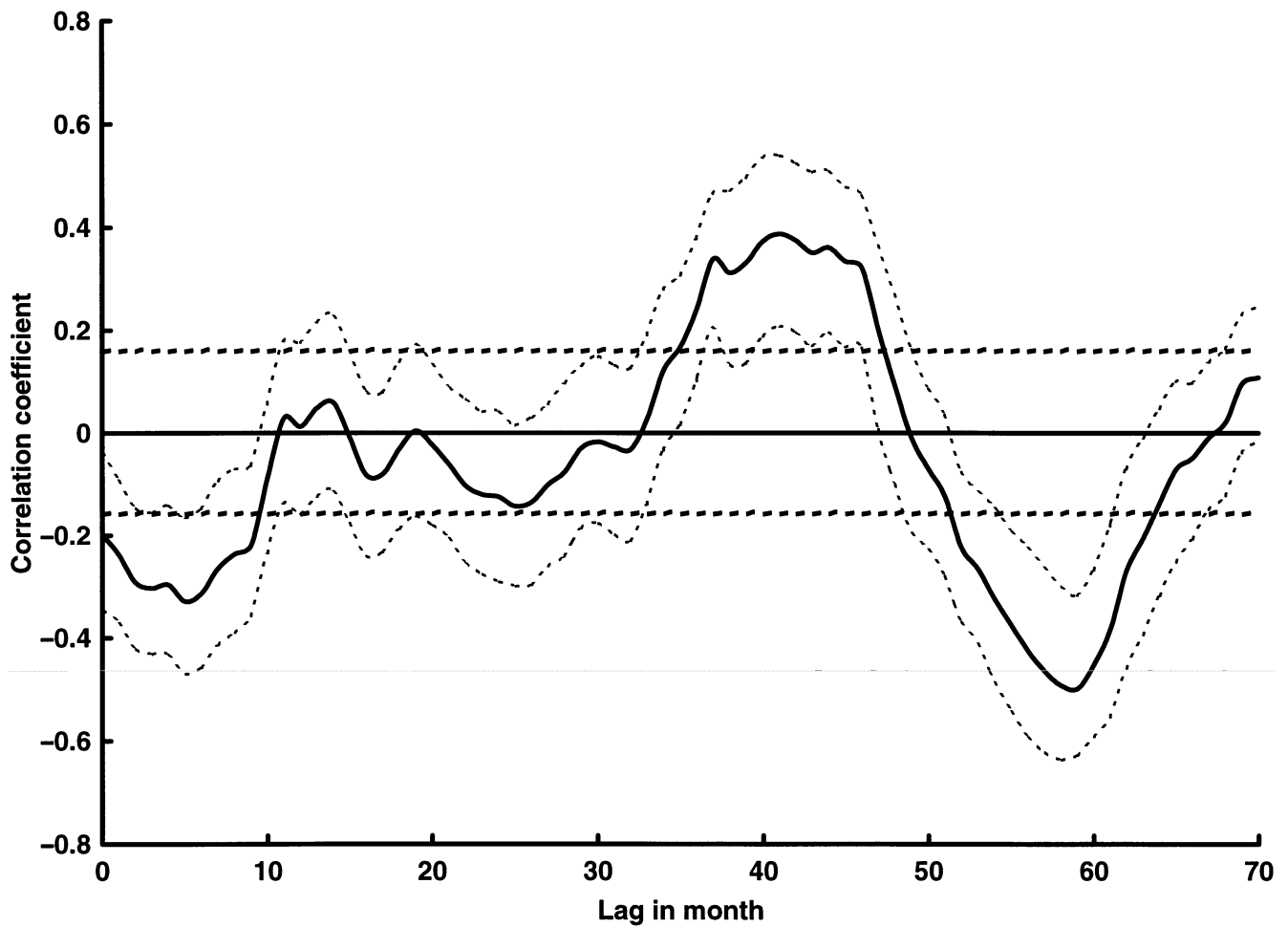


Figure 4. Lagged cross-correlation, r_m , between the SST anomalies for a lag (m) ranging from 0 to -70 months (see text for detailed description) observed south of the Kerguelen Islands from 1982 to 1995 and the Southern Oscillation Index obtained from 1976 to 1995. Limits of the 95% confidence interval are indicated by the short, dashed lines. Statistical significance of the correlation coefficient at $p=0.05$ is indicated by a bold, dashed line on the figure.

relation to warming waters, as recently described for seabirds foraging over the California Current waters (Veit *et al.* 1996, 1997). Such a shift in at-sea distribution of the blue petrel is likely to affect profoundly the breeding performances of that species at Kerguelen.

This study is part of the programme 109 'Ecologie des oiseaux et mammifères marins Antarctiques' (Director: P. Jouventin), and is supported by the 'Institut Français pour la Recherche et la Technologie Polaire' and by the programme bio-indicators of the 'groupement de Recherche écosystèmes polaires et anthropisation'. We thank all the field workers involved in banding and recovery on Mayes Island, D. Besson and D. Capdeville for the data processing, C. Barbraud and X. Bonnet for drawing the figures and A. Hedd and M. Kersten for correcting the English. We thank W. A. Montevecchi and two anonymous reviewers for their useful comments on the first version of this manuscript.

REFERENCES

- Aebischer, N. J., Coulson, J. C. & Colebrook, J. M. 1990 Parallel long-term trends across four marine trophic levels and weather. *Nature* **347**, 753–755.
- Boersma, P. D. 1978 Breeding patterns of Galapagos penguins as an indicator of oceanographic conditions. *Science* **200**, 1481–1483.
- Boyd, I. L. 1993 Tooth growth in male Antarctic fur seals (*Arctocephalus gazella*) from South Georgia: an indicator of long term growth history. *J. Zool. Lond.* **229**, 177–190.
- Chastel, O., Weimerskirch, H. & Jouventin, P. 1993 High annual variability in reproductive success and survival of an Antarctic seabird, the snow petrel *Pagodroma nivea*. *Oecologia* **94**, 278–285.
- Chastel, O., Weimerskirch, H. & Jouventin, P. 1995a Influence of body condition on reproductive decision and reproductive success in the blue petrel. *Auk* **112**, 964–972.
- Chastel, O., Weimerskirch, H. & Jouventin, P. 1995b Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* **76**, 2240–2246.
- Chaurand, T. & Weimerskirch, H. 1994a The regular alternation of short and long foraging trips in blue petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *J. Anim. Ecol.* **63**, 275–282.
- Chaurand, T. & Weimerskirch, H. 1994b Incubation routine, body mass regulation and egg-neglect in the blue petrel *Halobaena caerulea*. *Ibis* **136**, 285–290.
- Croxall, J. P. 1984 Seabirds. In *Antarctic ecology* (ed. R. M. Laws), pp. 533–619. London: Academic Press.
- Croxall, J. P. 1992 Southern Ocean environmental changes: effect on seabirds, seal and whale populations. *Phil. Trans. R. Soc. Lond. B* **338**, 319–328.
- Deacon, G. E. R. 1982 Physical and biological zonation in the Southern Ocean. *J. Deep-Sea Res.* **29**, 1–15.

- Gleason, J. R. 1988 Algorithms for balanced bootstrap simulations. *Am. Statist.* **42**, 263–266.
- Guinet, C., Jouventin, P. & Georges, J.-Y. 1994 Long term population changes of fur seals (*Arctocephalus gazella* and *Arctocephalus tropicalis*) on subantarctic (Crozet) and subtropical (St Paul and Amsterdam) islands and their possible relationship to El Niño Southern Oscillation. *Antarc. Sci.* **6**, 473–478.
- Hall, P. 1992 *The bootstrap and Edgeworth expansion*. Berlin: Springer Verlag.
- Hays, C. 1986 Effect of the 1982–1983 El Niño on Humboldt penguin colonies in Peru. *Biol. Conserv.* **36**, 169–180.
- Hunt, G. L. & Schneider, D. C. 1987 Scale-dependent processes in the physical and biological environment of marine birds. In *Seabirds: feeding biology and role in marine ecosystems* (ed. J. P. Croxall), pp. 7–41. Cambridge University Press.
- Hunt, G. L., Gould, P., Forsell, D. & Peterson, H. 1981 Pelagic distribution of marine birds in the eastern Bering Sea. In *The eastern Bering Sea Shelf: oceanography and resources*, vol. 2 (ed. D. W. Hood & J. A. Caulder), pp. 689–717. Washington DC: National Oceanographic and Atmospheric Administration.
- Hunt, G. L., Priddle, J., Whitehouse, M. J., Veit, R. R. & Heywood, R. B. 1992 Changes in seabird species abundance near South Georgia during a period of rapid change in sea surface temperature. *Antarc. Sci.* **4**, 15–22.
- Ivanchenko, O. P., Klyausov, A. V., Pavlukhin, S. V. & Semelinka, A. N. 1989 On the position of the Polar Frontal Zone and the state of the planktonic community in the region of the Kerguelen Archipelago in 1987. In *Union conference on the world ocean geography at the service of the national utilisation of marine resources*, pp. 64–65. Leningrad.
- Jaquet, N., Whitehead, H. & 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.
- Lomakina, N. B. 1966 The euphausiids fauna of the Antarctic and notal regions. In *Biological reports of the soviet Antarctic expedition 1955–1958*, vol. 2 (ed. A. P. Andriashev & P. V. Usshakov), pp. 260–342. Jerusalem: Israel Programme for Scientific Translation.
- Nagata, Y., Michida, Y. & Umimura, Y. 1988 Variation of positions and structure of the oceanic fronts in the Indian Ocean sector of the Southern Ocean in the period from 1965 to 1987. In *Antarctic Ocean and resources variability* (ed. D. Saharage), pp. 92–98. Berlin and Heidelberg: Springer-Verlag.
- Pakhomov, E. A. & McQuaid, C. D. 1996 Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biol.* **16**, 271–286.
- Rasmusson, E. M. & Wallace, J. M. 1983 Meteorological aspects of the El Niño/Southern Oscillation. *Science* **222**, 1195–1202.
- Reynolds, R. W. 1988 A real-time global sea surface temperature analysis. *J. Clim.* **1**, 75–86.
- Reynolds, R. W. & Marsico, D. C. 1993 An improved real time global sea surface temperature analysis. *J. Clim.* **6**, 114–119.
- Ridoux, V. 1994 The diets and dietary segregation of seabirds at the subantarctic Crozet Island. *Mar. Orn.* **22**, 1–183.
- Ryan, P. G. & Cooper, J. 1989 The distribution and abundance of aerial seabirds in relation to Antarctic krill in the Pridz Bay region, Antarctica, during late summer. *Polar Biol.* **10**, 199–209.
- Schreiber, R. W. & Schreiber, E. A. 1984 Central Pacific seabirds and the El Niño Southern Oscillation: 1982 to 1983 perspectives. *Science* **225**, 713–716.
- Semelkina, A. N. 1993 Development of the zooplankton in the Kerguelen Island region in the year 1987–1988. In *Les rapports des campagnes à la mer: campagnes SKALP 1987 et 1988 aux Iles Kerguelen à bord des navires SKIFF et KALPER* (ed. G. Duhamel), pp. 90–103. Paris: Terres Australes et Antarctiques Françaises.
- Stahl, J. C., Jouventin, P., Mougin, J. L., Roux, J. P. & Weimerskirch, H. 1985 The foraging zones of seabirds in the Crozet Islands sector of the Southern Ocean. In *Antarctic nutrient cycles and food webs* (ed. W. R. Siegfried, R. Condy & R. M. Laws), pp. 478–486. Berlin and Heidelberg: Springer-Verlag.
- Veit, R. R., Pyle, P. & McGowan, J. A. 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. R., McGowan, J. A., Ainley, D. G., Wahls, T. R. & Pyle, P. 1997 Apex marine predators declines ninety per cent in association with changing oceanic climate. *Global Change Biol.* **3**, 23–28.
- Weimerskirch, H., Zotier, R. & Jouventin, P. 1989 The avifauna of the Kerguelen Islands. *Emu* **89**, 15–29.
- White, W. B. & Peterson, R. G. 1996 An Antarctic circumpolar wave in surface pressure, wind, temperature and sea-ice extent. *Nature* **380**, 699–702.
- Woehler, E. J., Hodges, C. L. & Watts, D. J. 1991 An atlas of the pelagic distribution and abundance of seabirds in the southern Indian Ocean. *ANARE Res. Notes* **77**, 1–406.