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Marie Nevoux · Christophe Barbraud

Relationships between sea ice concentration, sea surface temperature and demographic traits of thin-billed prions

Abstract Understanding the effects of environmental variations on ecosystems is a major topic in ecology. In this study, we estimated demographic parameters of a seabird population, the thin-billed prion (*Pachyptila belcheri*) at Kerguelen Islands, and then tested for relationships with inter-annual variations of climatic indices, using long-term capture–recapture data. The annual adult survival probability was 0.825 ± 0.009 and the breeding success was 0.519 ± 0.090. Sea surface temperature anomalies were negatively related with breeding success. By contrast, winter sea ice concentration in the Antarctic seasonal ice zone seemed to negatively influence adult survival. This suggests a connection between sub-Antarctic and Antarctic ecosystems. The actual context of large climatic changes in the Austral Ocean seems to explain a large part of the decreasing trends observed for both the breeding success and the adult survival. Thus, a decrease of the population size of thin-billed prions at Kerguelen could be strongly suspected in the near future.

Introduction

During the last decades, climate fluctuations have been particularly intense, and it is now admitted that we are in a context of a global warming, with an average increase of 0.3–0.6°C throughout the twentieth century (IPCC 2001). Consequences of a potential impact on the functioning of ecosystems are very difficult to predict (Hughes 2000) and in this context the study of the influence of climatic fluctuations on populations is a major topic in ecology (Stenseth et al. 2002; Sæther et al. 2004). Recent investigations have shown that global warming leads to dramatic effects on plant and animal populations, through changes in their physiology, phenology, distribution and demography (see reviews in Hughes 2000; Walther et al. 2002; Stenseth et al. 2002, 2003; Root et al. 2003). Furthermore, climatic indices calculated from field observations and satellite data are considered as good proxies of the climatic conditions (Ottersen et al. 2001; Stenseth et al. 2003). Hence, it may be possible to investigate some of the interactions between climatic fluctuations and populations by the use of such indices.

Oceans and atmosphere are strongly linked, and it is known that climatic conditions affect the structure and the functioning of the oceans, determining favourable or unfavourable growing conditions for marine species (Hayward 1997; McGowan et al. 1998; Edwards and Richardson 2004). If there is an alteration of the structure and abundance of prey communities (Hayward 1997; McGowan et al. 1998; Edwards and Richardson 2004; Winder and Schindler 2004), it would potentially affect the dynamics of predator populations (Veit et al. 1997). Indeed, seabirds, as other top predators, are assumed to integrate perturbations occurring on lower trophic levels (Veit et al. 1997). They also represent one of the few marine components that are easily monitored and for which long-term datasets on breeding populations exist.

The thin-billed prion (*Pachyptila belcheri* Mathews), a small sub-Antarctic Procellariiform, is one of these seabirds. Spending the winter at sea and breeding in summer on sub-Antarctic islands of the Southern Ocean, it has to deal with this highly variable oceanic environment all year round. Moreover, climatic anomalies may amplify environmental constraints that birds have to face (Sillett et al. 2000). Theoretical and few empirical studies suggest that winter is the most difficult period for seabirds, where the majority of the annual mortality occurs (Fretwell 1972; Barbraud and Weimerskirch 2003) depending upon their ability to restore their body

M. Nevoux (✉) · C. Barbraud
Centre d'Etudes Biologiques de Chizé,
Centre National de la Recherche Scientifique,
79360 Villiers en Bois, France
E-mail: stagbarb@cebc.cnrs.fr
Tel.: +33-549-096111
Fax: +33-549-096526

condition (Chastel et al. 1995b; Barbraud and Weimerskirch 2001a; Pinaud and Weimerskirch 2002). During summer, breeders have to ensure both chick development and their own survival. Thus, the breeding success is dependent of the availability of resources that determine their ability to cover their energetic expenditures (Goodman 1974). We can predict that environmental fluctuations may affect demographic parameters through different mechanisms affecting the food web. Indeed, studies have already mentioned a probable negative impact of warm climatic anomalies on the dynamics of seabird populations that seemed to be associated with a perturbation of trophic resources (McGowan et al. 1998; Hughes 2000; Thompson and Ollason 2001; Jenouvrier et al. 2003). Previous studies also showed that both the Southern Oscillation Index (SOI) and the sea surface temperature anomalies (SSTA) occurring in the Southern Indian Ocean negatively affected the dynamics of the blue petrel population (Halobaena carerulea) (Guinet et al. 1998; Barbraud and Weimerskirch 2003). The blue petrel is a small Procellariiform of the Kerguelen seabird community known to be genetically and ecologically very close to the thin-billed prion. Thus, we can expect that close relative species, sharing the same oceanic environment, may be affected in the same way by the same climatic changes. We could also expect that warm temperatures, potentially linked to the SOI, may have a negative impact on the survival of both seabirds.

Analyses of the fluctuations of the main demographic traits of thin-billed prions over a 15-year period allowed us to investigate the possible influence of climatic changes occurring on the large sub-Antarctic foraging grounds of thin-billed prions. First, from a long-term capture-mark-recapture data set, we estimated the inter-annual variations of adult survival probability and breeding success, never previously documented for this species. Then, we tested for a possible link with recent climate changes by studying fluctuations of the demographic parameters of this population in relation to the inter-annual variability of oceanographic conditions.

Materials and methods

Biological model and field protocol

The thin-billed prion is a small (150 g) pelagic Procellariiform that forages from sub-Antarctic to Antarctic waters, up to the boundary of the pack ice (Marchant and Higgins 1990; Warham 1990), and that preys mainly on small crustaceans, fishes and squids (Warham 1990; Cherel et al. 2002). After a juvenile stage of a few years spent at sea, adults return each summer to breeding colonies where they nest in burrows and fledge one chick per year at best (Weimerskirch et al. 1989; Marchant and Higgins 1990; Warham 1990). As in many long-living seabirds, thin-billed prions are known to be par-

ticularly faithful to their breeding site (Marchant and Higgins 1990; Warham 1990). This characteristic allows the development of long-term studies, based on individual monitoring of ringed birds through the use of capture-mark-recapture (CMR) methods.

The study took place on Mayes Island (48°38′S 68°38′E), Kerguelen Archipelago–Southern Indian Ocean, a 5 ha island supporting several tens of thousands of breeding pairs of thin-billed prion (C. Barbraud, personal communication), among which 150–200 pairs were monitored each year from seasons 1986/1987 to 2001/2002 (noted thereafter as 1986–2001). Birds nest in burrows dig in mixed substrates of coarse gravel and soil. Burrows, fitted with an observation window above the nest chamber if necessary, were inspected during the course of the breeding period from mid-November to mid-January, as soon as breeders arrived on the colony to lay (Strange 1980; Marchant and Higgins 1990; Warham 1990). Each burrow was visited at least three times, which permitted to record each member of a breeding pair and to measure its breeding performance. Every year all fledglings as well as all unringed adults found during burrow inspections were ringed with a stainless steel ring. Fieldworkers applied the same sampling protocol each year.

Environmental parameters

Since the development of high-resolution satellite data, climatic fluctuations have been defined by a growing number of indices. To limit chance in the correlations between environmental variability and demographic parameters, we restricted the range of indices used in these analyses to a few factors known to affect the ecology of some Antarctic (Trathan et al. 1996; Barbraud and Weimerskirch 2001a; Croxall et al. 2002; Jenouvrier et al. 2003; Sun et al. 2004) and sub-Antarctic marine top predators (Guinet et al. 1998; Pinaud and Weimerskirch 2002; Barbraud and Weimerskirch 2003; Inchausti et al. 2003).

We chose two categories of climatic indices: global and local indices. Global indices reduce the complex spatio-temporal variability of weather fluctuations to a single measure, and are being used in a growing number of empirical studies (Stenseth et al. 2002, 2003). We chose the SOI that reflects climatic environment on a large scale, linked to the El-Niño phenomena. Some studies revealed that the effects of the SOI can be detected in the Indian Ocean within a few years time lag since the development of a particular event in the Eastern Pacific (Guinet et al. 1998; Xie and Annamalai 2002). SOI is computed by the Commonwealth Bureau of Meteorology (http://www.bom.gov.au/climate/current/soihtm1.shtml). We also used the Antarctic Oscillation Index (AAOI) that is constructed by projecting the daily (00Z) 700 mb height anomalies poleward of 20°S. It allowed us to characterise atmospheric condi-

tions at the sea surface of the Austral Ocean. Data are available on the National Oceanic and Atmospheric Administration web site (http://www.cpc.noaa.gov/products/precip/CWlink/daily_ao_index/aao/aao_index.html).

Local indices such as SSTA and Sea Ice Concentration (SIC) reveal variations in the oceanographic environment on a more regional scale. Monthly SSTA derived from ship, buoy and satellite data (Reynolds and Smith 1994) are available from the Integrated Global Ocean Service System (IGOSS—http://ingrid.ldgo.columbia.edu/SOURCES/.IGOSS/.nmc/.monthly/.ssta/). Monthly SIC, as a percentage, are also provided by IGOSS (http://ingrid.ldgo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv2/.monthly/.sea_ice/).

Distribution of the thin-billed prion

To use these local indices in a relevant way, it was necessary to define restricted geographic areas consistent with the seasonal distribution of the thin-billed prion, for which climatic data were averaged.

The summer distribution of the thin-billed prion is relatively well known. Birds are present from the continental shelf around Kerguelen Islands to Antarctic waters, up to the pack ice boundary (Woehler et al. 1991; Cherel et al. 2002; Stahl et al., unpublished data). Sea surface temperature anomalies were separately calculated for these two distinct areas: the continental shelf zone (CS) and the Antarctic zone (AAW) (Fig. 1), and sea ice concentration was calculated for the Antarctic sector south of Kerguelen (for the latitude 70°E). In contrast, the winter distribution of this prion species is poorly known and the few data available were not sufficient for defining a winter area to which to apply local indices. Therefore, global climatic indices, acting at the scale of an oceanic basin, were used for the whole period.

Estimating demographic parameters

Breeding parameters   In the study colony, burrows were checked several times during the breeding season, which allowed us to measure breeding performance of ringed birds. The overall breeding success (proportion of laid eggs that fledged a chick) represented two different measures: the hatching success (proportion of laid eggs that hatched) and the fledging success (proportion of hatched eggs that fledged a chick). To investigate relationships between climatic variability and breeding performances, Pearson's correlations were carried out with the SYSTAT software (Wilkinson 1996), using Bonferroni corrected probabilities to test for the significance of the relationships. All breeding performances are given ± 1 standard deviation.

Capture and survival models   Demographic parameters were estimated with CMR models, using individual capture-recapture histories, over the whole 1986–2001 period. The return rate of birds ringed as chicks within their colony of birth was very small (M. Nevoux and C. Barbraud, unpublished data). To limit this source of heterogeneity, only individual capture histories from adult-ringed birds were considered in this study. Although the field protocol was assumed to be the same all along the study, the recapture probability was integrated in the models to obtain unbiased estimates of survival probability. Capture and adult survival probabilities were estimated using the Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992) implemented in the MARK software (White and Burnham 1999). The starting model, considered to be biologically consistent with the data, was the general model: ϕ (t), p (t) where both probabilities of survival (ϕ) and capture (p) were time-dependent (t). The fit of the general model to the data was determined using goodness-of-fit (GOF) tests under the U-CARE software (Choquet et al. 2003). The GOF test indicated a severe lack of fit ($\chi^2 = 570.918$, $df = 104$,

Fig. 1 Geographic sectors on which local indices were applied. *CS* continental shelf (lat. 46.5–55.5°S, long. 62.5–78.5°E), *AAW* Antarctic waters (lat. 60.5–65.5°S, long. 30.5–90.5°E)
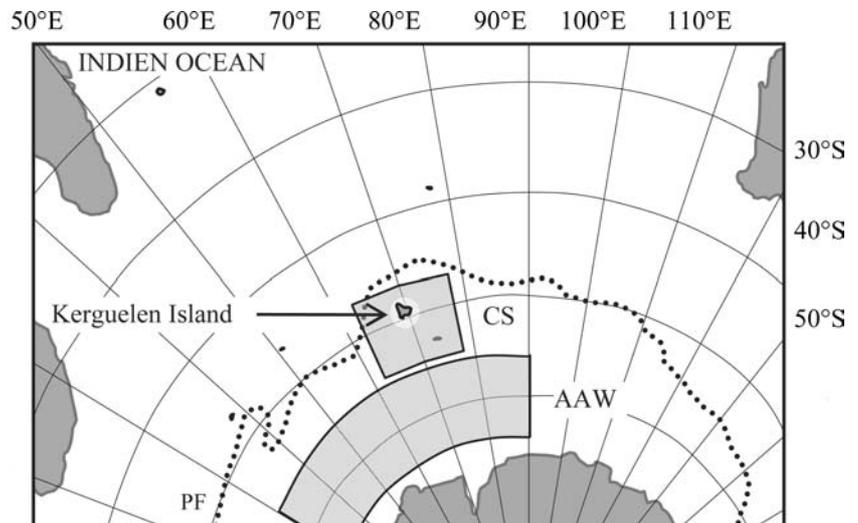
$P < 0.001$) mainly explained by the 2.CT test ($\chi^2 = 236.027$, $df = 14$, $P < 0.001$) indicating a positive trap-dependence effect (Lebreton et al. 1992). It was adjusted in a model with "two age classes" for resighting probabilities following Pradel (1993). The general model then became $\phi(t)$, $p(t*m)$, where (m) represents the Markovian dependence in capture probability. Analyses were run on a sample size of $N = 636$ birds for $k = 15$ occasions.

Adult survival as well as capture probability, which is partly dependent of the propensy of adults to breed, might be expected to be affected by climatic fluctuations. To test this hypothesis, climatic indices were incorporated in models as numerical covariates in a logit-linear relationship of capture and/or survival with climatic indices: Logit $\phi = \alpha + \beta.C$, where C is the covariate and β the slope parameter, indicating a positive ($\beta > 0$) or a negative ($\beta < 0$) effect of the covariate on capture and/or survival. To assess the effects of covariates, we estimated the proportion of explained variation in survival or capture probabilities accounted by covariates as: $r^2 = [\text{Dev } (M_c) - \text{Dev } (M.)] / [\text{Dev } (M_t) - \text{Dev } (M.)]$, where Dev represented the deviance for survival or capture models with covariates (M_c), constant ($M.$) and time (M_t) effects, respectively.

The effect of a given climatic anomaly to the whole trophic food web up to top predators can be indirect and thus delayed (Thompson and Ollason 2001). Covariates were thus introduced into the models with different lags. The SOI and the AAOI data were gathered into seasonal means, which were incorporated in models with a lag from 0 to 5 years (Guinet et al. 1998; Barbraud and Weimerskirch 2003). For local indices, monthly means and means of 2, 3 or 4 consecutive months were tested with up to 1-year lag. All estimations of survival

parameters are given ± 1 standard error.

Model selection was done using a second order Akaïke's Information Criterion (AICc) (Burnham and Anderson 1998). The smaller the AICc, the better the model, considering that two models i, j are different for ΔAICc > 2, where ΔAICc $= |\text{AICc}_i - \text{AICc}_j|$ (Anderson and Burnham 1999). When confidence intervals were not computed for some parameters, we used the profile likelihood method to obtain more precise estimates (implemented in the MARK software).

Results

Capture and survival models

We did not find evidence of a lack of fit of the general model $\phi(t)$, $p(t*m)$ to the data (GOF test: $\chi^2 = 32.579$, $df = 40$, $P = 0.438$). We thus considered model $\phi(t)$, $p(t*m)$ as appropriate for modelling the underlying processes that generated the data.

Inter-annual variations of the capture probability were better explained with an additive time-dependent model (Table 1, model a_2) than with the general model which considered the interaction between the time and the Markovian dependence in capture probability (model a_3). However, capture probabilities varied with time (model a_2 vs model a_4), and the average capture probability was 0.519 ± 0.028 (estimated from model a_2). A model with constant adult survival (model a_1) was preferred to a time dependent model (model a_2). Mean adult survival probability was estimated at 0.825 ± 0.009 from model a_1.

Contrary to what could be expected, none of the climatic indices tested to model capture probability improved the estimate of this parameter, whether it was the

Table 1 Modelling annual capture and survival probabilities for the thin-billed prion at Mayes Island, Kerguelen

	Models	AICc	ΔAICc	np	Dev
a_1	$\phi(.) \ p(t+m)$	4,150.832	3.795	16	2,272.654
a_2	$\phi(t) \ p(t+m)$	4,154.172	7.135	28	2,251.415
a_3	$\phi(t) \ p(t*m)$	4,166.559	19.522	39	2,240.992
a_4	$\phi(t) \ p(m)$	4,272.774	125.737	15	2,396.630
b_1	$\phi(t) \ p(\text{AAOI}_{\text{Feb}} + m)$	4,189.814	42.777	18	2,307.561
b_2	$\phi(t) \ p(\text{SSTA-CS}_{\text{Sept to Nov}} + m)$	4,200.366	53.329	19	2,316.073
b_3	$\phi(t) \ p(\text{SSTA-AAW}_{\text{Sept to Nov}} + m)$	4,207.840	60.803	18	2,325.587
b_4	$\phi(t) \ p(\text{SIC}_{\text{Max}} + m)$	4,229.034	81.997	18	2,346.781
c_1	**$\phi(\text{SIC}_{\text{Aug to Sept}}) \ p(t+m)$**	**4,147.037**	**0.000**	**17**	**2,266.825**
c_2	$\phi(\text{SOI}_{\text{Mar to Oct y-3}}) \ p(t+m)$	4,152.140	5.103	17	2,271.925
c_3	$\phi(\text{SSTA-AAW}_{\text{Mar to Jun}}) \ p(t+m)$	4,152.366	5.329	17	2,272.151
c_4	$\phi(\text{SSTA-CS}_{\text{Sept to Nov}}) \ p(t+m)$	4,152.573	5.536	17	2,272.359

a: modelling time dependence on capture and survival, b: modelling capture probabilities as a function of climatic indices, c: modelling survival probabilities as a function of climatic indices. Only models with lowest AICc values are presented for each covariate. In bold characters: model selected

AICc Akaïke's Information Criterion, *ΔAICc* difference between the current and the lowest AICc model, *np* number of parameters estimated for the model, *Dev* relative deviance of the model. Climatic covariates: *AAOI* Antarctic Oscillation Index, *SSTA* Sea Surface Temperature Anomaly on the Continental Self zone (*CS*) and on the Antarctic Waters zone (*AAW*), *SIC* Sea Ice Concentration. Subscripts indicate monthly values for covariates, or periods during which values were averaged (e.g. $SIC_{\text{Aug to Sept}}$ SIC value averaged over the August to September period)

AAOI (model b_1), the SSTA on the continental shelf zone (model b_2), on the Antarctic waters zone (model b_3) or the maximum winter SIC (model b_4).

For survival, neither a model with SOI with a three-year lag (model c_2) nor models with SSTA (models c_3 and c_4) were preferred over the constant model (model a_1). However, the average SIC in August and September significantly affected survival (model c_1 vs model a_1; slope $= -4.228 \pm 1.747$). During the 14 years of the study, the SIC in autumn tended to increase, although not significantly at the 0.05 level ($r = 0.477$, $N = 14$, $P = 0.085$; Fig. 2a). The pattern of survival variation was characterised by high survival probabilities in 1991 and 1992, and by a decreasing trend from 1996 up to 2001 (Fig. 2b).

Breeding performance

The breeding success was strongly correlated with both the hatching success ($r = 0.912$, $N = 14$, $P < 0.001$) and the fledging success ($r = 0.826$, $N = 14$, $P = 0.010$) (Table 2). The average breeding success was 0.519 ± 0.090 (Fig. 3b), and significantly decreased during the whole study period (logistic regression: $\chi^2_{Wald} = 18.580$, $df = 1$, $P < 0.001$), as well as the hatching success $\chi^2_{Wald} = 20.234$, $df = 1$, $P < 0.001$). In contrast, the fledging success remained stable ($\chi^2_{Wald} = 1.226$, $df = 1$, $P = 0.268$). Among the tested climatic indices, only one significant correlation was detected between breeding performance and an environmental covariate: the sea surface temperature anomaly in the Antarctic water zone during summer months. During the whole study period, this index tended to increase ($t_{Pearson} = 2.029$, $df = 12$, $P = 0.065$; Fig. 3a), suggesting a warming of the sea surface temperature. Years of low hatching and breeding success corresponded to years with high temperatures of Antarctic waters from October to December ($r = 0.682$, $N = 14$, $P = 0.039$ and $r = 0.712$, $N = 14$, $P = 0.020$, respectively) (Fig. 3c).

Discussion

Survival

In marine top predators, which are generally long-lived animals, adult survival rate is particularly high, and it has a major influence on population growth rates (Lebreton and Clobert 1991; Sæther and Bakke 2000). Estimates of the adult survival probability of the thin-billed prion are in accordance with this pattern (average annual probability $\phi = 0.825 \pm 0.009$). To our knowledge this is one of the first survival estimate obtained for a prion species (genus *Pachyptila*) with the Salvin's Prion (*P. salvini*, $\phi = 0.84$, Schreiber and Burger 2001). Comparison with data available for species of similar body mass like the Kerguelen's population of blue petrel
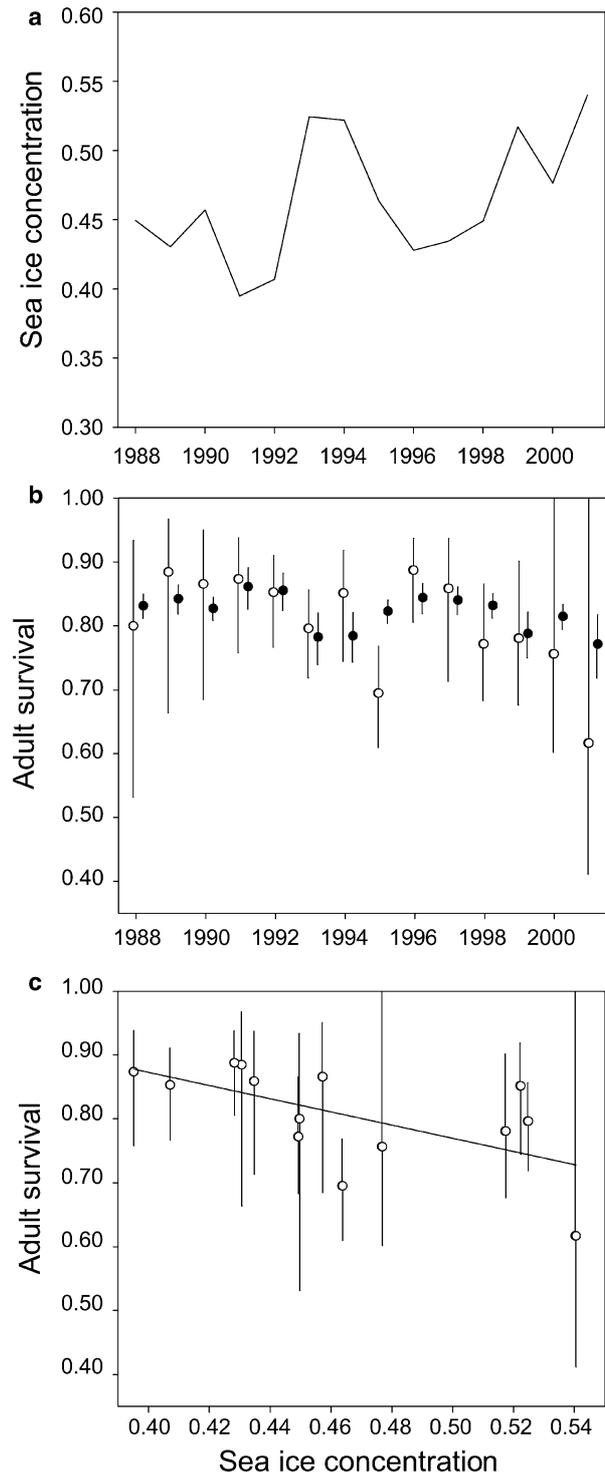

Fig. 2 Estimates of survival probabilities of the thin-billed prion at Mayes Island, Kerguelen and relationships with climatic indices. **a** Winter sea ice concentration south of Kerguelen, **b** annual adult survival probability, *open circle* estimated as a function of time from model $a_2^\ddagger$ (Table 1) and *filled circle* estimated as a function of sea ice concentration (*SIC*) from model c_1 (Table 1), **c** annual adult survival probability estimated as a function of time ‡ plotted as a function of SIC. The *line* indicates the linear relation between adult survival and SIC. (*Bars* indicate ± 1 standard error). (‡ The confidence intervals of the last four parameters of this model were obtained with the profile likelihood method)

Table 2 Results of Pearson's correlations between breeding parameters of the thin-billed prion and climatic indices

Climate indices breeding success	Hatching	Fledging	Total	SOI $_t$	SOI $_{t-1}$	SOI $_{t-2}$	SOI $_{t-3}$	SOI $_{t-4}$	SIC summer	SIC winter	SSTA-CS winter	SSTA-CS summer	SSTA-AAW winter	SSTA-AAW summer
Hatching		.	.	.	.	.	.	.	.	.	.	.	.	.
Fledging			+	.	.	.	.	.	.	.	.	.	.	.
Total			+	.	.	.	.	.	.	.	.	.	−	.

'.' non-significant correlation, +/− positive/negative correlation at the 0.05 level (Bonferroni corrected)

($\phi = 0.894 \pm 0.030$, Barbraud and Weimerskirch 2003), gave an homogeneous estimation for adult survival in medium-sized petrels, apart from uncertainties. These estimates correspond to the apparent adult survival that gathers both mortality and permanent emigration. During inspections of burrows outside the studied colony on Mayes Island, no ringed individuals were found (J.L.Chil and C.Marteau, personal communication), suggesting that permanent emigration was low in the vicinity of the colony. However, the number of birds controlled represented only a little proportion of the whole breeding population and permanent emigration could occur outside Mayes Island and could be increased due to the sensitivity of birds to handling or to less faithful individuals. Field observations revealed that some burrows became increasingly damaged during years (C.Barbraud and C.Marteau, personal communication) probably leading to less attractive sites. Nevertheless, we believe that even if the survival probability of the Mayes Island population was underestimated it could however be a good indicator of its inter-annual variations and of the relations between survival and climatic indices.

Concerning the impact of climatic conditions on survival, analyses revealed that survival was affected by Antarctic winter sea ice concentration south of Kerguelen, probably by controlling the productivity of the main foraging areas, as supposed in previous studies. Indeed, correlations between demographic parameters and sea ice conditions have been found for several Antarctic seabirds [Adélie penguin (*Pygoscelis adeliae*, Trathan et al. 1996); emperor penguin (*Aptenodytes forsteri*, Barbraud and Weimerskirch 2001a); snow petrel (*Pagodroma nivea*, Barbraud and Weimerskirch 2001b); southern fulmar (*Fulmarus glacialoides*, Jenouvrier et al. 2003)], but to our knowledge this has not been previously shown for a sub-Antarctic species breeding at lower latitudes (typically north of 50°S). This finding suggests that variations in sea ice conditions around the Antarctic continent may also affect the population dynamics of several sub-Antarctic species that forage in the seasonal ice zone. To our knowledge, this study presents for the first time a significant connection between sub-Antarctic and Antarctic ecosystems through the importance of sea ice for a Kerguelen population. However, whereas a positive correlation between sea ice extent and demographic parameters was typically found for several Antarctic populations, an inverse relationship was found for the thin-billed prion of Kerguelen. The negative relationship between winter sea ice concentration and adult survival indicated that cooler winters corresponded to less favourable conditions for the survival of thin-billed prions.

The oceanic sector covered by the winter sea ice had probably a major importance for prions. From at-sea observations, it is known that prions forage in this zone during summer. We suggest that winter sea ice conditions may greatly influence the food available for prions in summer, probably through an effect on prey species
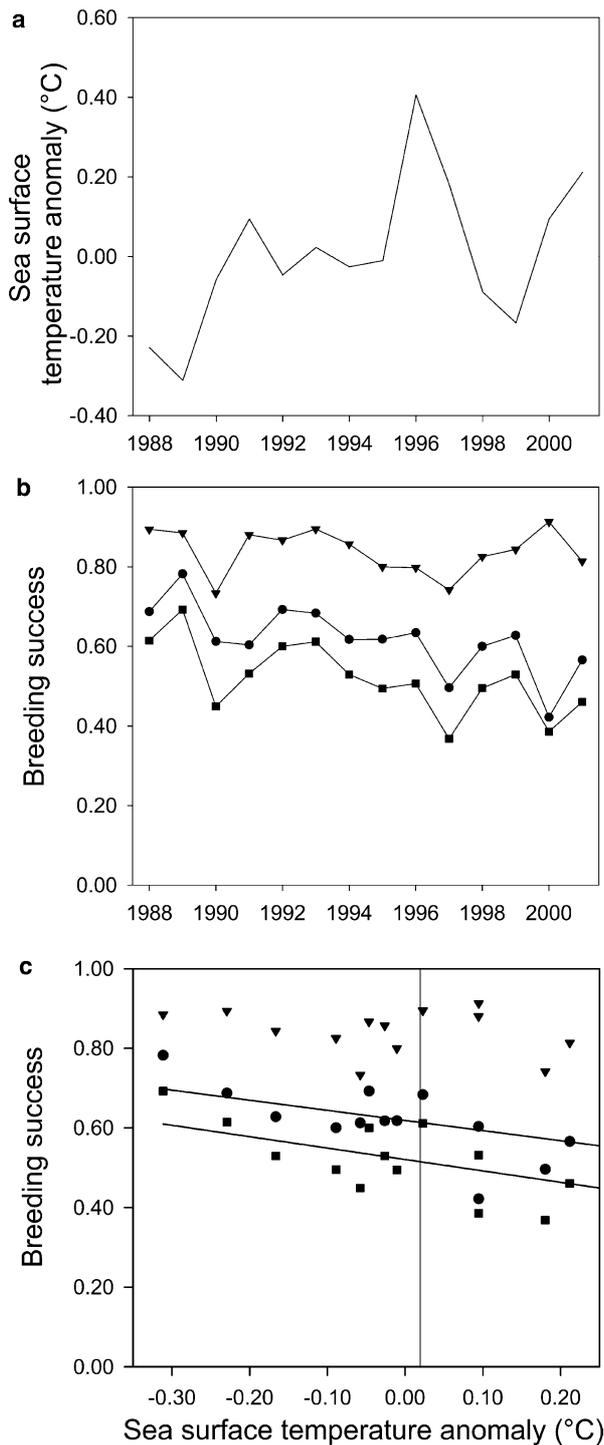
Fig. 3 Estimates of breeding parameters of the thin-billed prion at Mayes Island, Kerguelen and relationships with climatic indices. **a** Summer sea surface temperature anomaly (*SSTA*) in the Antarctic water zone, **b** annual breeding performance: *filled circle* hatching success, *filled inverted triangle* fledging success and *filled square* total breeding success, **c** breeding performance plotted as a function of sea surface temperature anomaly: *filled circle* hatching success, *filled inverted triangle* fledging success and *filled square* total breeding success, with lines for linear regressions of hatching, fledging and total breeding success, respectively

growing conditions. If an extensive winter sea ice cover has been shown to represent favourable conditions for the Antarctic krill *Euphausia superba* (Loeb et al. 1997; Veit et al. 1997; Fraser and Hofmann 2003), it was not enough to explain the present relation between sea ice cover and the survival probabilities of thin-billed prions, contrary to what is usually proposed for Antarctic sea-birds. Indeed, krill is not the major prey species for thin-billed prions, which prey mainly on the amphipod *Themisto gaudichaudii* (Cherel et al. 2002). To understand the mechanisms involved between sea ice, prey abundance and population dynamics, it seems necessary to further investigate the life cycle of the main prey species of thin-billed prions, as well as the foraging tactics of the birds.

Breeding performance

Our results and those of a previous study (Guinet et al. 1998) highlight the importance of the variability of the Antarctic oceanographic sector on the hatching success of sub-Antarctic seabirds, which corresponds to an area prospected by thin-billed prions during the incubation period. In addition, the relationship we found between sea surface temperature anomaly during incubation and hatching success is consistent with the study of Quillfeldt et al. (2003) who found a high egg desertion rate in the Falkland's thin-billed prion population in 2003, that coincided with an episode of warm sea surface temperatures. In sub-Antarctic waters, a warm anomaly leads to unfavourable growing conditions for primary production (Wilson and Adamec 2002). This situation of low prey availability should allow birds to compensate for the decrease of their body condition caused by incubation fasts on the nest, in an extended amount of time. In the same time, it would increase the length of the fasts and the weight loss imposed to the partner that remained on the nest. In this long-lived species, if the incubating bird has not been relieved before reaching a minimal body mass, it deserts the egg to go foraging in order to preserve its own chances of survival (Chaurand and Weimerskirch 1994; Chastel et al. 1995a), thus reducing the hatching success (Warham 1990).

On the other hand, the influence of environmental fluctuations during the chick-rearing period on fledging success seemed to be much less significant. As suggested by Chauraud et al. (1994), food resources may be more abundant during the second part of the summer, and breeding birds might therefore find sufficient food for their chicks and themselves. Another hypothesis to explain this lack of relationship between environmental variation and fledging success could be that lower quality individuals would have failed before egg hatching, so that only the most efficient pairs, which would be able to face fluctuations of the trophic resources to rear their chick, would remain.

Changes in the environment are highly susceptible to affect ecosystem components by a huge variety of climatic parameters and through a high number of different mechanisms. However, we could assume populations to be plastic enough to attenuate the effect of these perturbations. In addition, climatic indices have to be considered as indirect parameters reflecting physicochemical conditions that should be integrated by the system. Thus, the sensitivity of populations to this kind of factors could be considered to be generally weaker. Nevertheless, the relationships found between demographic parameters and oceanographic indices highlighted links that were strong enough to impact the population dynamics of the thin-billed prion population at Kerguelen. Based on our results, we could expect that an increase in the frequency of warm sea surface temperature anomalies, a consequence of a global warming of the Southern Indian Ocean (Levitus et al. 2000; Gille 2002), may deteriorate the hatching success and the whole breeding performance. By contrast, the observed decreasing trends of both the sea ice extent (Curran et al. 2003) and the length of sea ice season (Parkinson 1998), may lead to more favourable oceanographic conditions for adult survival. It is known that the population growth rate of long-lived species is mainly sensitive to fluctuations in adult survival (Sæther and Bakke 2000). So, we can predict that if the trends observed for oceanographic parameters are confirmed in the years to come, the thin-billed prion population at Kerguelen will probably increase in the short term, given that survival and reproductive success are not affected by other factors. By contrast, our results suggest that the population has probably declined during last years given the low adult survival and the decreasing reproductive success. This situation is probably the result of time-restricted climatic events, such as the episode of high sea ice concentration observed between 1993 and 1995. The changes of that population are probably driven by interactions between global trends and occasional extreme climatic episodes. Further modelling, using population matrix models, will be necessary to better understand the demographic parameters that control population growth rate and their sensitivity to environmental fluctuations.

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