OIKOS 108: 511–522, 2005

Modelling population dynamics of seabirds: importance of the effects of climate fluctuations on breeding proportions

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Jenouvrier, S., Barbraud, C., Cazelles, B. and Weimerskirch, H. 2005. Modelling population dynamics of seabirds: importance of the effects of climate fluctuations on breeding proportions. – Oikos 108: 511–522.

Environmental factors and their interactions are likely to have shaped specific breeding and survival strategies in top predators. Understanding how climatic factors affect populations requires detailed investigation of the demographic parameters and population modelling. Here, we focus on the modelling of a southern fulmar population over a 39 year period in Terre Adélie, Antarctica, using Leslie matrix models to understand from a prospective and retrospective point of view, how vital rates and their variations, affect the cyclic population dynamics. The elasticity of population growth rate to adult survival was very high (0.95), as predicted by a slow–fast continuum in avian life histories. However, adult survival varied little between years (mean ± SD: 0.92 ± 0.07), and could not explain the strong fluctuations observed in the number of breeders and chicks. The high temporal fluctuations of the proportion of breeders (0.57 ± 0.22) and breeding success (0.70 ± 0.14) had the strongest impact on population dynamics, despite their weak elasticities (0.05). Before the 1980s, population fluctuations were mainly explained by a direct impact of sea-ice extent (SIE) anomalies during summer (by a threshold effect) on the proportion of breeders. After 1980s, 3 years periodic population fluctuations were best predicted by 3 years cyclic variations in the proportion of breeders. SIE showed a marked change of periodicity during the 1980s, and SIE during winter fluctuated with a 3 years periodicity during 1980–1995. The marked change in population dynamics, through a change of the variations of the proportion of breeders, may be explained in the light of a regime shift that probably occurred around the 1980s, and which affected the sea ice environment, the availability of prey, and thus the demographic parameters and population dynamics of southern fulmars.

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The biotic and abiotic environments to which individuals are exposed may vary importantly over time and can, through phenotypic plasticity as well as microevolutionary processes, shape individual life histories (Stearns 1992). It is widely appreciated that life history can produce time lags in population dynamics (Turchin 2003). Coulson et al. (2001) and Thompson and Ollason (2001) showed that time lags in life history are important in explaining temporal patterns of population fluctuations in the Soay sheep (*Ovis aries* L.) and in the northern fulmar (*Fulmarus glacialis* L.). Seabirds are longlived species and factors affecting their demographic parameters, such as recruitment, could be expected to have a delayed effect on population size (Thompson and Ollason 2001, Wilson et al. 2001). A decrease in adult survival, would, for example, have an immediate effect on the breeding population (Barbraud and Weimerskirch 2001), whereas a decrease in fecundity,

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Accepted 9 September 2004

ISSN 0030-1299

or on immature survival, could have a lagged effect on population size (Weimerskirch et al. 1997). Moreover, density dependent and climatic conditions experienced by individuals early in life differ considerably between cohorts, and can also have delayed, long term effects arising from its influence on their survival and/or breeding performance (Gaillard et al. 1997, Lindström 1999, Forchhammer et al. 2001, Lande et al. 2002, Lindström and Kokko 2002). Modelling is a crucial way to understand how the environmental fluctuations, e.g. due to a climate change, will affect future population fluctuations through its impact on vital rates.

Temporal variation in vital rates and population growth rate may be due to environmental fluctuations and/or density dependence (Saether 1997, Grant and Benton 2000, Neubert and Caswell 2000). Usually it is difficult to distinguish the effect of density dependence and the impact of the environment (Leirs et al. 1997, Barbraud and Weimerskirch 2003). This makes it difficult to understand the mechanisms generating the feedback between demography and population dynamics. In this study we focus on a southern fulmar (*Fulmarus glacialoides* Smith) population, where no density dependence in life history trait was detected, probably because of the small population size and the high availability of nesting sites (Jenouvrier et al. 2003). This enables us to study the influence of environmental fluctuations on the temporal variation in vital rates and how this affect population dynamics.

In marine ecosystems, interannual variability is a well recognised phenomenon with very variable, and sometime unpredictable, fluctuations in oceanographic parameters, or cyclic patterns such the El Niño southern oscillation and the North Atlantic oscillation (Stenseth et al. 2002). This variability is expected to affect all levels of the trophic web and especially marine top predator populations (Aebischer et al. 1990, Croxall 1992). Variations in the physical marine environment are likely to affect the availability and accessibility of resources for foraging predators, and therefore may influence how individuals allocate resources towards competing energy demanding processes such as maintenance and reproduction (Stearns 1992). Tradeoffs might thus be affected by environmental variability, and strong oceanographic anomalies might even affect survival of predator species.

Although several studies have investigated the effects of environmental variability on some demographic parameters of top predator populations such as population size, breeding performances, or survival (Fraser et al. 1992, Guinet et al. 1998, Smith et al. 1999, Barbraud et al. 2000), few have simultaneously explored the influence of the environment variability on all parameters and its consequences on the population size. From an ecological perspective this means to understand how environmental factors affect the vital rates, and therefore the population dynamics. From a purely demographic point of view, this means to understand how vital rates, such as survival and fecundity, and their variations, affect the population dynamics.

Several studies have showed that demographic parameters that strongly influence variation in population growth rate show small temporal variation (Horvizt et al. 1997 for plants, Gaillard et al. 1998 for ungulates). For instance, in birds, the species can be placed along a "slow–fast continuum", where species with a high fecundity rate, but low survival are found at one end (Saether and Bakke 2000). In contrast, at the other end of this continuum are located species that mature late, produce few chicks, and have a long life expectancy. The sensitivity of their population growth rate to adult survival is very high. Retrospective analysis (Caswell 2000) highlighted a negative relationship between the sensitivity of vital rates and their temporal variations, between, and within species (Saether and Bakke 2000). This can be interpreted as the result of an evolution of a bet-hedging strategy (Seger and Brockman 1987) among longlived species to spread the risk of reproductive investments over several breeding seasons. Most seabirds are located in the extreme part of this gradient, since they lay only a single egg, mature at very high age, and have a high adult survival rate. For these species, we therefore expect a high sensitivity of growth rate to adult survival, but small temporal variation. In the other hand, we predict that the fluctuations of fecundity will greatly influence the population dynamics.

The Antarctic community of seabirds shows different population dynamical responses to environmental variability (Croxall et al. 2002). This emphasizes the need to a better understanding of the impact of environmental fluctuations on population dynamics through their effects on vital rate. In a previous study (Jenouvrier et al. 2003), we showed a very high variability over a 39-year period of the southern fulmar population size. Demographic parameters, like adult survival or the proportion of breeders were influenced by environmental fluctuations and particularly by sea ice conditions. This long term population monitoring, therefore provides a good system to study the influence of environmental fluctuations on the temporal variation in vital rates and how this affect population dynamics. Here, we focus on the modelling of the southern fulmar population with Leslie matrix models to understand from a prospective and retrospective point of view, how vital rates and their variations, affect the cyclic population dynamics.

Methods

Description of the study

Southern fulmars are cliff nesting seabirds that forage over Antarctic waters, occasionally up to subantarctic waters, and prey mainly on euphausiids, fishes, crustaceans and squids (Ainley et al. 1984, Ridoux and Offredo 1989). The censusing and marking of southern fulmars was carried out every year from 1963 to 2002 on Ile des Pétrels, Pointe Géologie Archipelago (66°40′S, 140°01′E), Terre Adélie, Antarctica. The only colony of southern fulmars at Pointe Géologie is located on a cliff 20 meters from the Dumont d'Urville station. Breeding pairs were censused towards the end of December, just after egg laying. Nests were checked just before fledging to count the number of chicks fledged. Every year, all adult birds captured in the colony were marked with a stainless steel band during the incubation, and all chicks were marked just before fledging. Each nest with an egg was checked two to three times during the first half of the incubation period, which permitted to read the ring of all breeding birds present on the colony. Non breeders were defined as those birds that were not observed incubating an egg during the visits to the colony. Although the probability that they laid an egg and failed before the first control is not null, it was considered as negligible since most birds lay their egg around mid December, and the first visit to the colony occurs the 20th of December.

Time series analysis

Because our time series showed marked changes in cycle period through time, we applied wavelet analysis to take into account the non-stationarity of the period of the different population dynamics. By decomposing a time series into time and frequency domains, wavelet analysis can determine both the dominant modes of variability, and how those modes vary in time (Torrence and Compo 1998, Klvana et al. 2004).

We used the Morlet wavelet function ψ_0 that is essentially a damped complex exponential function, which can quantify local cyclic fluctuations in the time series. The frequency-time range over which it does this is set by a scale parameter, s, relating to the conventional Fourier period of oscillations, and a translation parameter n. The Morlet wavelet function is $\psi_0(\eta) = \pi^{1/4} \exp(i\omega_0\eta)\exp(-\eta^2/2)$, where ω_0 is the non-dimensional frequency and $\eta = n/s$ (Torrence and Compo 1998).

With $\omega_{0=} = 6$, the wavelet scale s is inversely proportional to the central frequency of the wavelet, and the frequency is equal to 1/s, or the period p is equal to s. The continuous wavelet transformation (CWT), $W_n(s)$, of the time series X_n is calculated as the convolution of X_n with ψ_0. The wavelet transform coefficients $W_n(s)$ represent the contribution of the scale s to the signal at different time position n. By taking into account a range of s and n values, one can explore and identify the structures relating to time and frequency.

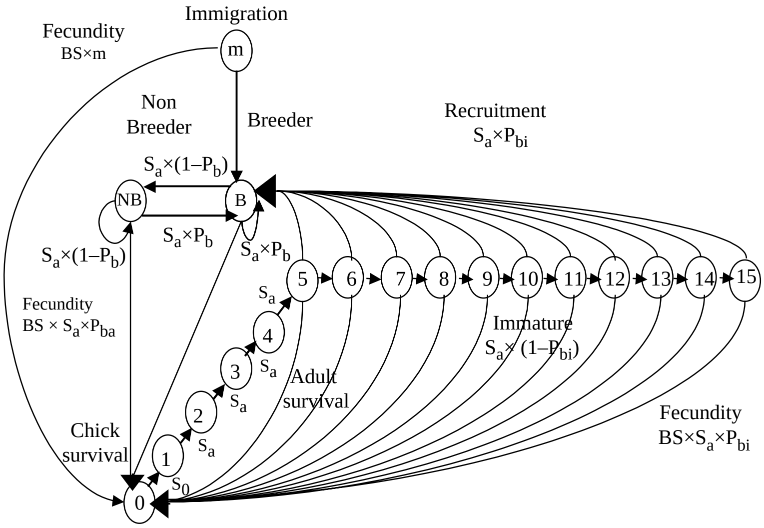
The wavelet power spectrum (WPS), at time point n and scale s, is then given by $|W_n(s)|^2$. The WPS gives a measure of the variance distribution of the time series at time point n and scale s. To compare WPS with classical spectral methods, global wavelet spectrum is computed as the time average of the WPS for each frequency components. It has been shown that the global wavelet spectrum provides an unbiased and consistent estimation of the Fourier spectrum (Percival 1995).

As with classical Fourier analysis using fast Fourier transform, the data were padded with zero up to the next-highest power of two (Torrence and Compo 1998). The 'cone of influence' is a reflection of a consequent loss in statistical power near the start and the end of the series. This area in the WPS figure delimited by a white line (Results) should be interpreted cautiously. Nevertheless, the zero padding, owing to numerous introduced zeros, mainly induces reduction in the CWT and in the associated quantities.

The 5% and 10% significance levels were determined with bootstrapped simulations. We consider the null hypothesis as the observed time series being different from that expected through chance alone. We constructed 1000 surrogate data sets, and calculated for each surrogate the CWT. Based on these surrogate series, one constructs the distribution under the null hypothesis of WPS, global WPS. These distributions are then used to establish the 5% and 10% significance levels for the WPS, global WPS.

Population modelling

We constructed a population model structured by age and reproductive status classes. Modelling was done using a post-breeding matrix (Caswell 2001; Fig. 1, Table 1). Observed minimum age at first breeding was 6 years, and the age at which all birds were recruited was 16 years (Jenouvrier et al. 2003). During the first year, chicks survive with the probability S_0. We cannot estimate the immature survival because birds stayed at sea and were not observable. Therefore, we estimated S_0 using the return rate from fledging to recruitment, and assuming that the survival of immature birds was similar to that of adults after the first year at sea. Each year, birds have the probability S_a to survive without senescence, S_a corresponding to the adult survival estimated with capture recapture methods (Jenouvrier et al. 2003). The probability to breed for the first time at age i was $(S_a \times P_{bi})$, $i \in [6, 15]$, where P_{bi} was the proportion of birds banded as chicks that breed for the first time at i years old (Jenouvrier et al. 2003). Once recruited, birds reproduce every year with the probability $(S_a \times P_b)$, where P_b is the proportion of breeders, estimated as the number of breeders on the number of birds alive calculated from the capture recapture data. The southern



$$
n_{t+1} = \overset{A}{\begin{pmatrix}
0 & 0 & 0 & 0 & 0 & (1+m)\times BS\times S_a\times P_{b6} & (1+m)\times BS\times S_a\times P_{b7} & (1+m)\times BS\times S_a\times P_{b8} & (1+m)\times BS\times S_a\times P_{b9} & (1+m)\times BS\times S_a\times P_{b10} & (1+m)\times BS\times S_a\times P_{b11} & (1+m)\times BS\times S_a\times P_{b12} & (1+m)\times BS\times S_a\times P_{b13} & (1+m)\times BS\times S_a\times P_{b14} & (1+m)\times BS\times S_a\times P_{b15} & (1+m)\times BS\times S_a & (1+m)\times BS\times S_a\times P_b & (1+m)\times BS\times S_a\times P_b \\
S_0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & S_a & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & S_a & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & S_a & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & S_a & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & S_a\times(1-P_{b6}) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & S_a\times(1-P_{b7}) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & S_a\times(1-P_{b8}) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_a\times(1-P_{b9}) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_a\times(1-P_{b10}) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_a\times(1-P_{b11}) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_a\times(1-P_{b12}) & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_a\times(1-P_{b13}) & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_a\times(1-P_{b14}) & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_a\times(1-P_{b15}) & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_a\times(1-P_b) & S_a\times(1-P_b) \\
0 & 0 & 0 & 0 & 0 & (1+m)\times S_a\times P_{b6} & (1+m)\times S_a\times P_{b7} & (1+m)\times S_a\times P_{b8} & (1+m)\times S_a\times P_{b9} & (1+m)\times S_a\times P_{b10} & (1+m)\times S_a\times P_{b11} & (1+m)\times S_a\times P_{b12} & (1+m)\times S_a\times P_{b13} & (1+m)\times S_a\times P_{b14} & (1+m)\times S_a\times P_{b15} & (1+m)\times S_a & (1+m)\times S_a\times P_b & (1+m)\times S_a\times P_b
\end{pmatrix}} n_t
$$

Fig. 1. Upper: lifetime cycle graph for the southern fulmar population. Minimum age at first breeding was assumed to be 6 years, and the age at which all birds were recruited 16 years. During the first year, chicks survive with the probability S_0. Each year, adults survive with the probability S_a. The probability to breed for the first time at age i was ($S_a \times P_{bi}$), $i \in [6,15]$, where P_{bi} was the proportion of birds that breed for the first time at i years old. Once recruited, birds reproduce every year with the probability ($S_a \times P_b$), P_b being the proportion of breeders. The southern fulmars are able to skip a reproduction with the probability ($S_a \times (1 - P_b)$). The number of chicks is determined by the reproductive success of breeders, noted BS. We consider also a proportion of immigrants, m. Lower: population projection matrix A is multiplied to n(t), a vector describing the state of the population at time t, to obtain the state of the population at t+1. The projection interval (from t to t+1) is one year.

fulmars are able to skip a reproduction with the probability ($S_a \times (1 - P_b)$). The number of chicks are determined by the reproductive success of breeders, noted BS, estimated as the proportion of eggs producing fledglings. A previous analysis (Jenouvrier et al. 2003), highlighted the importance of immigration in this population. The number of immigrants was estimated from 1978 as those adults found breeding for the first time and not banded as chick in the colony. We showed that the number of immigrants was correlated both with the number of local breeders at the colony, and with the number of local recruits (Jenouvrier et al. 2003). To take into account the fact that the temporal variations of immigration and breeding population are related, we considered a proportion of immigrants, m, calculated as the number of immigrants on the number of breeders.

The resulting model (Fig. 1) was a linear, time invariant system of difference equation:

$$n(t+1) = A\ n(t) \tag{1}$$

where A is the population projection matrix (Fig. 1), and n(t) a vector describing the state of the population, whose entries n(t) give the numbers in each class. For further details, see Fig. 1 and Table 1.

We started setting up a constant model (1), where the matrix A is a constant that included the mean values of the demographic rates (Table 1). The matrix analysis yielded the deterministic population growth rate, stable age distribution and the sensitivities of the growth rate to variations in demographic rates (Caswell 2001). In order to compare the model's prediction with the observed number of breeding pairs (or chicks), we calculated

Table 1. Parameters entered in the matrix population models for southern fulmars at Dumont d'Urville. We used post breeding Leslie matrix for a female population (Fig. 1). The matrix analysis yielded stable age distribution (Caswell 2001). NB for non breeders, B for breeders. The 0 class represents the chicks, and the classes from 1 to 15 years old the immatures.

Age class	Survival	Proportion of breeders	Fecundity	Stable age distribution	Initial number
0	0.45	–	–	0.1528	22
1	0.92	–	–	0.0685	10
2	0.92	–	–	0.0629	9
3	0.92	–	–	0.0578	8
4	0.92	–	–	0.0532	8
5	0.92	–	–	0.0489	7
6	0.92	0.07	0.07 × 0.92 × 0.70	0.0418	6
7	0.92	0.13	0.13 × 0.92 × 0.70	0.0334	5
8	0.92	0.14	0.14 × 0.92 × 0.70	0.0264	4
9	0.92	0.13	0.13 × 0.92 × 0.70	0.0211	3
10	0.92	0.11	0.11 × 0.92 × 0.70	0.0173	2
11	0.92	0.09	0.09 × 0.92 × 0.70	0.0145	2
12	0.92	0.07	0.07 × 0.92 × 0.70	0.0124	2
13	0.92	0.06	0.06 × 0.92 × 0.70	0.0107	1
14	0.92	0.05	0.05 × 0.92 × 0.70	0.0093	1
15	0.92	1	0.92 × 0.70	0.0082	1
NB	0.92	0.57	0.57 × 0.92 × 0.70	0.1426	22
B	0.92	0.57	0.57 × 0.92 × 0.70	0.2183	32

growth rate as the slope of a least square fit of the log-transformed number of breeding pairs (or chicks) versus time.

Second, we included temporal variability in the elements of the transition matrix (Fig. 2) using a linear time varying model:

$$n(t+1) = A_t \; n(t) \tag{2}$$

We used in the projection matrix of a year t ($\mathbf{A}_t$), the breeding success of a year t+1, the proportion of breeders a year t+1, and the chick survival rate between year t and t+1. Indeed, in a postbreeding matrix, breeders have to survive before breeding, and therefore the fecundity rate was function of reproductive parameters at year t+1. We kept the adult survival rate constant since we showed in a previous analysis (Jenouvrier et al. 2003) that adult survival varied little between years. We started with an initial vector of the number of recorded breeding pairs and chicks. Numbers of individuals in the other age classes were obtained by the stable age distribution produced by the left eigenvector compared to the mean number of breeding pairs (Table 1). To compare numbers of breeding pairs (or chicks) observed and predicted by matrix models, we calculated a fitting criteria based on a χ^2 value defined as the sum of the square distance between the number of breeding pairs (or chicks) observed and predicted, divided by the number observed.

Third, we included temporal cyclity of demographic parameters by integrating equation (3) in the projection matrix of a year t (A_t) of the Eq. 2:

$$\begin{aligned} d(t) = \bar{d} &+ (\sigma^2(d) \times \cos((2\pi \times t)/\text{period})) \\ &+ (\sigma^2(d) \times \sin((2\pi \times t)/\text{period})) \end{aligned} \tag{3}$$

where d(t) is the value of the demographic parameter at year t, $\bar{d}$ and $\sigma^2(d)$ are respectively the mean and variance of the parameter computed over the study.

Finally, to study the effect of environment variability on the population dynamics through the influence of climate fluctuations on vital rates, we considered the model $n(t+1) = A_t \, n(t)$, where each entries of A_t may be function of an environmental variable. We used sea ice extent (SIE) since 1973 (Jenouvrier et al. 2003). SIE data were available from the Antarctic CRC and Australian Antarctic Division Climate Data Sets (http://www.antcrc.utas.edu.au/ ~jacka/seaice_C_html). We considered that anomalies on demographic parameters were linked to SIE anomalies. We used the mean of anomalies to simulate multi annual environmental fluctuations, and the mean of exceptional anomalies, defined as anomalies above the mean of anomalies (Table 2), to simulate exceptional environmental conditions. For example, when a 47 km decrease, compared to the mean, in winter sea ice extent occurred during warm events, adult survival decreased by 6% (Table 2). If exceptional warm events occurred, when a 71 km decrease of sea ice extent occurred, adult survival decreased by 10% (Table 2).

Results

Demographic parameters

The number of southern fulmar breeding pairs increased during the study (Fig. 2a), although it fluctuated strongly, especially since the early 1980s. The observed growth rate of the breeding population was 1.0046. Time series analysis showed that the population fluctuated with a periodicity around 3 years after the eighties (Fig. 2b). Indeed, the global wavelet power spectrum showed a main periodic component around 3 years (Fig. 2b, right). These main cyclic characteristics were not constant, and the wavelet analysis revealed that they significantly changed over time (Fig. 2b, left). Wavelet

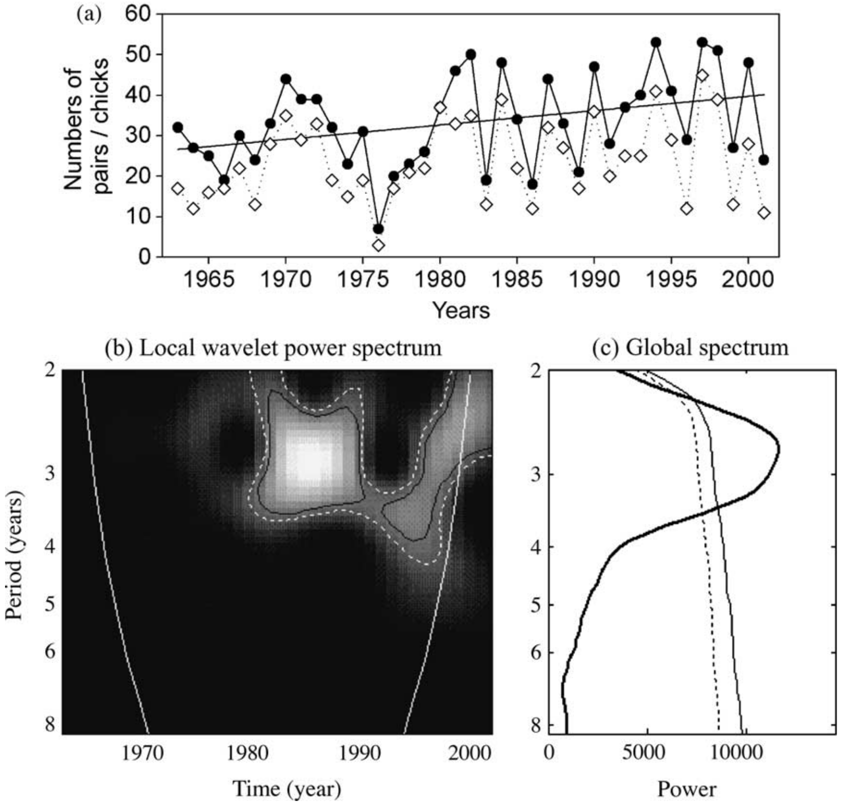


Fig. 2. (a) Annual variation of the number of breeding pairs (filled circle) and fledged chicks (open diamond) for southern fulmars between 1963 and 2002. The number of breeding pairs increased significantly since 1963 (linear regression: p = 0.026, $R^2 = 35.6\%$, growth rate: 1.0046). (b) Local wavelet power spectrum (using Morlet wavelet, left) and global wavelet power spectrum (right) of southern fulmars breeding population size between 1963 and 2001. For the global spectrum, the hair black line and dotted line respectively represent the 5% and 10% significance levels, calculated with bootstrap methods. For the local wavelet power spectrum, the black thick contour is the 5% significance level and the white dotted contour is the 10% significance level. The white contour indicates the cone of influence, where zero padding has reduced the variance. The local wavelet power spectrum gives a measure of the variance distribution of the time series according to time and for each periodicity; high variability is represented by white colour, whereas black colour indicates a weak variability.

power spectrum indicated that the fulmar population showed significant cyclic fluctuations only after 1980, with a marked periodicity around 3 years in 1980–1990, and from 1996.

The fluctuations of the number of chicks followed those of the breeding pairs, but the number of chicks produced did not increase significantly during the study (p = 0.124, Fig. 2a). The observed growth rate of the chick population was 1.0039.

The proportion of birds alive in the breeding population during a particular year and attempting to breed averaged (±SD) 0.57 ± 0.22. It fluctuated strongly between years (especially since the early 1980s), and was particularly low between 1975 and 1980 (Fig. 3a). The mean breeding success was 0.7 ± 0.14%, and showed high inter-annual variability (Fig. 3b). The juvenile survival rate showed high year to year variations (Fig. 3c), and was on average 0.26 ± 0.15. It was particularly low during the mid seventies and mid eighties.

Population modelling

The constant deterministic model predicted a long term annual geometric growth rate of 1.0117, thus providing good information of the trend on the population. Sensitivity and elasticity analyses indicate that the growth rate is mainly sensitive to adult survival (elasticity: 0.95). Survival during the first year at sea, breeding success, the proportion of breeders and the proportion of immigrants have low elasticities (0.05, 0.05, 0.05, and 0.003, respectively). The proportion of birds attempting to breed for the first time have less contribution on growth rate (elasticity at age 6 to 15 years: 0.002, 0.003, 0.003, 0.002, 0.001, 7.494×10^{-4}, 4.177

Table 2. Values of anomalies of demographic and environmental parameters used in the study of the impact of the environment on the population dynamics through its effect on demographic parameters (Methods). Chick survival was not related to sea ice extent, whereas the fluctuations of breeding success (BS), proportion of breeders (P_b), and adult survival (S_a) were linked to the variation of sea ice extent (SIE).

	BS	P_b	S_a	SIE_{winter} (km)	SIE_{summer} (km)
Mean of the anomalies ($\bar{a}$)	0.11	0.18	0.06	47	26
Maximum of the anomalies	0.30	0.54	0.17	110	65
Mean of anomalies $> \bar{a}$	0.19	0.3	0.10	71	46

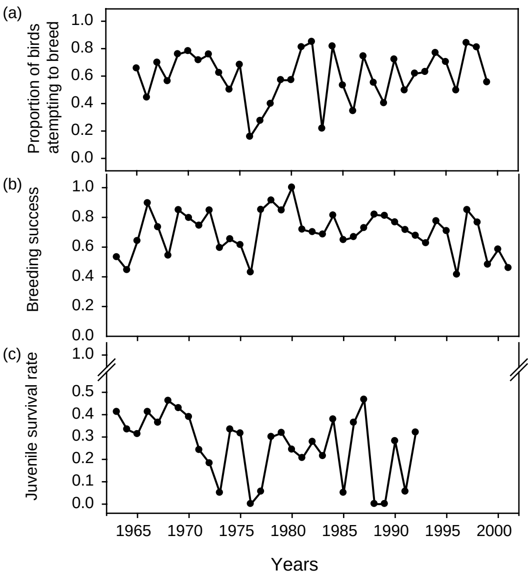


Fig. 3. Annual variation of (a) the proportion of breeders, (b) breeding success, and (c) juvenile survival rate for southern fulmars between 1963 and 2002.

$\times 10^{-4}$, 2.449×10^{-4}, 1.248×10^{-4}, and 4.604×10^{-5}, respectively).

Adult survival was less variable than chick survival, breeding success, and the proportion of breeders (mean ± SD: 0.92 ± 0.07, 0.45 ± 0.21, 0.70 ± 0.14, and 0.57 ± 0.22, respectively; Fig. 3). When we took into account the temporal variability in chick survival or in breeding success, the numbers of breeding pairs predicted by the matrix models were far from the observed values (Fig. 4a, b, left, Table 3). However, when we considered the temporal variation in the proportion of breeders the model predictions were close to the observed dynamics of the breeder population (Fig. 4c, left, Table 3). A model taking into account the temporal variability in breeding success, chick survival or both, in addition to the temporal variation of the proportion of breeders, did not improve the fit of the model (Table 3).

The numbers of chicks predicted by the matrix models taking into account the temporal variability in chick survival were far from the observed values (Fig. 4a, right, Table 3). However, the model considering the temporal variation in the proportion of breeders predicted very well the variation of the number of chicks (Fig. 4c, right, Table 3). The model taking into account the temporal variability in breeding success showed the best fit (Table 3), but graphically (Fig. 4b, right) the predictions described less well the observed number of chicks than the model considering the temporal variation in the proportion of breeders (Fig. 4c). The model considering both the temporal variability in breeding success and in the proportion of breeders showed the best fit, and predicted very well the variation of the number of chicks (Fig. 4d, right).

The model taking into account for temporal variability in both the proportion of breeders and breeding success, showed the overall best fit to observed numbers of chicks and breeders (Table 3, Fig. 4d). This model predicted very well the variation of both numbers of breeding pairs and chicks, but the estimates were in general too large (Fig. 4d). The number of recruits (sum of breeders and non breeders) increased at a rate of 0.63% per year (Fig. 4b, left). The number of immatures overall increased at a rate of 0.73% per year, but it decreased between 1975 and 1979 (Fig. 4b, right), probably due to a decrease in the proportion of breeders, breeding success, and juvenile survival in 1976 (Fig. 3a, b, c).

When a cyclic component of 3 years on the proportion of breeders was taken into account, the models fitted reasonably well the observed breeding population size from the eighties (Fig. 5a, Table 3). This indicates that the observed periodicity of the population dynamics (Fig. 2b) is due to a cyclicity of 3 years in the time series of the proportion breeders.

Modelling climate fluctuations

SIE showed strong year-to-year variations during the period 1973–2002 (Fig. 6a), especially during winter. An abrupt sea ice retreat during winter occurred between 1973 and 1981. The global spectrum for the winter SIE (Fig. 6b, right) showed a main significant periodic component around 2–3 years, whereas for summer SIE, two periodic components around 3 and 4–5 years appeared highly dominant (Fig. 6c, right). Wavelet power spectrum revealed that winter SIE showed a marked shift of periodicity from a weak periodicity of 4 years before 1980 to a stronger one of 2–3 years between 1980–1995 (Fig. 6b, left). Summer temperature showed a strong periodicity around 4 years before the end of the 1980s, and a 3 years periodicity at the end of the 1990s, without any noticeable signal between these time periods (Fig. 6b, left). The models considering the effect of SIE on demographic parameters with threshold effects (Methods, Table 2) poorly fitted the observed data (Table 3). A model where the proportion of breeders varied as a function of SIE during summer was among those that best explained the population dynamics (Table 3, Fig. 5b). Indeed, from 1973 to 1985, this model fitted reasonably well the observed number of breeding pairs. Taking into account for the effect of environmental factors on adult survival or breeding success, in addition to the environmental impact on the proportion of breeders, did not improve the fit of the model (Table 3).

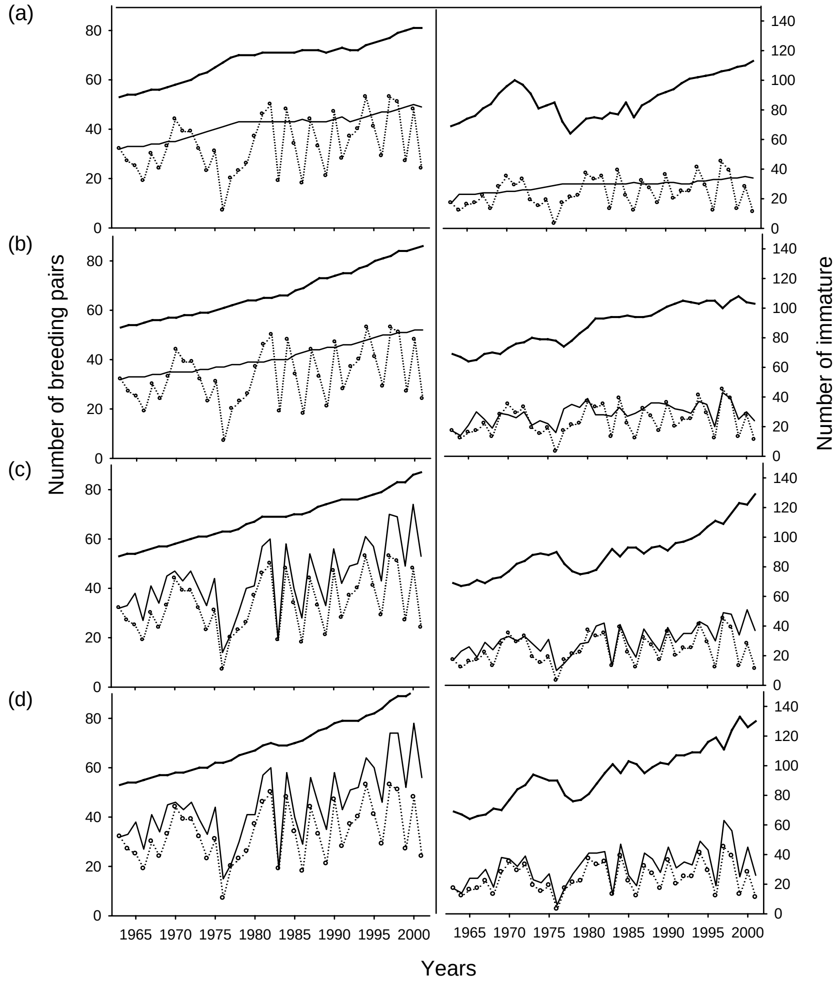


Fig. 4. Annual variation of the number of breeding pairs and recruits (left panels), chicks and immatures (right panels) for southern fulmars between 1963 and 2002. Models take into account the temporal variation of (a) chick survival, (b) breeding success, (c) proportion of breeders, and (d) of both proportion of breeders and breeding success. Symbols and lines indicate for both left and right panels: the observed number (circle and dotted line), the number predicted by matrix models (hair line). For left panels, the thick line indicates the number of recruited pairs (sum of breeding pairs and non breeding pairs that have recruited) whereas for right panels it designates the immatures.

Discussion

The elasticity of the southern fulmar population growth rate to adult survival was very high, as predicted by the position of the species along the slow–fast continuum of avian life histories (Saether and Bakke 2000). Saether et al. (1996) termed these species "survivor species". Accordingly, adult survival varied little between years, and could not explain the strong fluctuations observed in the population size. Rather, the high temporal fluctuations of the proportion of breeders had the strongest impact on the breeder population dynamics,

Table 3. Model fit (χ^2) calculated as the sum of squared distance between the numbers of breeding pairs (or chicks) observed and predicted, on the number of breeding pairs (or chicks) observed. P_b is the proportion of breeders, BS the breeding success, S_0 the chick survival and S_a the adult survival. The bold entries stand for the best model (lowest χ^2).

Models	χ^2 for the number of breeding pairs	χ^2 for the number of chicks	Sum of χ^2
$P_b(t)$–BS(t)	231.53	**143.48**	**375.02**
$P_b(t)$	**188.64**	241.29	429.93
$P_b(t)$–BS(t)–$S_0(t)$	318.71	200.43	519.13
$P_b(t)$–$S_0(t)$	252.42	293.18	545.60
BS(t)	375.39	218.25	593.64
BS(t)–$S_0(t)$	456.44	267.07	723.51
Constant	357.12	436.59	793.71
$P_b(SIE_{summer})$	409.69	436.73	846.42
$S_0(t)$	422.51	493.30	915.81
P_b(period 3 years)	447.49	528.54	976.03
$P_b(SIE_{summer})$–BS(SIE_{summer})	424.41	835.14	1259.55
P_b(period 3 years)–BS(period 3 years)	501.11	886.11	1387.22
$P_b(SIE_{summer})$–BS(SIE_{summer})–S_a (SIE_{winter})	968.18	1469.70	2437.88

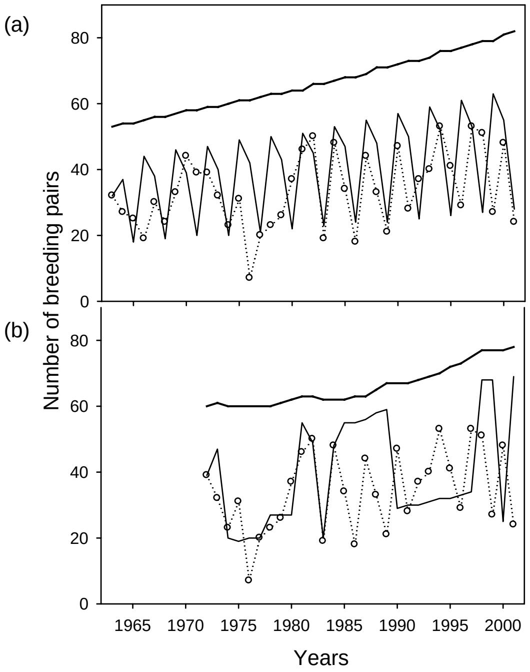


Fig. 5. Annual variation of the number of breeding pairs for southern fulmars observed between 1963 and 2002 (circle and dotted line), predicted number of breeders (hair line), and recruited (thick line) obtained using a matrix model considering (a) for a periodic variation of 3 years on the proportion of breeders, and (b) for the impact of SIE anomalies on the proportion of breeders.

despite its weak elasticity. The high temporal fluctuations of breeding success also influenced the population dynamics of chicks, despite its weak elasticity. A decrease in the contribution of a trait to the variance in the population growth rate with increasing sensitivity may be a common pattern, suggesting that a reduction in the variance of sensitive traits is favoured through selection (Saether and Bakke 2000).

We demonstrated that the model taking into account the temporal variations of the proportion of breeders and breeding success, showed the overall best fit. This model especially greatly increased the fit to the observed chick population dynamics. The second overall best-fit model considered only the temporal variation of the proportion of breeders. This suggests that there is a strong influence of the proportion of breeders on the population dynamics, and a smaller influence of breeding success variations. Interestingly, southern fulmars as other Procellariiforms, are longlived organisms that should be less prone to trade their own survival for that of their offspring, because any reduction in adult survival would greatly reduce lifetime reproductive success (Charlesworth 1980). Weimerskirch (1999) showed the important role of body condition in allocation decisions for foraging and breeding in albatrosses and petrels. These species behave as prudent parents (Drent and Dann 1980) in never allowing their body condition to deteriorate to a level that may jeopardize their lifetime reproductive success. Breeding abstention among longlived species may be a response to poor feeding conditions early in the breeding season (Chastel et al. 1995). When facing food shortage, individuals may not reach a threshold value of early body condition, below which established breeders will refrain from breeding. We showed here that the proportion of breeders was the demographic parameter that most influenced the breeder population inter-annual variations. Southern fulmars feed mainly on Antarctic krill (*Euphausia superba* Dana) in Terre Adélie. Interannual changes in the recruitment success of krill abundance may decline following successive winter of reduced ice coverage (Loeb et al. 1997), and lower krill abundance is associated with areas with less winter sea-ice cover (Nicol et al. 2000). During summer, krill density increases southward from the point where ice concentration is greater than about 40% (Brierley et al. 2002), and any krill reduction may be in proportion to the reduction of ice-edge length. Fulmars may have difficulties in finding food in years with high sea surface temperature and low sea ice concentration, during which mortality may be increased, and the proportion of breeders decreased (Jenouvrier et al. 2003). Indeed, the southern fulmar is a capital breeder (Weimerskirch 1989) that needs to accumulate extra reserves to engage or to persevere a breeding attempt. Depletion of the capital in winter and before the reproduction, related to poor environmental conditions, probably results in a skip of the reproduction. This represents an extreme case of bet-hedging strategy where reproduction is probably largely determined by the environmental conditions.

The model considering the temporal variations of the proportion of breeders and breeding success predicted well the fluctuations of the numbers of chicks and breeders, but the estimates were in general too large, especially for the number of breeding pairs. If we considered a number of immature less than the number predicted by the stable age distribution, this overestimation disappears during the twenty first years of the study. Therefore, the overestimation of the number of breeders was probably due to an overestimation of the number of immatures. Indeed, we assumed that immature and adult survival were equal, which is probably not true. Unfortunately, immature survival is very difficult to estimate since birds stayed at sea until their first reproduction.

The number of breeding pairs was highly variable, reaching its lowest value in 1976, due to a low proportion of birds attempting to breed this year. Similarly, the number of chicks, the breeding success, and juvenile survival were also very low in 1976. During this particular year an important sea ice retreat occurred during winter that probably strongly affected the

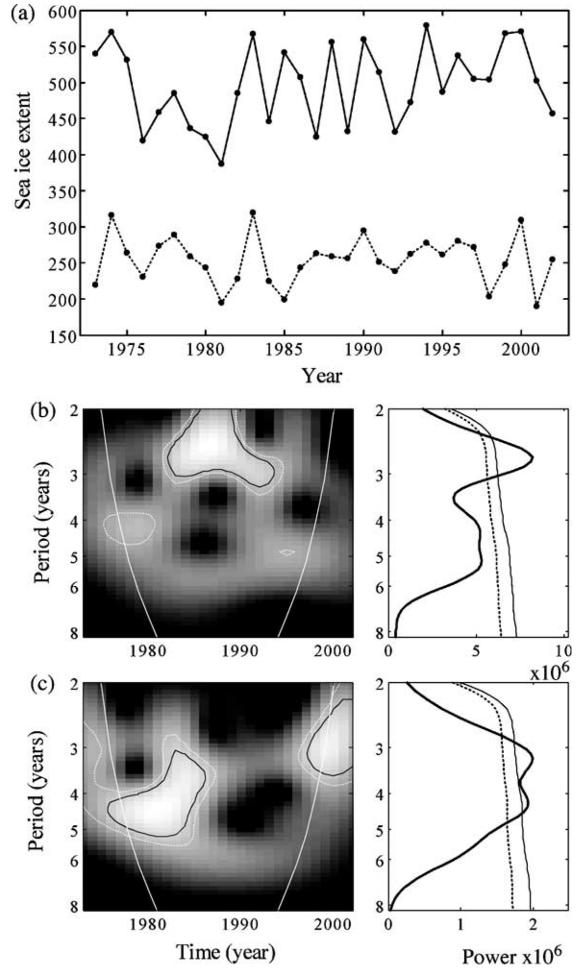


Fig. 6. (a) Annual variation of sea ice extent (SIE) during winter (black line) and during summer (dotted line) for a sector of 130E–150E off the Dumont d'Urville coast, Antarctica between 1973 and 2002. (b) Local wavelet power spectrum (left), and global wavelet power spectrum (right) of SIE during winter 1973 and 2002. (same legend as Fig. 2). (c) Local wavelet power spectrum (left) and global wavelet power spectrum (right) of SIE during summer 1973 and 2002. (same legend as Fig. 2).

abundance of krill (Loeb et al. 1997), and therefore the fecundity rate of fulmars. Heterogeneity in environmental conditions early in life have the potential to induce fitness differences among cohorts. Environmental conditions affecting birth weight and/or early growth may have a considerable impact on later survival and reproductive performance (Lindström 1999, Forchhammer at al. 2001). We showed that, following the unfavourable year in 1976, major decreases in fecundity, juvenile survival rate (equal to zero), and number of immatures occurred. Interestingly, the recruited population (sum of breeders and non breeders) did not show such a reduction, probably because the recruitment of breeders is spread over a long time period, given that the age at first breeding varies between 6 to 15 years of age (Jenouvrier et al. 2003). Therefore, the fluctuations of the population were not directly related to strong cohort effects, but to a strong environmental forcing on the reproductive decisions of birds. Indeed, we showed previously (Jenouvrier et al. 2003) that local recruitment and immigration were related to the number of local breeders, and that local recruitment, the number of local breeders and the proportion of birds attempting to breed were lower when sea ice during summer was low.

In this study, we showed that the population dynamics of breeders from 1973 to 1985 could be explain by the fluctuation of the proportion of breeders linked directly to SIE anomalies during summer. After 1980s the effect of summer SIE anomalies on the proportion of birds attempting to breed did not fully explain population fluctuations, indicating that the relationship between SIE anomalies and the proportion of breeders was more complex. Indeed, SIE during summer showed fewer fluctuations after the 1980s, and the proportion of breeders was probably influenced by other factors or by a mechanism different from our hypothesised threshold effect. Interestingly, the southern fulmar population dynamics exhibited a 3 years periodicity after 1980. Results from the present study indicate that this cyclicity of 3 years is due to 3 years periodic variations of the proportion of breeders. SIE present a well known periodicity between 3–5 years (Zwally et al. 2002), and also showed a change in cyclicity around the 1980s. Winter SIE periodicity was especially marked around 3 years from 1980 to 1995, but no linear correlation was detected between winter SIE and the proportion of breeders, possibly because variability was the result of a combination of confounding factors related to environmental conditions at sea, but also in the colony (Jouventin and Weimerskirch 1991). Brierley et al. (1999) showed that krill density near the Antarctic peninsula, fluctuates according to a cyclical pattern with a main periodicity of 8, 5 and 3 years, which can be broadly described by the fluctuations in environmental parameters. These changes in periodicity may be interpreted in the light of a climatic regime shift that probably occurred during that period in both sub Antarctic (Weimerskirch et al. 2003), and Antarctic ecosystems (Reid and Croxall 2001, Ainley et al. unpubl.). This regime shift resulted in changes in coastal wind strength and air temperature, which in turn affected the sea ice environment, and therefore the demographic parameters and population dynamics of southern fulmars. In fact, recent analysis of ice core data in Antarctic, underlines a change during the 1970s, with an abrupt meridional atmospheric circulation change, bringing more moisture from "warm" subtropical moisture sources to the Antarctic coast (Masson-Delmotte et al. 2003). Our local meteorological data confirm this by showing that the winter SIE decreased steadily from 1975 to 1981, reaching the smallest ice cover in 1981.

Acknowledgements – We greatly acknowledge all the wintering fieldworkers involved in the long term monitoring programs in Terre Adélie since 1963, and Dominique Besson for her constant support and help in the management of the database. This long term study was supported by Expéditions Polaires Françaises, by Institut Paul Emile Victor (Programme IPEV n°109), and by Terres Australes et Antarctiques Françaises.

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