Effects of climate variability on the temporal population dynamics of southern fulmars

STEPHANIE JENOUVRIER, CHRISTOPHE BARBRAUD and HENRI WEIMERSKIRCH

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

Summary

1. Ecological and population processes are affected by large-scale climatic fluctuations, and top predators such as seabirds can provide an integrative view on the consequences of environmental variability on ecosystems. Here, we examine the dynamics of a southern fulmar population in Antarctica over a 39-year period and evaluate the impact of environmental variability on the life history traits of this top predator species.

2. Between 1963 and 2002, the number of breeding pairs fluctuated between seven and 53 in relation to variations in sea ice concentration, and increased overall (annual growth rate: 1·0035). Breeding performance tended to be lower in years with low sea ice concentration. The proportion of birds attempting to breed varied strongly from one year to the next despite the birds were alive, indicating strong environmental forcing on the decision to breed. The number of new local recruits and immigrants was correlated highly with the number of local breeders, and capture probabilities were positively related to the breeding population size. Local recruitment, number of local breeders and proportion of birds attempting to breed were lower when sea ice concentration during summer was low.

3. Adult survival between 1964 and 2002 was on average 0·923 ± 0·006, and decreased during years with high sea surface temperature and low sea ice concentration.

4. Modelled population growth rate, estimated using matrix models, of the population was 0·9728, a difference of 3·6% compared to the observed rate of increase. This discrepancy is due probably to the immigration rate (3 ± 3%).

5. Demographic parameters were affected by sea ice concentration and sea surface temperature anomalies, probably through an impact on krill availability, the main prey of southern fulmars. During warm anomalies, birds skip breeding probably because the food availability was low and limiting for the highly energy demanding reproductive activities.

6. We also emphasize that demographic parameters were very low during the period 1975–80 and showed a higher variability after 1980, which could be interpreted in the context of a regime shift. Our study indicates that the southern fulmar population dynamics may be very susceptible to environmental variability. Further long-lasting warm anomalies are likely to affect negatively their populations.

Key-words: Antarctic environment, demography, matrix population model, seabirds, survival analysis.

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Introduction

The way that environmental variability and the present climatic change will affect populations is a major concern in ecology. Ecological and population processes are affected by large-scale climatic fluctuations (Saether *et al*. 2000; Sillett, Holmes & Sherry 2000; Stenseth *et al*. 2002; Walther *et al*. 2002). Putative effects of El Niño on ecosystems and populations have been studied extensively (Karl *et al*. 1995; Polis *et al*. 1997; Chavez *et al*. 1999; Schreiber 2001), and in the Northern Hemisphere it has been shown that climatic fluctuations associated with the North Atlantic

Correspondence: Stéphanie Jenouvrier, Centre d'Etudes Biologiques de Chizé, F-79360 Villiers en Bois, France. Tel. +335 49 09 61 11; Fax: +335 49 09 65 26; E-mail: jenouvrier@cebc.cnrs.fr

Oscillation had important effects on animal populations (Post & Stenseth 1998; Post *et al.* 1999; Thompson & Ollason 2001). Top predators can provide an integrative view of the ecological consequences of environmental variability because changes in the population processes of top predators reflect the direct, indirect and interlinked influences of biological and physical environmental variables (Furness & Greenwood 1993). Biological changes are likely to have their main effect through modification of food web processes. Even physical changes, while exerting important direct impacts, may have most influence through indirect effects acting on the nature and extent of breeding habitat, on feeding habitat, or on the distribution and abundance of food supplies (Newton 1998). The environmental factors and their interactions are likely to have shaped specific breeding and survival strategies in top predators. 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 (Aebischer 1986; Veit *et al.* 1997; Post *et al.* 1999; Stenseth *et al.* 1999; Reid & Croxall 2001), few have explored simultaneously the influence of the environment variability on all parameters and its consequences on the population size.

In Antarctic ecosystems, environmental conditions can have an important influence on food availability either directly or indirectly (Pakhomov & McQuaid 1996), and thus are likely to influence population dynamics of top predators. Seabirds are long-lived upper trophic-level predators that appear to integrate environmental variability over large spatial and temporal scales (Ainley & Boekelheide 1990; Furness & Greenwood 1993; Smith *et al.* 1999). Sea surface temperature (SST) and/or sea ice extent or concentration have been shown to affect population dynamics of seabirds via an effect on demographic traits (Croxall 1992; Fraser *et al.* 1992; Chastel, Weimerskirch & Jouventin 1993; Guinet *et al.* 1998; Smith *et al.* 1999; Barbraud *et al.* 2000; Barbraud & Weimerskirch 2001). The mechanism proposed was an effect of SST and sea ice anomalies on food availability of seabirds as, for example, reduced sea ice extent and warm SST affect the abundance of krill negatively (Pakhomov & McQuaid 1996; Loeb *et al.* 1997; Brierley *et al.* 2002), and consequently breeding and/or survival parameters. Changes in SST and sea ice have profound and contrasted effects on populations, decrease in sea ice extent having for example positive impact on some species and negative on others (Croxall, Trathan & Murphy 2002).

Long-term studies provide the unique opportunity to observe how changes of the physical environment affect the marine ecosystems at long time-scales. Most of the studies on the impact of the fluctuation of the Antarctic environment on populations focused on penguins (Croxall 1992; Fraser *et al.* 1992; Smith *et al.* 1999; Barbraud & Weimerskirch 2001), and few on flying seabirds. In this study we examine for the first time the dynamics of a southern fulmar (*Fulmarus glacialoides* Smith) population, over a 39-year period, in order to evaluate the impact of the variability of the Antarctic environment on the demographic traits of this population. In the light of previous studies (Croxall 1992; Fraser *et al.* 1992; Chastel *et al.* 1993; Smith *et al.* 1999; Barbraud *et al.* 2000; Barbraud & Weimerskirch 2001; Wilson *et al.* 2001) and from a study on the effect of environmental variability on the dynamics of the closely related northern fulmar *F. glacialis* L. (Thompson & Ollason 2001), we examine whether southern fulmar population dynamics are influenced by the sea surface temperature and sea ice concentration anomalies. Because fulmars forage mainly over Antarctic waters (Ainley, O'connor & Boekelheide 1984; Veit & Hunt 1991; Ainley, Ribic & Spear 1993), we test whether demographic parameters are affected negatively by warm events through a negative effect of SST and sea ice concentration on southern fulmar food resources (mainly krill, Ridoux & Offredo 1989). We also measure recruitment and immigration rate; a parameter that has rarely been measured in previous studies. Finally, we model the population growth rate with Leslie matrix models (Caswell 2001) to understand the intrinsic southern fulmar population dynamics.

Materials and methods

DESCRIPTION OF THE STUDY

Southern fulmars are cliff-nesting seabirds that forage over Antarctic waters, occasionally up to sub-Antarctic waters, and prey mainly on euphausiids, fishes, crustaceans and squids (Ainley *et al.* 1984; Ridoux & 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 m from the Dumont d'Urville station. Breeding pairs were censused towards the end of December, just after egg-laying. Hatched eggs were checked in late January and live chicks were counted just before fledging from mid- to late February. 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 us to read the ring of all breeding birds present on the colony. Southern fulmars are very tame and could be approached easily. The ring could often be read without capturing the incubating bird, but just by gently taking the incubating bird's tarsus and reading the ring.

In order to investigate the relationships between the fluctuations of the environmental and the demographic

parameters we used SST and sea ice concentration (SIC), which were derived from satellite radiometer measurements from January 1981 to March 2002. Data were obtained on a 1° scale and averaged over a chosen sector and were available off the internet on-line information maintained by the International Research Institute for Climate Prediction (http://ingrid.ldgo.columbia.edu/). In our analysis, we used SST obtained from different spatial sectors. Indeed, satellite tracking during summer (H. Weimerskirch *et al.* unpublished data) indicated that southern fulmars from this colony forage during breeding in a sector between 68°–64°S and 136°–152°E. However, because the exact winter distribution of the population from Terre Adélie is unknown, we explored three different spatial sectors extending to sub-Antarctic waters: 70–60°S, 70–50°S, and 70–40°S where southern fulmars are known to occur in winter (Woehler, Hodges & Watts 1990).

BREEDING ANALYSES

The number of breeding pairs was estimated as the number of nests containing an egg. The proportion of birds attempting to breed was calculated as the number of individuals breeding in the colony during a particular year over the number of breeders known to be alive that season. Reproductive parameters were estimated as follows: the overall breeding success as the proportion of eggs producing fledglings, the hatching success as the proportion of hatched eggs and the fledging success as the proportion of hatched eggs producing fledglings. The local recruitment rate was the proportion of marked chicks that returned to breed for their first time; it was measured from 1978 because all chicks were marked from 1963 and most birds have started to breed after the age of 15 years old (see Results). Immigration was estimated from 1978 as those adults found breeding for the first time and not banded as chicks in the colony. Recruitment is the sum of local recruitment and immigration. We also considered the number of local breeders as the birds that breed at least one time at the colony, i.e. the breeding population size minus the number of recruits.

In order to investigate the relationships between the SST and SIC time-series and demographic parameters, we used a randomization procedure to evaluate the statistical significance of Spearman correlation coefficients. We calculated a 95% confidence interval (CI) using a bootstrap estimation method (Hall 1992), and to account for Bonferroni corrections we calculated a 99% CI. Demographic parameters were randomly rearranged to SST and SIC values 10 000 times. The resulting set of coefficients provided an approximate sampling distribution of the correlation coefficient, and consequently 95% (or 99%) approximate CI of the observed value of the correlation coefficient. This procedure allowed us to detect when the correlation coefficient differed significantly from 0 at a 0·05 (0·01) level

(indicating a significant shift toward a positive or a negative relationships) of the 10 000 random rearrangements of the data. Results were found to be significant when the Spearman correlation coefficient was significant at the 0·05 (0·01) level, and when a correlation coefficient value of 0 was not included within the 95% (99%) CI.

SURVIVAL ANALYSES

From 1963 to 1992, the juvenile survival rate was estimated for each cohort as the proportion of chicks that survived until recruitment over the number of marked chicks for each year. To estimate adult survival, we used the developments of the Cormack–Jolly–Seber (CJS) models (Lebreton *et al.* 1992), which provide unbiased estimators of survival probabilities. To test whether different models fitted the data, we used the U-CARE software (Choquet *et al.* 2000). To test the main effects of different factors and their interaction we used the MARK software (White & Burnham 1999).

We removed the first capture to limit heterogeneity amongst individuals, and thus worked with a total of 434 individual capture histories. We fitted the data to the CJS model $\{\phi_t p_t\}$, where both the survival (ϕ) and recapture probability (p) are time-dependent (t). The CJS model fitted the data poorly (test 2 + test 3, $\chi^2_{152} = 291·5$, $P < 0·0001$). However, a large part of this χ^2 statistic was explained by test 2 ($\chi^2_{79} = 185·79$, $P < 0·0001$), whereas test 3 explained a smaller part of total χ^2 ($\chi^2_{73'} = 105·59$, $P = 0·008$). This indicated a 'trap dependence' effect on capture (Pradel 1993). Indeed, the test 2.CT presented a 'trap happiness' effect ($P < 0·001$), indicating that capture probability at year $t + 1$ was higher for individuals captured at year t than for individuals not captured at year t. Consequently, we fitted a model numerically $\{\phi_t p_{t*m}\}$ to account for the trap effect in the capture probabilities. A goodness-of-fit test for this model was calculated considering only the components of test 3 and test 2.CL, but it still fitted the data poorly ($\chi^2_{117} = 190·76$, $P < 0·0001$). To account for this extra binomial variation, we calculated a variance inflation factor $\hat{C}$ (Lebreton *et al.* 1992) as the χ^2 goodness-of-fit statistic of model $\{\phi_t p_{t*m}\}$ over its number of degrees of freedom. The variance inflation factor ($\hat{C} = 1·63$) did exceed 1 (when $\hat{C} = 1$ the model fits data perfectly), indicating either true excess variation and correct model structure or failure of the model used to account for the structure in the data (Lebreton *et al.* 1992). However, $\hat{C}$ remained well below 3, above which the model structure is grossly inadequate (Lebreton *et al.* 1992).

To select the most appropriate model we used the Akaike Information Criterion (AICc) corrected for the effective sample size (Lebreton *et al.* 1992). AICc was calculated as AICc = DEV + $2k$ + $2k(n/(n − k$-1)), where DEV represented the deviance ($−2\ln(L)$), L the likelihood of the model evaluated at maximum likelihood estimates, k the number of separately estimable

parameters in the model and *n* the effective sample size. To account for $\hat{C}$, we used the AICc corrected for extrabinomial variation defined as QAICc = (DEV/$\hat{C}$) + $2k + 2k(n/(n - k - 1))$. The best model was the lowest QAICc model, and we considered that two models were different when the ΔQAICc was greater than 1 or 2 (Anderson & Burnham 1999).

We then modelled the yearly variation in adult survival as a function of covariates that might be relevant to the ecology of fulmars. To assess the effects of these covariates, we compared constant and time-dependent survival models (Gaillard *et al.* 1997; Barbraud *et al.* 2000). The amount of variation accounted for covariates was calculated as [DEV($\phi_{covariate}$)-DEV($\phi_.$)]/[DEV(ϕ_t) – DEV($\phi_.$)], where DEV was the deviance for survival models with covariate, constant and time effects, respectively. This corresponded to the proportion of explained variation and was comparable to a squared correlation coefficient (Schemper 1990). We chose to model the adult annual survival rate as a function of three time periods for both SST and SIC. These time periods corresponded to the chick rearing period (January–March), the non-breeding period (April–October) and the laying and incubation period of the same year (November–December). Survival and recapture probability estimates are given ± 1 SE.

POPULATION MODELLING

To determine whether the estimated demographic parameters accounted for the observed changes in population size, we constructed deterministic and stochastic matrix population models accounting for environmental or demographic stochasticity, or both. In addition, we studied how the fluctuation of demographic traits, such as breeding success and survival, affected the population growth rate.

Modelling was conducted using a post-breeding matrix (Caswell 2001) with the software ULM (Legendre & Clobert 1995). We started setting-up a constant model, which included the mean values of the demographic rates. Factors entering the model were fecundity and mean adult survival estimated with capture–recapture methods. Fecundity was the proportion of breeding individuals multiplied by the average breeding success and the mean survival during the first year at sea. The proportion of breeding individuals was estimated by cumulating the number of individuals breeding for the first time in each class of age, multiplied by the mean proportion of birds attempting to breed. The mean survival during the first year at sea was estimated from the survival from fledging to recruitment, and assuming that the survival of immature birds was similar to that of adults after the first year at sea. The matrix analysis yielded the deterministic population growth rate and the sensitivities of the growth rate to variation in demographic rates.

In order to compare the model's prediction with the observed population dynamics of fulmars, we estimated the observed population growth rate using capture–recapture methodology (Pradel 1996). By 'reading' the capture histories backwards, it is possible to estimate the probability γ that an individual caught at the time *t* + 1 was present in the population at time *t*. Such probabilities, called seniority probabilities (Pradel 1996), can be estimated using similar approaches to those used in survival rate estimations (see Material and methods for survival analysis). The seniority probabilities (γ) represent the resident fraction of the population and can be used to directly estimate population growth rates (Pradel 1996). To estimate the growth rate, we modelled recapture probabilities as time-dependent, as we cannot account for trap dependence, and survival rate and growth as constant.

As a result of a small population size and because we suspected an influence of the environmental fluctuations on population dynamics, we also modelled the effects of demographic and environmental stochasticity, and both together. Demographic stochasticity refers to individual probabilities of death and reproduction in a finite population. Environmental stochasticity refers to exogenous perturbations that, similarly, affect survival and breeding performance (Akçakaya 1991; Burgman, Ferson & Akçakaya 1993). When individual vital rates are affected by stochastic factors, population growth rate is a random variable. Estimates of the stochastic growth rate can be obtained by running 1000 Monte-Carlo simulations during 50 years with ULM (Legendre & Clobert 1995).

Results

POPULATION SIZE

The number of breeding pairs increased during the study (growth rate = 1·0035, *P* = 0·026, R^2 = 12·7%, Fig. 1a), although it fluctuated strongly, especially since the early 1980s. It was particularly low between 1975 and 1980 (Fig. 1a). The fluctuations of the number of chicks produced followed those of the breeding pairs, but the number of chicks produced did not increase significantly during the study (*P* = 0·124, Fig. 1a). The number of breeding pairs was correlated positively with SIC observed during January and February (Fig. 2a).

BREEDING SUCCESS

The mean breeding, hatching and fledging successes were, respectively, 70 ± 14%, 76 ± 13%, and 92 ± 9%. The breeding and hatching successes showed high interannual variability (Fig. 1b). The fledging success was less variable and higher before 1981 (96 ± 8%) than after (89 ± 9%; Mann–Whitney *U*-test *P* = 0·006; Fig. 1b). No reproductive parameter was related to SST or SIC (Fig. 2), although fledging success tended
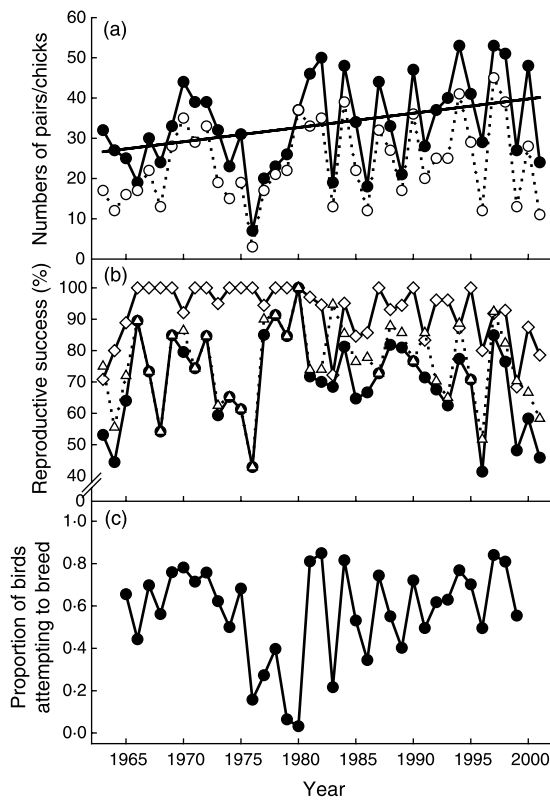
Fig. 1. Annual variation of (a) the number of breeding pairs (filled circle) and fledged chicks (open circle); (b) breeding success (filled circle), hatching success (open triangle) and fledging success (open diamond); and (c) the proportion of birds attempting to breed, for southern fulmars at Dumont d'Urville, Terre Adélie, Antarctica, between 1963 and 2002. The number of breeding pairs increased significantly since 1963 ($P = 0.26$, slope = 0.335 ± 0.15, $R^2 = 35.6\%$).

Fig. 2. Variation in Spearman correlation coefficients calculated between SIC from April (end of the breeding season) to March of the following year and (a) the number of breeding pairs, (b) the overall breeding success, (c) the hatching success and (d) the fledging success of southern fulmars at Dumont d'Urville since 1982. Upper and lower limits of the 99% CI are indicated by the dotted lines. Statistical significance of the Spearman correlation coefficient at $P = 0.01$ level is indicated by dashed lines. Results were regarded as significant when the correlation coefficient was significant at the 0.01 level and when correlation coefficients of 0 were not included within the 99% CI (Bonferroni corrections).

to be related positively to the SIC during the rearing period (Fig. 2d). There was no correlation between the breeding success and the number of breeding pairs (Pearson's correlation coefficient $r = 0.33$, $P = 0.23$).

PROPORTION OF BIRDS ATTEMPTING TO BREED

The proportion of birds alive in the breeding population during a particular year and attempting to breed averaged 0.57 ± 0.22. It fluctuated strongly between years (especially since the early 1980s), and was particularly low between 1975 and 1980 (Fig. 1c). The proportion of birds attempting to breed was correlated positively with SIC during summer (correlation coefficient = 0.4, $P < 0.05$, bootstrap method, see Material and methods).

RECRUITMENT AND IMMIGRATION

A total of 297 adults and 915 chicks were marked from 1963 to 2001. The juvenile survival rate showed a high year-to-year variation (Fig. 3a) and was on average $26 \pm 15\%$. It was particularly low during the mid-1970s
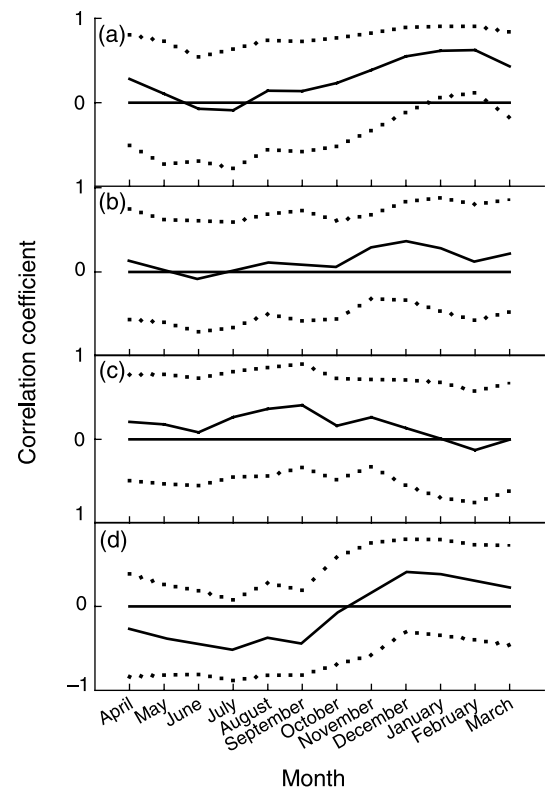
and mid-1980s. No significant relationship was found between the juvenile survival rate and SST or SIC.

Most breeders and non-breeders came back for the first time at the colony around 7 years of age (modal values for age at first return and first breeding are 7 years; Fig. 4). The mean age of first return to the colony was 8 ± 3 years ($n = 184$), and was 11 ± 4 years ($n = 159$) for the first reproductive attempt.

The number of new local recruits fluctuated strongly between years (Fig. 5b), and averaged $11 \pm 11\%$ of the breeding population. The number of local recruits was correlated with the number of breeders at the colony (correlation coefficient = 0.75, $P < 0.05$, bootstrap method, Fig. 5), and related positively to SIC during summer (correlation coefficient = 0.49, $P < 0.05$, bootstrap method).

The number of birds recorded for the first time and not banded as chicks (called hereafter immigrants) did exhibit a high year-to-year variation (Fig. 5c). The mean proportion of immigrants that bred was $3 \pm 3\%$ of the breeding population. The number of immigrants was correlated both with the number of local breeders
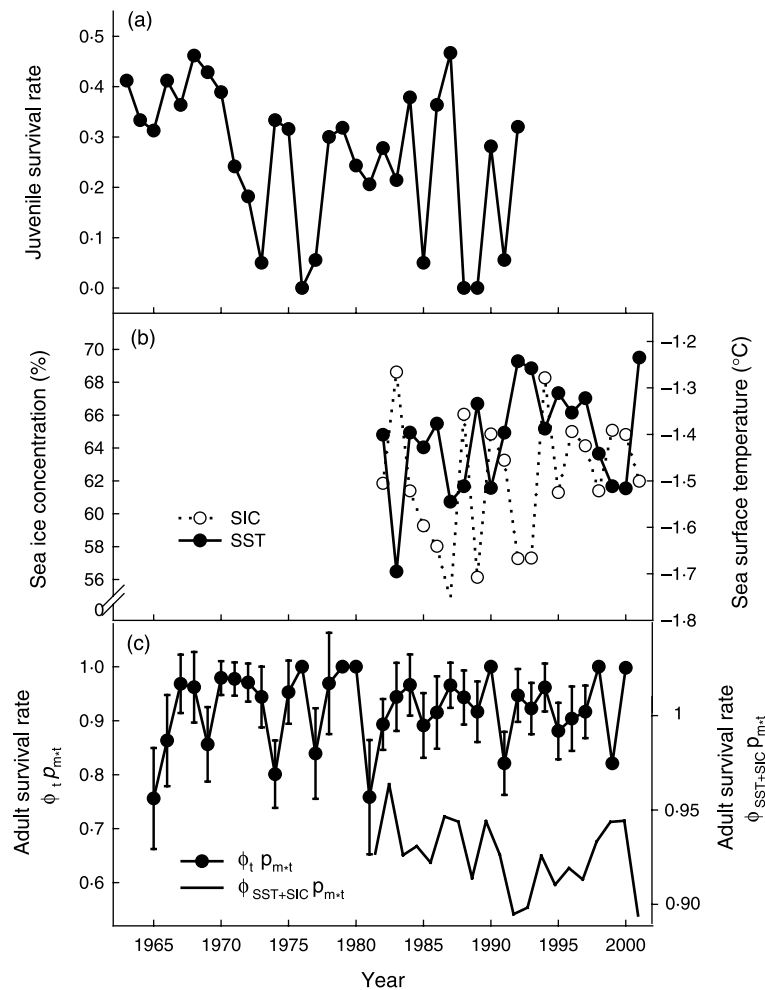
Fig. 3. Annual variations in (a) juvenile survival rate of southern fulmars at Dumont d'Urville; (b) sea surface temperature (SST, filled circle) and sea ice concentration (SIC, open circle) during winter between 70°S and 60°S; (c) adult survival rate of southern fulmars at Dumont d'Urville. Adult survival was estimated from the time and trap dependent model ($\phi_t p_{m*t}$), and constrained by SST and SIC ($\phi_{SST+SIC} p_{m*t}$). Because trap-dependent models have severe identifiability problems (Pradel 1993), no estimate from the time and trap-dependent model is available for 2001.
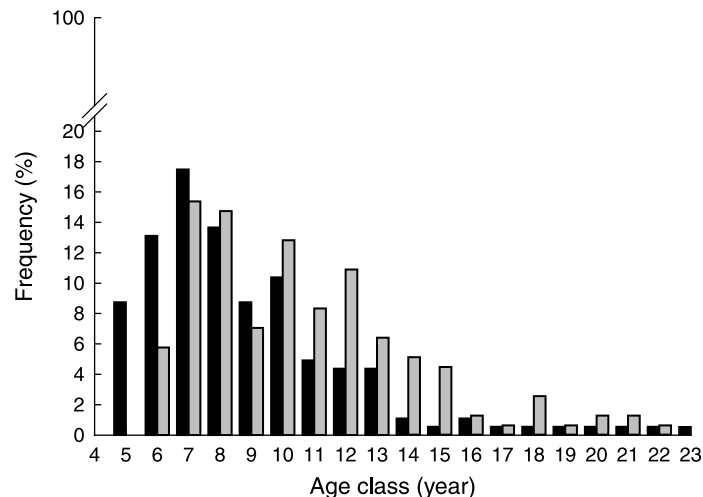

Fig. 4. Proportion of adults marked as chicks that came back for the first time to the colony (black bars) or that were breeding for the first time at the colony (grey bars) as a function of age.

at the colony (Fig. 5, correlation coefficient = 0·43, $P < 0·05$, bootstrap method) and with the number of local recruits (correlation coefficient = 0·65, $P < 0·05$, bootstrap method, Fig. 5).

The number of local breeders was related positively to SIC during summer (correlation coefficient = 0·57, $P < 0·05$, bootstrap method) emphasizing the relation between the population size and the SIC during summer.
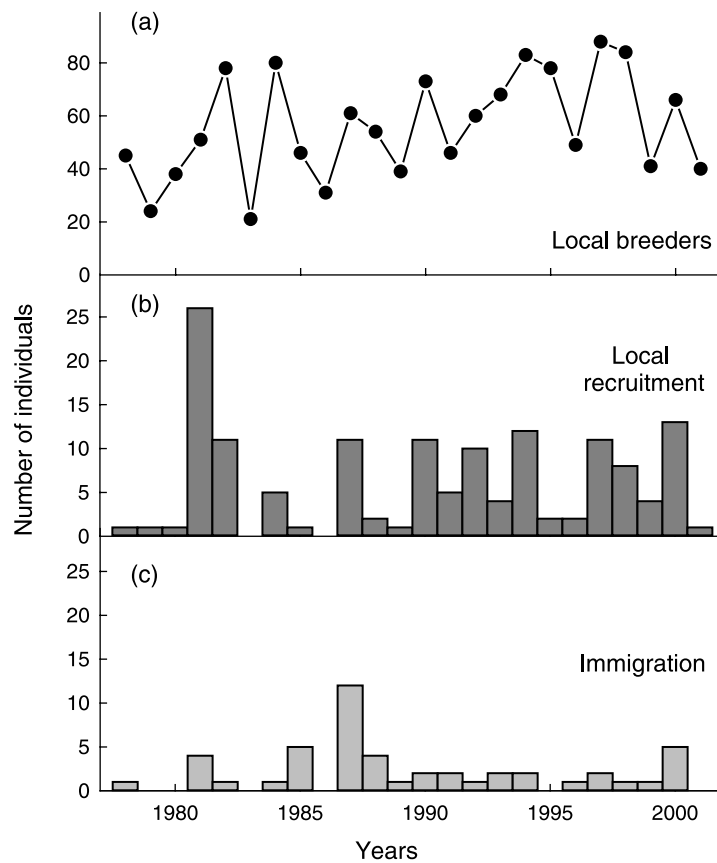
Fig. 5. Annual variation of (a) the number of local breeders, which represent the birds that bred at least once before; (b) the number of local recruits; and (c) the number of immigrants at the colony of southern fulmars at Dumont d'Urville. The sum of local recruits and of immigrants represents the recruitment. The number of local breeders, local recruits and immigrants is calculated from 1978 as more than 90% of the birds at 15 years old have bred at least once (see Fig. 4).

Table 1. Modelling capture and survival probabilities for adult southern fulmars at Dumont d'Urville between 1965 and 2000. The model selected (lowest Akaike Information Criterion, QAICc) is in bold type and k refers to the number of parameters estimated

Biological hypothesis	Model	QAICc	k	QDeviance
Additive trap effect on capture probabilities	$\{\phi_t p_{m*t}\}$	3444·941	108	1302·649
	vs.			
	$\{\phi_t p_{m+t}\}$	3538·920	68	1482·884
Constant trap effect on capture probabilities	$\{\phi_t p_{m*t}\}$	3444·941	108	1302·649
	vs.			
	$\{\phi_t p_m\}$	3748·370	39	1753·041
Time dependence in survival	$\{\phi_t p_{m*t}\}$	3444·941	108	1302·649
	vs.			
	$\{\phi \cdot p_{m*t}\}$	**3401·024**	**74**	**1332·239**

ADULT SURVIVAL

Capture probabilities were time-dependent (Table 1) and correlated with the number of breeding pairs [slope = 0·06, 95% CI = (0·05; 0·07), R^2 = 44%], indicating that birds do not breed every year at the colony despite being alive. Capture probabilities were particularly low from 1976 to 1981 (1965–75: 0·76 ± 0·12 and 0·58 ± 0·16; 1976–81: 0·22 ± 0·16 and 0·21 ± 0·29; 1982–2000: 0·65 ± 0·21 and 0·49 ± 0·16, for the first and second age classes, respectively; Kruskal–Wallis

test: $P = 0·001$ and $P = 0·023$ for the first and second age classes, respectively; Fig. 6).

Model $\{\phi_t p_{t*m}\}$ was used for modelling survival probabilities (Table 1). The adult annual survival rate showed little year-to-year variation from 1965 to 2000 (Fig. 3c), and the model $\{\phi \cdot p_{m*t}\}$ had a lower QAICc than model $\{\phi \cdot p_{m+t}\}$ (Table 1). The survival estimate for the model $\{\phi_t p_{t*m}\}$ was $\phi = 0·923 ± 0·006$. There was no effect of the number of breeding pairs on survival [slope = $-0·0005 ± 0·01$, 95% CI = ($-0·02$; $0·02$)].
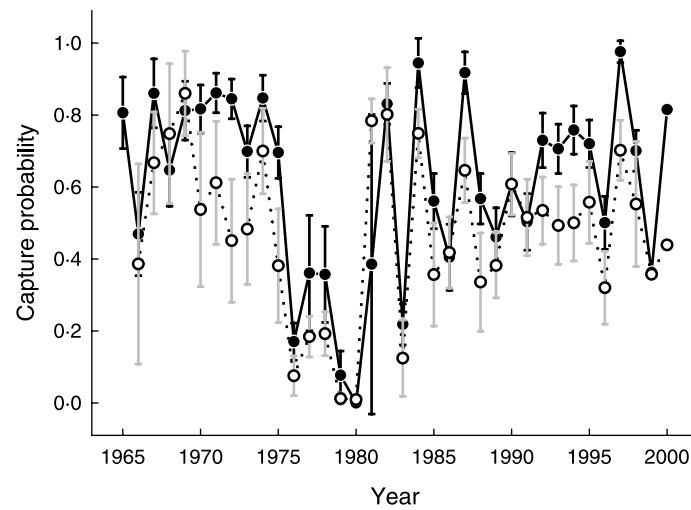
Fig. 6. Annual variation of the capture probabilities for the first age class (filled circle) and the second age-class (open circle) estimated from the time and trap-dependent model ($\phi_t p_{m*t}$). Because trap-dependent models have severe identifiability problems (Pradel 1993), no estimate is available for 2001.

Table 2. Modelling time dependence in fulmar survival. The model selected (lowest QAICc) is in bold type. SE indicates the standard error of the slope estimate. R^2 refers to the proportion of variance explained by the model. Models with one covariate are sorted by increasing QAICc

Type	Covariate	slope	SE	QAICc	R^2
Time-dependent survival					
One covariate	$\phi(t)$	–	–	2186·64	1
SST	Winter$_{70-60}$	−2·4581	1·6499	2160·37	0·2402
SIC	Winter	0·0123	0·0431	2160·67	0·0079
SIC	Chick rearing	−0·0239	0·0370	2162·42	0·0428
SST	Chick rearing	−0·4650	0·7617	2162·50	0·0351
SST	Winter$_{70-50}$	−0·7597	1·4215	2162·55	0·0304
SST	Winter$_{70-40}$	0·3389	0·9314	2162·73	0·0126
SST	Incubation	0·2109	1·1555	2162·83	0·0033
SIC	Incubation	0·0026	0·0269	2162·86	0·0009
Two covariates					
SST	**Winter**	**−2·4482**	**1·6610**	**2160·36**	**0·2405**
	+				
SIC	**Winter**	**0·0025**	**0·0459**		
Constant survival	$\phi(.)$	–	–	2160·75	0

Among the eight covariates, SST between 70° and 60°S during winter accounted for 24% of the yearly variation in survival (Table 2). Adult fulmars survived better when sea surface temperatures were lower. The proportion of variation accounted for by SIC was very low (Table 2). A model with both covariates SST and SIC during winter since 1981 had the lowest QAICc (Table 2), indicating that annual survival was influenced by both SST and SIC (Fig. 3b,c). We noted that the SST for the other sectors (70°−50°S and 70°−40°S) had a higher QAICc and explained a very small part of the yearly variation observed (Table 2). The environmental parameters during the reproductive period did not affect the annual adult survival rate (Table 2).

POPULATION MODELLING

We constructed a matrix population model with 15 age classes (the minimum age at first breeding being 6 years and the age at which all birds were recruited being 15 years), without senescence. The parameters used for modelling population dynamics are given in Table 3. The deterministic model predicted a long-term annual geometric growth rate of 0·9789 (Table 4), indicating that the population would be declining at an average rate of 2·11% per year. The analysis of growth rate sensitivities and elasticities to demographic rates showed that the growth rate is mainly sensitive to adult survival (elasticity 96·18%). Survival during the first year at sea, breeding success and proportion of breeders had little influence on the population growth rate (elasticity 3·8%). Therefore, fecundity has very low elasticity in the matrix (Table 3).

When modelling demographic or environmental stochasticity, or both, mean growth rate was lower than the one predicted by the deterministic model (Table 4). The estimated growth rate by the recapture model was 1·009 ± 0·002, 95% CI = (1·004; 1·014), indicating an

Table 3. Parameters entered in the matrix population models for southern fulmars at Dumont d'Urville, and elasticities of growth rate to changes in the matrix entries. We used post-breeding Leslie matrix for a female population

Age class	Adult survival (%)	Survival at the first year at sea (%)	Breeding success (%)	Proportion of birds attempting to breed (%)	Cumulative frequencies of first breeding in each age class (%)	Fecundity (%)	Fecundity elasticities (%)	Survival elasticities (%)
1	92·3	45	70	60	0	0	0	3·818
2	92·3	45	70	60	0	0	0	3·818
3	92·3	45	70	60	0	0	0	3·818
4	92·3	45	70	60	0	0	0	3·818
5	92·3	45	70	60	0	0	0	3·818
6	92·3	45	70	60	9	0·85	0·247	3·793
7	92·3	45	70	60	24	2·27	0·622	3·731
8	92·3	45	70	60	38	3·59	0·928	3·632
9	92·3	45	70	60	45	4·25	1·036	3·534
10	92·3	45	70	60	57	5·39	1·237	3·411
11	92·3	45	70	60	65	6·14	1·330	3·278
12	92·3	45	70	60	76	7·18	1·467	3·131
13	92·3	45	70	60	82	7·75	1·492	2·982
14	92·3	45	70	60	87	8·22	1·493	2·833
15+	92·3	45	70	60	100	9·45	2·833	4·676

Table 4. Modelled growth rates of the population of southern fulmars at Dumont d'Urville. We modelled the effect of demographic and environmental stochasticity (1000 Monte Carlo simulations). SE indicates the standard error of the mean growth rate

Model	Growth rate	Mean growth rate	SE
Constant	0·9789	–	–
Demographic stochasticity	–	0·9761	0·0002
Environmental stochasticity	–	0·9752	0·0003
Demographic and environmental stochasticity	–	0·9728	0·0048

estimated increase of 0·9% per year. This contrasted with the matrix population model estimate accounting for demographic and environmental stochasticity, which predicted a decline of the fulmar population at an average rate of 2·72% per year.

Discussion

Changes in population size reflect the sum of various factors, which may operate more or less independently and react on different time-scales. The fluctuations of the breeding population reflect the interactions between environmental variability and the trade-off between reproductive effort and survival (Stearns 1992). The data presented in this study are the only available data for Antarctic seabirds, and the few data for birds, that provide a long-term record of all demographic parameters and population size. The results of the study showed a very high variability over time in population size that is influenced mainly by adult survival, but also to the tendency of fulmars to skip breeding during some years, both parameters being related to environmental factors.

Climatic oscillations can drive the interannual variation of some populations (Barbraud & Weimerskirch 2001; Schreiber 2001; Stenseth *et al.* 2002). Thompson & Ollason (2001) showed recently that the North

Atlantic Oscillation affects the northern fulmar population dynamics. The modelling of the southern fulmar population dynamics showed that growth rate is influenced mainly by adult survival, as demonstrated previously for long-lived species (Lebreton & Clobert 1991). Moreover, adult mortality increased in years with high winter SST and low winter SIC. SST and SIC during the breeding season had less impact on the adult survival, which is consistent with the prediction that adult survival of birds is probably influenced mainly by winter conditions (Fretwell 1972; Newton 1998). The breeding, hatching and fledging successes showed a high year-to-year variability, especially since 1980 for fledging success. However, these breeding parameters were not related to SST or SIC, possibly because variability was the result of a combination of confounding factors related to environmental conditions at sea but also in the colony (Jouventin & Weimerskirch 1991). In addition, because the population is small, the stochastic processes may have masked any relationship with environmental parameters. No density dependence was detected, probably because of the small population size and the high availability of nesting sites.

Interestingly, the capture probability of southern fulmars was correlated positively with the breeding population size, indicating that birds do not reproduce

every year. In other terms, the probability to recapture an individual bird in a given year was related closely to the probability that this individual bred that year, indicating that individuals that skipped breeding stayed at sea. Local recruitment and immigration, which represented recruitment, were related to the number of local breeders, pointing to a strong environmental forcing on the reproductive decision of birds. Indeed, local recruitment, number of local breeders and proportion of birds attempting to breed were lower when SIC during summer was low.

The modelling of the fulmar population, which accounted for demographic or environmental stochasticity (or both), predicted a decline in the population at an average rate of 2–3% per year, although we estimated with capture–recapture methods an increase of 0·9% per year since 1963. The observed discrepancy between modelled and estimated population growth rates is explained by the recruitment of birds not born in the colony. Indeed, another population was discovered in the vicinity of Dumont d'Urville (250 km) (Barbraud *et al.* 1999). The emigration rate from the colony of Dumont d'Urville is probably very low, as individuals marked in Dumont D'Urville were not found in these more distant colonies (C. Barbraud & K. Delord unpublished data). Our study is the first to provide evidence that immigration plays a significant role in population dynamics of Antarctic seabirds, with immigrants representing on average 3% of the breeders each year. Although immigration is low, it can nevertheless play a significant role in the population dynamics of seabird populations (Inchausti & Weimerskirch 2002).

Sea ice variability during winter seems to affect the population dynamics of several Antarctic birds. The lack of winter sea ice has negative effects on the size of Adélie penguin (*Pygoscelis adeliae* Hombron and Jacquinot) populations, and the loss of sea ice in the northern Bellingshausen Sea has led to the gradual disappearance of that species on the western side of the northern Antarctic Peninsula (Fraser *et al.* 1992; Trathan, Croxall & Murphy 1996; Fraser & Patterson 1997). In addition, the population of emperor penguins (*Aptenodytes forsteri* Gray) has declined by 50% during the late 1970s because of a decrease in adult survival due to warm SST and decrease in sea ice extent (Barbraud & Weimerskirch 2001). On the other hand, adult survival of snow petrels was influenced positively by the latitudinal extent of sea ice during winter (Barbraud *et al.* 2000). Therefore, species of the Antarctic community of seabirds show contrasted responses to the fluctuations of environmental variability, emphasizing the need to better understand their role in the Antarctic ecosystem (Croxall *et al.* 2002).

Several authors have emphasized the important role of krill in the Antarctic food web to explain the link between the role of sea ice and the population dynamics of top predators (Croxall 1992; Tynan 1998; Nicol *et al.* 2000; Reid & Croxall 2001), and particularly seabirds (Fraser *et al.* 1992; Smith *et al.* 1999; Barbraud

et al. 2000; Barbraud & Weimerskirch 2001). Loeb *et al.* (1997) showed that low krill abundance was associated with less winter sea ice cover. Southern fulmars feed mainly on Antarctic krill (*Euphausia superba* Dana) in Terre Adélie (Ridoux & Offredo 1989). Recent satellite tracking during summer in Terre Adélie indicates that fulmars feed in light pack ice (40–60% of ice concentration) (H. Weimerskirch *et al.* unpublished data), where the density of krill is very high (Brierley *et al.* 2002). Therefore, in years with high SST and low SIC, fulmars may have difficulties in finding food, which could increase mortality during winter and decrease the proportion of birds attempting to breed during summer.

In this study, the lowest number of breeding pairs was observed during the period 1975–80. Interestingly, several studies showed the same drop in the number of breeding pairs for the emperor penguin (Barbraud & Weimerskirch 2001), the Adélie penguin (Jouventin & Weimerskirch 1991) and the snow petrel *Pagodroma nivea* Forster (Chastel *et al.* 1993) in Terre Adélie. In addition, the number of breeding pairs of southern fulmars seems to be more variable after this period. This may reinforce the hypothesis of a regime shift that may have occurred during the mid-seventies in the Antarctic ecosystem as suggested by Weimerskirch *et al.* (2003) and D. Ainley *et al.* (unpublished data). This long-term data set, unbiased by economic pressures (fishing or whaling records), potentially provides a proxy for environmental conditions in the Southern Ocean since 1960, well before the launching of satellites that now provide climate data. The frequency and intensity of interannual variation in SST are expected to increase with global warming (IPCC 2001). We showed that southern fulmars may be very susceptible to environmental variability, and that further long-lasting warm anomalies are likely to affect negatively their populations.

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References

Aebischer, N.J. (1986) Retrospective investigation of an ecological disaster in the shag, *Phalacrocorax aristotelis*: a general method based on long-term marking. *Journal of Animal Ecology*, **55**, 613–629.

Ainley, D.G. & Boekelheide, R.J. (1990) *Seabirds of the Farallon Islands. Ecology, Dynamics and Structure of an Upwelling System Community*. Stanford University Press, Stanford.

Ainley, D.G., O'connor, E.F. & Boekelheide, R.J. (1984) The marine ecology of birds in the Ross Sea, Antarctica. *Ornithological Monographs*, **32**, 1–97.

Ainley, D.G., Ribic, C.A. & Spear, L.B. (1993) Species–habitat relationships among antarctic seabirds: a function of physiological of biological factors? *Condor*, **95**, 806–816.

Akçakaya, H.R. (1991) A method for simulating demographic stochasticity. *Ecological Modelling*, **54**, 133–136.

Anderson, D.R. & Burnham, K.P. (1999) General strategies for the analysis of ringing data. *Bird Study*, **46**, 261–270.

Barbraud, C., Delord, K.C., Micol, T. & Jouventin, P. (1999) First census of breeding seabirds between Cap Bienvenue (Terre Adélie) and Moyes Islands (King George V Land), Antarctica: new records for Antarctic seabird populations. *Polar Biology*, **21**, 146–150.

Barbraud, C. & Weimerskirch, H. (2001) Emperor penguins and climate change. *Nature*, **411**, 183–186.

Barbraud, C., Weimerskirch, H., Guinet, C. & Jouventin, P. (2000) Effect of sea-ice extent on adult survival of an Antarctic top predator: the snow petrel *Pagodroma nivea*. *Oecologia*, **125**, 483–488.

Brierley, A.S., Fernandes, P.G., Brandon, M.A., Armstrong, F., Millard, N.W., McPhail, S.D., Stevenson, P., Pebody, M., Perrett, J., Squires, M., Bone, D.G. & Griffiths, A.M. (2002) Antarctic krill under sea ice: elevated abundance in a narrow band just south of ice edge. *Science*, **295**, 1890–1892.

Burgman, M.A., Ferson, S. & Akçakaya, H.R. (1993) *Risk Assessment in Conservation Biology*. Chapman & Hall, London.

Caswell, H. (2001) *Matrix Population Models*, 2nd edn. Sinauer, Sunderland, MA.

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.

Chavez, F.P., Strutton, P.G., Friederich, C.E., Feely, R.A., Feldman, G.C., Foley, D.G. & McPhaden, M.J. (1999) Biological and chemical response of the equatorial Pacific ocean to the 1997–98 El Niño. *Science*, **286**, 2126–2131.

Choquet, R., Reboulet, A.M., Pradel, R. & Lebreton, J.-D. (2000) *U-Care (Utilities – Capture – REcapture) user's guide*. http://www.cefe.cnrs-mop.fr/wwwbiom/default.htm.

Croxall, J.P. (1992) Southern Ocean environmental changes: effects on seabird, seal and whale populations. *Philosophical Transactions of the Royal Society of London B*, **338**, 319–328.

Croxall, J.P., Trathan, P.N. & Murphy, E.J. (2002) Environmental change and Antarctic seabirds populations. *Science*, **297**, 1510–1514.

Fraser, B. & Patterson, D.L. (1997) Human disturbance and long-term changes in Adélie penguin populations: a natural experiment at Palmer Station, Antarctic Peninsula. *Antarctic Communities: Species, Structure and Survival* (eds B. Battaglia, J. Valencia & D.W.H. Walton), pp. 445–452. Cambridge University Press, Cambridge.

Fraser, W.R., Trivelpiece, W.Z., Ainley, D.G. & Trivelpiece, S.G. (1992) Increase in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biology*, **11**, 525–531.

Fretwell, S.D. (1972) *Populations in a Seasonal Environment*. Princeton University Press, Princeton, New Jersey.

Furness, R.W. & Greenwood, J.J.D. (1993) *Birds as Monitor of Environmental Change*. Chapman & Hall, London.

Gaillard, J.M., Boutin, J.M., Delorme, D., Van Laere, G., Duncan, P. & Lebreton, J.-D. (1997) Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia*, **112**, 502–513.

Guinet, C., Chastel, O., Koudil, M., Durbec, J.-P. & Jouventin, P. (1998) Effects of warm sea-surface temperature anomalies on the blue petrel at the Kerguelen Islands. *Proceedings of the Royal Society of London B*, **265**, 1001–1006.

Hall, P. (1992) *The Bootstrap and Edgewort Expannon*. Springer Verlag, Berlin.

Inchausti, P. & Weimerskirch, H. (2002) Dispersal and meta-population dynamics of an oceanic seabird, the wandering albatros, and its consequences for its response to long-line fisheries. *Journal of Animal Ecology*, **71**, 771–779.

IPCC (2001) Climate change 2001: synthesis report. A Contribution of Working Groups I, II, and III to the Third Assessment Report of the IPCC (ed. R.T. Watson & Core Writing Team). Cambridge University Press, Cambridge.

Jouventin, P. & Weimerskirch, H. (1991) Changes in the population size and demography of southern seabirds: management implications. *Bird Population Studies, Relevance to Conservation and Management* (eds C.M. Perrins, J.-D. Lebreton & G.J.M. Hirons), pp. 297–314. Oxford University Press, Oxford.

Karl, D.M., Letellier, R., Hebel, D., Tupas, L., Dore, J., Christian, J. & Winn, C. (1995) Ecosystem changes in the North Pacific subtropical gyre attributed to the 19991–1992 El Niño. *Nature*, **373**, 230–234.

Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.

Lebreton, J.-D. & Clobert, J. (1991) Birds population dynamics, management, and conservation: the role of mathematical modelling. *Bird Population Studies: Relevance to Conservation and Management* (eds C.M. Perrins, J.-D. Lebreton & G.J.M. Hirons), pp. 105–125. Oxford University Press, Oxford.

Legendre, S. & Clobert, J. (1995) ULM, a software for conservation and evolutionary biologists. *Journal of Applied Statistics*, **22**, 817–834.

Loeb, V.J., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W. & Trivelpiece, S.G. (1997) Effects of sea-ice extend and krill or salp dominance on the Antarctic food web. *Nature*, **387**, 897–900.

Newton, I. (1998) *Population Limitation in Birds*. Academic Press, San Diego.

Nicol, S., Pauly, T., Bindoff, N.L., Wright, S., Thiele, D., Hosie, G.W., Strutton, P.G. & Woehler, E. (2000) Ocean circulation off East Antarctica affects ecosystem structure and sea-ice extent. *Nature*, **406**, 504–507.

Pakhomov, E.A. & McQuaid, C.D. (1996) Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biology*, **16**, 271–286.

Polis, G.A., Hurd, S.D., Jackson, C.T. & Piñero, F.S. (1997) El Niño effects on the dynamics and control of an island ecosystem in the gulf of California. *Ecology*, **78**, 1884–1897.

Post, E., Peterson, R.O., Stenseth, N.C. & McLaren, B.E. (1999) Ecosystem consequences of wolf behavioural response to climate. *Nature*, **401**, 905–907.

Post, E. & Stenseth, N.C. (1998) Large-scale variability and population dynamics of moose and white-tailed deer. *Journal of Animal Ecology*, **67**, 537–543.

Pradel, R. (1993) Flexibility in survival analysis from recapture data: handling trap-dependence. *Marked Individuals in the Study of Bird Population* (eds J.-D. Lebreton & P.M. North), pp. 29–37. Birkhauser. Verlag Basel, Switzerland.

Pradel, R. (1996) Utilization of capture–mark–recapture for the study of the recruitment and population growth rate. *Biometrics*, **52**, 703–709.

Reid, K. & Croxall, J.P. (2001) Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proceedings of the Royal Society of London B*, **268**, 377–384.

Ridoux, V. & Offredo, C. (1989) The diets of five summer breeding seabirds in Adelie Land, Antarctica. *Polar Biology*, **9**, 137–145.

Saether, B.E., Tufto, J., Engen, S., Jerstad, K., Rostad, O.W. & Skatan, J.E. (2000) Population dynamical consequences of climate change for a small temperate songbird. *Science*, **287**, 854–856.

Schemper, M. (1990) The explained variation in proportional hazards regression. *Biometrika*, **77**, 216–218.

Schreiber, E.A. (2001) Climate and weather effects on seabirds. *Biology of Marine Birds* (eds E.A. Schreiber & J. Burger), pp. 179–207. CRC Press, Boca Raton, FL.

Sillett, T.S., Holmes, R.T. & Sherry, T.W. (2000) Impacts of global climate cycle on population dynamics of a migratory songbird. *Science*, **288**, 2040–2042.

Smith, R.C., Ainley, D., Baker, K., Domack, E., Emslie, S., Fraser, B., Kenett, J., Leventer, A., Mosley-Thompson, E., Stammerjohn, S. & Vernet, M. (1999) Marine ecosystem sensitivity to climate change. *Bioscience*, **49**, 393–404.

Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.

Stenseth, N.C., Chan, K.S., Tong, H., Boonstra, R., Boutin, S., Krebs, C.J., Post, E., O'Donoghue, M. & Yoccoz, N.G. (1999) Common dynamic structure of Canada lynx population within three climatic regions. *Science*, **285**, 1075–1073.

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurell, J.W., Chan, K.S. & Lima, M. (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292–1295.

Thompson, P.M. & Ollason, J.C. (2001) Lagged effects of ocean climate change on fulmar population dynamics. *Nature*, **413**, 417–420.

Trathan, P.N., Croxall, J.P. & Murphy, E.J. (1996) Dynamics of Antarctic penguin populations in relation to inter-annual variability in sea ice distribution. *Polar Biology*, **16**, 321–330.

Tynan, C.T. (1998) Ecological importance of the southern boundary of the Antarctic Circumpolar Current. *Nature*, **392**, 708–710.

Veit, R.R. & Hunt, G.L. Jr (1991) Broadscale density and aggregation of pelagic birds from a circumnavigational survey of the antarctic ocean. *Auk*, **108**, 190–800.

Veit, R.R., McGowan, J.A., Ainley, D.G., Wahls, T.R. & Pyle, P. (1997) Apex marine predator declines ninety percent in association with changing oceanic climate. *Global Change Biology*, **2**, 23–28.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Weimerskirch, H., Inchausti, P., Guinet, C. & Barbraud, C. (in press) Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science*, in press.

White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46** (Suppl.), 120–138.

Wilson, P.R., Ainley, D.G., Nur, N., Jacobs, S.S., Barton, K.J., Ballard, J.C. & Comiso, J.C. (2001) Adélie penguin population change in the pacific sector of Antarctica: relation to sea-ice extend and the Antarctic Circumpolar Current. *Marine Ecology Progress Series*, **213**, 301–309.

Woehler, E.J., Hodges, C.L. & Watts, D.J. (1990) *ANARE Research Notes 77: an Atlas of the Pelagic Distribution and Abundance of Seabirds in the Southern Indian Ocean, 1981–90*. Australian Antarctic Division, Kingston, Tasmania.