LONG-TERM CONTRASTED RESPONSES TO CLIMATE OF TWO ANTARCTIC SEABIRD SPECIES

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Abstract. We examined the population dynamics of two Antarctic seabirds and the influence of environmental variability over a 40-year period by coupling the estimation of demographic parameters, based on capture–recapture data, and modeling, using Leslie matrix population models. We demonstrated that the demographic parameters showing the greatest contribution to the variance of population growth rate were adult survival for both species. Breeding success showed the same contribution as adult survival for Emperor Penguins, whereas the proportion of breeders had the next stronger contribution for Snow Petrels.

The sensitivity of population growth rate to adult survival was very high and the adult survival variability was weak for both species. Snow Petrel males survived better than females, whereas Emperor Penguin males had lower survival than females. These differences may be explained by the different investment in breeding. Emperor Penguin adult survival was negatively affected by air temperature during summer and winter for both sexes; male survival was negatively affected by sea ice concentration during summer, autumn, and winter. On the other hand, there was no effect of environmental covariates on Snow Petrel adult survival. The Emperor Penguin population has declined by 50% because of a decrease in adult survival related to a warming event during a regime shift in the late 1970s, whereas Snow Petrels showed their lowest numbers in 1976, but were able to skip reproduction.

Indeed, the retrospective analysis of projection population matrix entries indicated that breeding abstention played a critical role in the population dynamics of Snow Petrels but not Emperor Penguins. Snow Petrels did not breed either when air temperature decreased during spring (probably reducing nest attendance and laying) or when sea ice decreased during autumn (reducing food availability).

Emperor Penguin and Snow Petrel breeding population sizes were positively influenced by sea ice through its effect on adult survival for Emperor Penguins and on the proportion of breeders for Snow Petrels. Therefore, we hypothesize that the population sizes of the two species could be negatively affected by reduced sea ice in the context of global warming.

Key words: Antarctic seabirds; Aptenodytes forsteri; *capture–recapture survival analysis; climate variability; demography; Emperor Penguin; matrix models;* Pagodroma nivea; *population dynamics; prospective and retrospective analysis; Snow Petrel.*

INTRODUCTION

Climate changes have already affected species physiology, phenology, abundance, and distribution, and thus the structure and composition of communities (Hughes 2000). One of the mechanisms by which climate warming may induce changes in ecosystems is by disrupting the evolved life history strategies of key component species (Rhodes and Odum 1996). Studying the effect of environmental fluctuations on population dynamics of sympatrically breeding species is crucial to understanding their contrasting demographic responses to climate change, and to predicting the effect of global warming at the community level.

Variability in ecosystems is probably a major constraint in the evolution of life history traits of organisms

(Stearns 1992). In marine ecosystems, interannual variability is a well-recognized phenomenon with very variable, and sometimes 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, especially marine top-predator populations (Aebischer et al. 1990). 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 toward competing energy-demanding processes such as maintenance and reproduction (Stearns 1992). Thus, trade-offs may be affected by environmental variability, and strong oceanographic anomalies may affect the survival of predator species (Barbraud and Weimerskirch 2001*a*).

Although several studies have investigated the effects of environmental variability on some demograph-
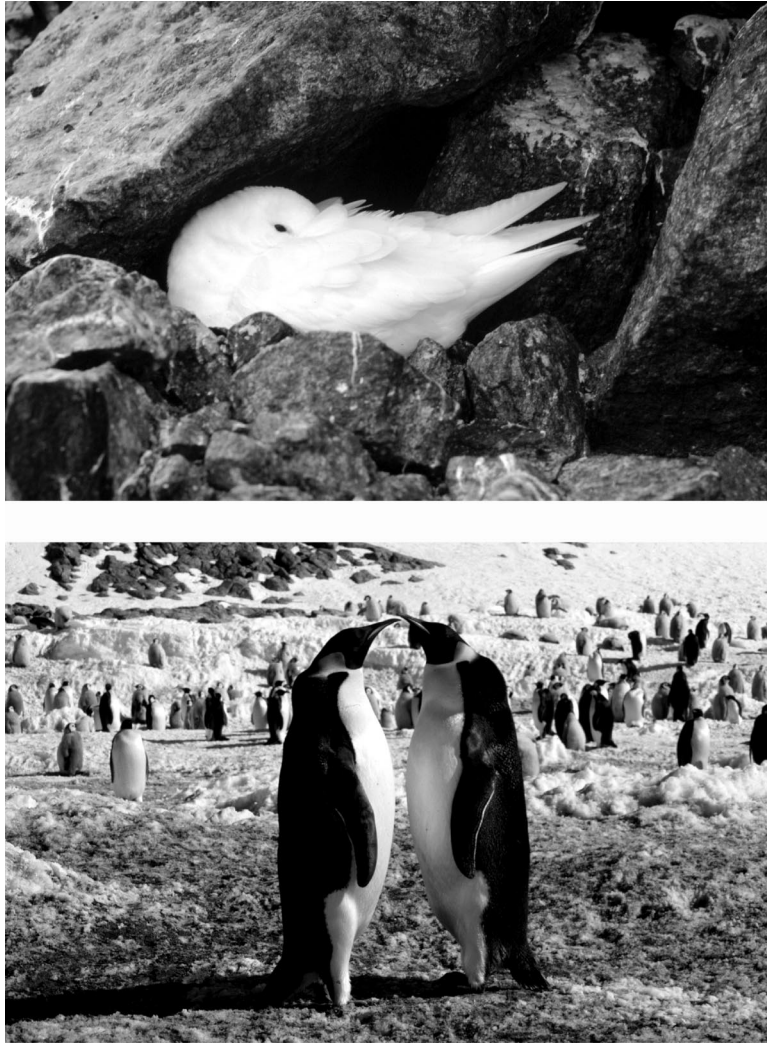
PLATE 1. (Top) Adult Snow Petrel on its nest in boulders. The oldest known individual is at least 46 years old. (Bottom) Adult male and female Emperor Penguins, with chicks and adults in the background. The oldest known individual is at least 36 years old. Photo credit: C. Barbraud.

ic parameters of top-predator populations (e.g., population size, breeding performances, or survival; for a review, see Croxall et al. [2002]), few studies have simultaneously explored the influence of environmental variability on several parameters and its consequences for population size. This implies understanding how vital rates such as survival and fecundity, and their variations, affect population dynamics (Caswell 2001), and how environmental factors affect the vital rates.

In the Southern Ocean, seabirds are long-lived, upper-trophic-level predators that integrate environmental variability over large spatial and temporal scales (Smith et al. 1999). Sea surface temperature and sea ice extent have been shown to affect the population dynamics of seabirds through effects on demographic traits such as productivity and adult survival (e.g., Barbraud and Weimerskirch 2001a, Ainley 2002). Several

authors have emphasized the important role of krill in the Antarctic food web in explaining the link between sea ice and the population dynamics of top predators (Tynan 1998, Nicol et al. 2000, Croxall et al. 2002), particularly seabirds (Fraser et al. 1992, Smith et al. 1999, Barbraud et al. 2000, Barbraud and Weimerskirch 2001a, b). The proposed mechanism is an effect of sea surface temperature and sea ice anomalies on food availability. For example, reduced sea ice extent and warm sea surface temperature negatively affect the abundance of krill (Pakhomov and McQuaid 1996, Loeb et al. 1997, Brierley et al. 2002) and, as a consequence, the demographic parameters of krill predators. These environmental variables have contrasting effects on populations and species: a decrease in sea ice extent may have a positive impact on some species and a negative impact on others (Croxall et al. 2002). Thus, population models are necessary to comprehend

demographic responses to climatic variations within and among species.

Understanding changes in seabird populations requires knowledge of the dynamics of marine ecosystems, which are among the most complex, most difficult to study, and least understood of Earth's biomes (Croxall et al. 2002). Studies are few, time series are short, and quantitative knowledge of the dynamics of interactions between predators, their prey, and the environment remains very limited. Nevertheless, some of the most plausible inferences of the effects of changes in ice distribution and extent on the distribution and ecology of Antarctic seabirds have come through studies of the Adélie Penguin (*Pygoscelis adeliae*), the Emperor Penguin (*Aptenodytes forsteri*), and the Snow Petrel (*Pagodroma nivea*) (Croxall et al. 2002). In addition, few long-term studies at the individual level, recording the survival and reproduction of marked individuals, exist. Long-term studies that monitor several sympatric species are even scarcer. In this study, we compare sympatric Snow Petrel and Emperor Penguin populations over a 40-year period in order to evaluate the impact of the variability of the Antarctic environment on their population dynamics.

The impact of environmental variability on vital rates has already been approached by previous work on the two species, but only on some demographic parameters (Chastel et al. 1993, Barbraud et al. 2000, Barbraud and Weimerskirch 2001a, b). Here we specify the impact of sea ice and air temperature, during different seasons, on demographic parameters, especially capture probabilities and adult survival. We analyze the two data sets conjointly. In addition, we construct appropriate life history models using a state-based approach (McNamara and Houston 1996), estimate demographic parameters for those models between 1962 and 2002, analyze the models from a prospective and retrospective point of view (Caswell 2001), and make comparisons among species.

Methods

Study site and species

Both species were studied on Ile des Pétrels, Pointe Géologie Archipelago (66°40′ S, 140°01′ E), Terre Adélie, Antarctica (see Plate 1). Snow Petrels are cliff-nesting procellariiforms that forage over Antarctic waters, prey mainly on fish, crustaceans, and squids, and breed in summer (Ridoux and Offredo 1989). The Emperor Penguin is the only Antarctic winter breeder, and forages within the pack ice on fish, cephalopods, and Antarctic krill (*Euphausia superba*) (Offredo and Ridoux 1986). Breeding population censuses were carried out every year from 1963 to 2002 for the Snow Petrel, and from 1962 to 2001 for the Emperor Penguin. For the Snow Petrel, three colonies (Damier, Hybride, and Pylone) were intensively surveyed each year. Because no significant difference between the breeding perfor-

mances of pairs nesting in each of the three colonies was detected, data from the three colonies were pooled, except for the survival analysis. More details on the monitoring methodology are provided in Chastel et al. (1993) and Barbraud and Weimerskirch (2001a).

Environmental variables

Based on previous studies (Barbraud et al. 2000, Barbraud and Weimerskirch 2001a, b), we tested for the effect of four environmental variables on demographic parameters and population size of the two species: sea ice concentration, sea ice extent, air temperature, and Southern Oscillation Index (SOI).

The sea ice concentration data begin in 1982, because data derived from satellite radiometer measurements were not available prior to the 1980s. Sea ice concentration data were averaged over the area covered by ice, excluding regions with <15% ice concentration, for a sector 120 km wide off the colonies. Data were maintained by the International Research Institute for Climate Prediction (*available online*).[2] The sea ice extent data (i.e., the distance from the colonies to the limit of a ≥15% ice concentration) begin in 1973, and were extracted for longitude 140° E from the Antarctic CRC and Australian Antarctic Division Climate Data Sets (*available online*).[3] Air temperature data were obtained from the Météo France station at Dumont d'Urville, situated a few hundred meters from the studied colonies. Although ocean temperature is more relevant for marine organisms than is air temperature, the latter represents a useful proxy for sea surface temperature, as it is strongly influenced by the ocean surface temperature (Pearson correlation monthly data: $r = 0.40$, $P < 0.001$). Finally, we used the SOI as a proxy for the overall climate conditions because evidence of ENSO (El Niño Southern Oscillation) teleconnections in southern high-latitude climate has been identified (Liu et al. 2002). SOI is available from the Climatic Research Unit (*available online*).[4] To study the effect of environmental variables on demographic parameters, we divided the year into four seasons reflecting the species' life histories (Table 1). The winter season plays a critical role for the abundance and availability of resources during summer (Loeb et al. 1997) and affects the survival or breeding performance of Snow Petrels and Emperor Penguins (Barbraud et al. 2000, Barbraud and Weimerskirch 2001a, b). We used the season of the year t or $t + 1$, depending on which demographic parameter was studied and according to the biology of the species. For example, to study the effect of environmental variables on Emperor Penguin breeding success, we used the summer before the breeding season of year t, and autumn and winter during the breeding season of year t. For the number of

TABLE 1. Specification of biological meaning of seasonal periods used in analysis of the effect of environmental variables on demographic parameters of Snow Petrels and Emperor Penguins.

Year	Months	Season	Snow Petrel	Emperor Penguin
t	Jan–Mar	summer	**rearing and fledging**	not breeding
t	Apr–Jun	autumn	not breeding	**laying and incubation**
t	Jul–Sep	winter	not breeding	**rearing**
t	Oct–Dec	spring	**laying and incubation**	**fledging**
$t + 1$	Jan–Mar	summer	**rearing and fledging**	not breeding
$t + 1$	Apr–Jun	autumn	not breeding	**laying and incubation**

Note: Breeding season periods are set in boldface.

breeding pairs and proportion of breeders of Emperor Penguins, we used the previous autumn and winter (during the calendar year $t - 1$) for a breeding season during year t, and the summer (during the calendar year t) before the breeding season during year t. To investigate the relationships between environmental variables and demographic parameters, we used Pearson correlation coefficients (r) after checking the normality and homoscedasticity of the data.

Estimation of the demographic parameters

We estimated breeding success for each species as the proportion of eggs that fledged a chick. The proportion of birds attempting to breed was calculated as the number of individuals breeding in the colony during a particular year divided by the number of breeders known to be alive that season. The number of breeders known to be alive during a season t was calculated, from the capture–recapture studies conducted on each species, as the number of individuals that were observed at least during one preceding season. The proportion of adults marked as chicks that bred for the first time at the colony in each age class was estimated (see Appendix A). The proportion of birds attempting to breed for the first time as 6-year-olds or older was measured from 1980 to 2001 for Snow Petrels and from 1977 to 1987 for Emperor Penguins. Most (>90%) Snow Petrels started to breed before the age of 17 years, and most Emperor Penguins before the age of 8 years (see Appendix A). Juvenile survival rate was estimated for each cohort as the proportion of chicks that survived until recruitment divided by the number of marked chicks for each year. It was measured until the year when 90% of chicks had started to breed. Therefore, survival during the first year at sea was measured from 1963 to 1984 for Snow Petrels and from 1968 to 1977 for Emperor Penguins. To estimate the survival during the first year at sea, we assume that chicks recruited at the same age (the mode of the distribution of age at first breeding at the colony; see Appendix A: Fig. A1). We could not estimate immature survival for either species, because in these species with a delayed sexual maturity, individuals stay at sea for several years and remain unobservable. Therefore, we estimated survival during the first year at sea from the juvenile survival (from fledging to recruitment), and assumed that the survival of immature birds after the first year at sea was similar to adult survival. We corrected the survival estimates during the first year at sea by the proportion of immigrants for the Snow Petrel, and by tag loss for Emperor Penguins.

Recent developments of multistate models permit one to account for detection rates in the estimation of juvenile survival, age-specific breeding probabilities, or transition rates from nonbreeder to skipped breeder (Spendelow et al. 2002, Beauplet et al. 2005). Unfortunately, we could not apply this approach to estimate the temporal variability of our demographic parameters, due to severe problems of convergence of this model and the estimability of the parameters, probably because of our data (censuses and studied species). It is also possible to consider detection probability in the population count data (Williams et al. 2001), but our censuses did not permit us to apply such models. However, due to a high sampling effort on breeding colonies, we could consider that detection probabilities of breeders were close to 1.

Capture–recapture modeling of survival

To estimate adult survival, we used the developments of the Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992), which provide unbiased estimators of survival probabilities. Our data set contains capture histories referring to the members of a same pair; thus the fates of paired individuals are not independent. We therefore separately analyzed data sets for males and females. For the Snow Petrel, we removed the first capture to limit heterogeneity among individuals, and worked with a total of 630 male and 640 female individual capture histories from 1967/1968 to 2001/2002. For the Emperor Penguin, we removed the first two captures to limit heterogeneity among individuals, and removed the important impact of tag loss that may have occurred during the first two years after banding. Consequently, we worked with a total of 327 male and 381 female individual capture histories from 1971 to 2002.

For penguins, tag loss may be important, and the bands may cause problems (Ainley 2002, Jackson and Wilson 2002). Marking was stopped in 1988, when there were some doubts about the costs induced by flipper banding. Mortality of penguins with flipper

bands may result from complications arising when the wings swell during molt and the band constricts blood flow (Ainley 2002). Tag loss arises when the flipper band is slack after the molt, probably mostly after the first molt. From a survival analysis with doubly marked individuals, we estimated the importance of tag loss (see *Results*) and corrected the survival estimates by $1/\tau$, where τ is the probability of retaining the tag.

To examine the goodness of fit of the most general models, we used tests implemented in U-CARE software (Choquet et al. 2002). We first started with the CJS model with time-dependent survival (ϕ_t) and capture probabilities (p_t) for each sex for Emperor Penguins, and with time-dependent survival (ϕ_t) and capture probabilities (p_t) for each sex and for each colony for the Snow Petrel. The CJS model fitted the data for females, but not for males, for the Snow Petrel (see Appendix B). For Emperor Penguins, it fitted the data poorly for both sexes. The CJS does not permit survival to differ between newly and previously marked animals, contrary to the transient model $\{\phi_{a2*t} p_t\}$, nor does it permit capture to differ between animals captured at the previous occasion and those currently captured, contrary to the trap-dependent model $\{\phi_t p_{t*m}\}$. Here, $a2$ is the age-2 class, and was used to model the transient effect; m is the trap-dependent effect. For the two species and both sexes, Test 2 explained a large part of the CJS χ^2 statistic, whereas Test 3 explained a smaller part of the total χ^2. This indicates a "trap-dependence" effect on capture (Pradel 1993). Indeed, the Test 2.CT presents a "trap-happiness" effect, indicating that capture probability at year $t + 1$ was higher for individuals captured at year t than for individuals not captured at year t. The trap-dependent model correctly fitted the data for both species and both sexes. Consequently, for both sexes we numerically fitted a model $\{\phi_t p_{t*m}\}$ to account for the trap effect in Emperor Penguin capture probabilities. In addition, a strong trap-dependent effect was found for the three colonies of Snow Petrels for both sexes. We numerically fitted a model $\{\phi_{t*c} p_{t*m*c}\}$ in order to account for the trap effect in the capture probabilities for each colony; c is the colony effect.

To test the main effects of different factors and their interaction, we used MARK software (White and Burnham 1999). The inferential statistic used for comparing the relative ability of each model to explain variation in the data was the Akaïke Information Criterion (AIC$_c$), corrected for the effective sample size (Lebreton et al. 1992). We partitioned the variance of the survival estimates into sampling variance and process variance following Link and Nichols (1994), and used the process variance in the retrospective analysis.

The fieldwork protocols have important implications for the interpretation of recapture probabilities. Previous studies have shown that procellariiforms can skip breeding, once recruited into the breeding population (Chastel et al. 1993, Jenouvrier et al. 2003, 2005a).

Because encounters occur only on breeding grounds, recapture probabilities for Snow Petrels should be low in years during which a high proportion of breeders skip reproduction. We therefore studied the impact of the number of breeding pairs and environmental covariables on capture probabilities.

We then modeled the yearly variation in adult survival as a function of environmental covariates that might be relevant to the ecology of Snow Petrels and Emperor Penguins. We also used the number of breeding pairs as a covariate to investigate the possibility of density dependence on adult survival. To assess the effects of covariates, we estimated the amount of variation in survival or capture probabilities accounted for by covariates (Gaillard et al. 1997, Barbraud et al. 2000). We calculated the proportion of explained variation in survival or capture probabilities accounted for by covariates, R^2, as [DEV(Model$_{cov}$) − DEV(Model)]/ [DEV(Model$_t$) − DEV(Model)], where DEV was the deviance for survival or capture models with covariate, constant, and time effects, respectively.

Modeling the population dynamics

For each species, we constructed a population model using a pre-breeding matrix (Caswell 2001) structured by age and reproductive status classes (Fig. 1). Factors entering the model were the proportion of birds attempting to breed and their fecundity, adult survival estimated with capture–recapture methods (S_a), and, for the Snow Petrel, immigration (m). Fecundity was the average breeding success (BS) multiplied by the mean survival during the first year at sea (S_0). We considered that the minimum age at first breeding was six years for the Snow Petrel and three years for the Emperor Penguin, according to the observed distribution of age at first breeding (see Appendix A). Once recruited, birds reproduce every year, with the probability ($S_a P_b$), P_b being the proportion of breeders. Birds are able to skip a reproductive event with the probability ($S_a(1 − P_b)$).

A previous analysis highlighted the importance of immigration in the dynamics of a procellariiform species (Jenouvrier et al. 2003). Therefore, we took into account the immigration rate for the Snow Petrel population. The number of immigrants was estimated from 1981 as those adults found breeding for the first time and not banded as chicks in the colony. This estimate is probably very reliable because Snow Petrels are highly philopatric once they started to breed in a colony, and all chicks from the study colonies were banded each year. The number of immigrants was correlated both with the number of local breeders and with the number of local recruits, pointing out a strong environmental influence on the reproductive decision of birds (see Appendix A: Fig. A2). To take into account the fact that temporal variations of immigration and breeding population are related, we considered a pro-
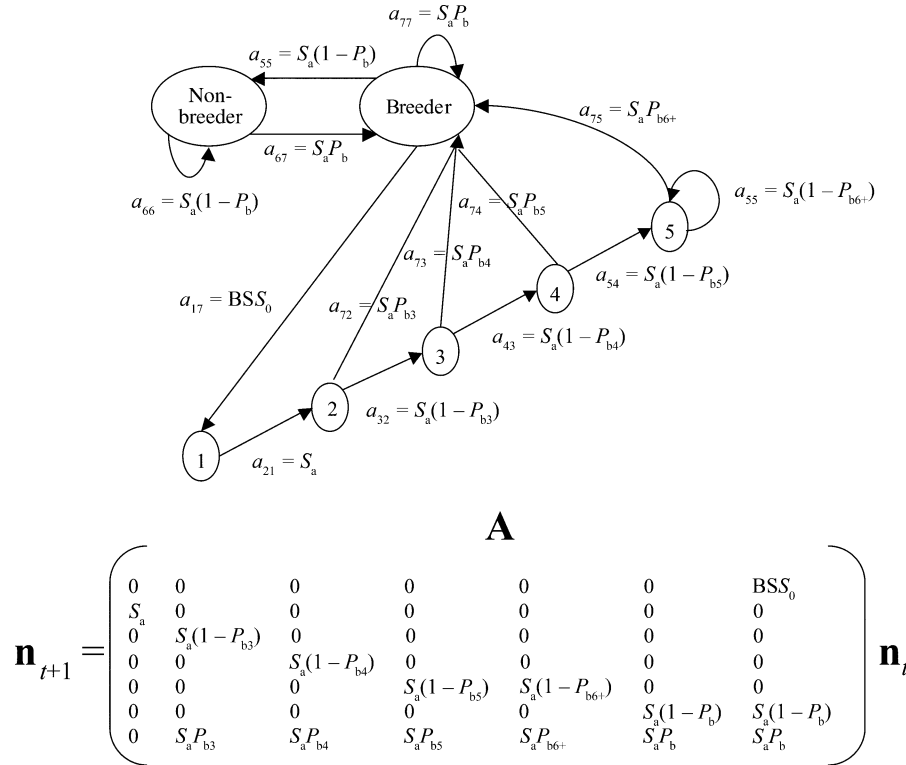
FIG. 1. Upper figure: Lifetime cycle graph for the Snow Petrel and Emperor Penguin populations at Dumont d'Urville, Terre Adélie, Antarctica. The probability of breeding for the first time at age i was ($S_a P_{bi}$), where P_{bi} was the proportion of birds banded as chicks that breed for the first time at i years old. We considered that the minimum age at first breeding was six years for the Snow Petrel ($P_{b3} = P_{b4} = P_{b5} = 0$) and three years for the Emperor Penguin. Once recruited, birds reproduce every year with the probability ($S_a P_b$), where P_b is the proportion of breeders. BS is the overall breeding success. The first year, chicks survive with the probability S_0. S_a corresponds to the adult survival estimated with capture–recapture methods. For Snow Petrels, we considered a proportion of immigrants of $P_{imm} = 0.05$. Lower figure: Population projection matrix $\mathbf{A}$ is multiplied to $\mathbf{n}(t)$, a vector describing the state of the population at time t, to obtain the state of the population at $t + 1$.

portion of immigrants, P_{imm}, calculated as the number of immigrants divided by the number of breeders.

The resulting model (Fig. 1) was a linear, time-invariant system of differential equation: $\mathbf{n}(t + 1) = \mathbf{A}$ $\mathbf{n}(t)$, where $\mathbf{A}$ is the population projection matrix, and $\mathbf{n}(t)$ is a vector describing the state of the population, whose entries $\mathbf{n}$ give the numbers in each class. The projection interval (from t to $t + 1$) is one year. The elements of the matrix $\mathbf{A}$ are shown in Fig. 1, and a_{ij} is the entry in the ith row and jth column of the matrix $\mathbf{A}$ (Caswell 2001).

We first focused on a matrix model with no stochasticity, which included the mean values of the demographic rates. The matrix analysis yielded the deterministic population growth rate (largest eigenvalue of $\mathbf{A}$), stable age distribution (right eigenvector of $\mathbf{A}$), and the sensitivities of the growth rate to variations in demographic rates θ ($\partial\lambda/\partial\theta$) or matrix entries a_{ij} ($\partial\lambda/\partial a_{ij}$). The sensitivities were log-scaled (elasticities) for the matrix entry sensitivities and vital rate sensitivities. We also used arcsine-scaled sensitivities for the vital rate sensitivities because demographic parameters were bounded by 0 and 1 (Link and Doherty 2002). In order

to compare the constant deterministic model's prediction, we calculated the observed growth rate as the slope of a least squares fit of the logged number of breeding pairs vs. time.

Second, we included temporal variability in the elements of the transition matrix using a linear time-varying model: $\mathbf{n}(t + 1) = \mathbf{A}_t \mathbf{n}(t)$. We used the adult survival rate between year t and $t + 1$, the proportion of breeders at year $t + 1$, the breeding success of a year t, and the chick survival rate between year t and $t + 1$ in the projection matrix of a year t ($\mathbf{A}_t$). We started with an initial vector where the number of breeding pairs and chicks were those observed, and the numbers in other classes were obtained by the stable age distribution produced by the left eigenvector compared to the initial number of breeding pairs.

Third, we conducted Life Table Response Experiments (LTRE) with random design analysis (Caswell 2001). The aim of this analysis is to quantify the contribution of each of the vital rates or matrix entries to the variability in the growth rate λ. This requires both the variability of the vital rates and the sensitivity analysis of λ because a particular vital rate may make a
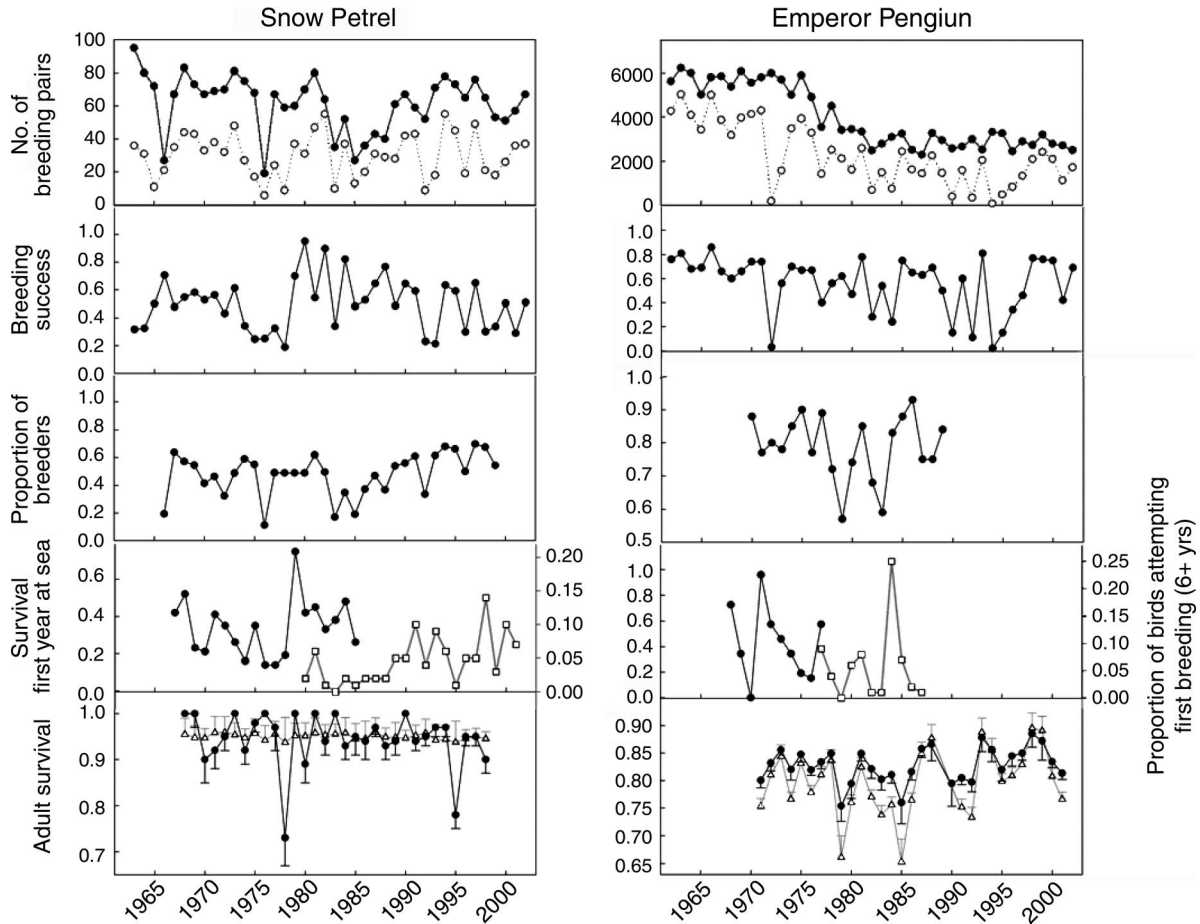
Fig. 2. Number of breeding pairs (solid circles) and fledged chicks (open circles); breeding success; proportion of birds attempting to breed; survival during the first year at sea (solid circles) and proportion of birds attempting to breed for the first time at ≥6 years old (gray squares); male (gray triangles) and female (solid circles) adult survival for Snow Petrels and Emperor Penguins at Dumont d'Urville, Terre Adélie, Antarctica, between 1962 and 2002. Survival estimates during the first year at sea were corrected by immigration for Snow Petrels and by tag loss for Emperor Penguins (see *Methods* and *Results*). Adult survival values were estimated from the best models (model averaging; Table 4), and error bars represent standard errors. Emperor Penguin adult survival was not corrected by tag loss.

small contribution, either because it does not vary much or because λ is not sensitive to its variation. Let $V(\lambda)$ denote the variance in λ among treatments (i.e., years). The first-order approximation to the variance in λ is

$$V(\lambda) \approx \sum_{ij} \sum_{kl} \mathbf{C}(ij, \, kl) s_{ij} s_{kl} = \mathbf{s}' \mathbf{Cs}$$

where $\mathbf{C}(ij,kl)$ is the covariance matrix of the matrix entries a_{ij} and a_{kl}. The sensitivity vectors s_{ij} and s_{kl} are evaluated at the mean matrix. We did not considered the covariance between matrix entries because they are due to the structure of the matrix **A** (Fig. 1). Contributions to $V(\lambda)$ can also be calculated in terms of lower-level parameters with the parameter vector $\mathbf{p} = (S_0 \, BS \, S_a, \, P_b \, P_{b6+})$, where P_{b6+} was the proportion of birds breeding for the first time at ≥6 years old. We could not include in the parameter vector the proportion of Emperor Penguins breeding for the first time before

age 6 because we did not have enough data to estimate its temporal variation. The effects of the temporal variation of a demographic parameter θ on the variability of λ can be approximated by using a first-order Taylor expansion, $V(\lambda) \approx s(\theta)^2 \, \text{var}(\theta)$, where $s(\theta)$ is the sensitivity of λ to demographic parameter θ. We also ignored covariation among demographic traits (see Brault and Caswell 1993).

Results

Population size, breeding parameters, and first-year survival

The number of breeding pairs of Snow Petrels showed strong year-to-year variation (Fig. 2) and increased when sea ice concentration during autumn and winter increased (Table 2). The number of breeding pairs of Emperor Penguins showed a dramatic decrease between 1975 and 1982 (Fig. 2), and was positively

TABLE 2. Pearson correlation coefficients between demographic parameters and environmental variables for each season.

Environmental variable	Snow Petrel				
	N	BS	S_0	P_b	P_{b6+}
SIC, sea ice concentration					
Summer					
Autumn	0.47*	−0.16		0.48*	0.47*
Winter	0.46*	0.12		0.19	0.42†
Spring	0.21	0.09		0.07	−0.02
SIE, sea ice extent					
Summer			0.39		
Autumn	−0.15	−0.29	−0.35	−0.10	0.24
Winter	−0.15	−0.16	−0.30	0.05	−0.07
Spring	0.24	0.12	0.20	−0.03	−0.07
T, air temperature					
Summer			0.20		
Autumn	0.09	0.25	0.21	−0.05	−0.16
Winter	0.16	−0.02	0.27	0.02	−0.08
Spring	−0.01	0.34*	0.41†	0.42*	−0.02
SOI	0.04	−0.23	0.02	0.00	0.14

Notes: Demographic parameters are: N, number of breeding pairs; S_0, survival during the first year at sea; BS, breeding success; P_b, proportion of breeders; and P_{b6+}, proportion of birds attempting to breed for the first time ≥6 years of age. SOI is the Southern Oscillation Index. A lag of 1 year for the environmental variable is shown in boldface. When the number of years is ≤10, Pearson correlation coefficients are not specified.

* $P \leq 0.05$; ** $P \leq 0.01$; † $P \leq 0.10$.

related to sea ice concentration, sea ice extent during summer, and SOI (Table 2). Fluctuations in the number of chicks produced followed fluctuations in the number of breeding pairs for both species (Fig. 2).

Survival during the first year at sea and breeding success showed high year-to-year variations for both species (Fig. 2). Emperor Penguin survival during the first year at sea increased when air temperature during autumn and winter increased (Table 2). Breeding success decreased for Snow Petrels when air temperature during spring decreased, and it decreased for Emperor Penguins when the SOI decreased (Table 2).

The proportion of birds alive in the breeding population during a particular year and attempting to breed was lower for Snow Petrels than for Emperor Penguins (Fig. 2). The relative variability of the proportion of breeders was similar to that of breeding success and survival during the first year at sea for Snow Petrels, but was lower for Emperor Penguins. The proportion of breeders increased for Snow Petrels when sea ice concentration during autumn and air temperature during spring increased (Table 2), and for Emperor Penguins when sea ice extent increased and air temperature decreased during the previous autumn (Table 2). The proportion of Snow Petrels attempting to breed for the first time at ≥6 years old was also positively related to sea ice concentration during autumn (Table 2).

Survival analysis

Modeling capture probabilities.—For both species and both sexes, the model selection procedure confirmed that there was a trap effect on capture probabilities (Table 3). For Snow Petrels, the trap effect was additive for both sexes, and there was no colony effect

on capture probabilities. For Emperor Penguins, the trap effect was additive for females but not for males. However, general trap-dependence models have severe identifiability problems, and the additive model is probably the best solution (Pradel 1993). In addition, considering the additive model for male Emperor Penguins instead of the model with interaction did not change the model selection results. Capture probabilities were time dependent for both species and both sexes. All of the models with a covariate effect on capture probabilities had a greater AIC$_c$ than did the best model without a covariate.

Modeling survival probabilities.—Model $\{\phi_t\ p_{t+m}\}$ was thus used for modeling survival probabilities (Table 3). Snow Petrel adult annual survival probabilities did not differ between colonies for either sex. For both species, model $\{\phi_.\ p_{t+m}\}$ did not differ from the model $\{\phi_t\ p_{t+m}\}$ (ΔAIC$_c$ < 2) for males, indicating that male adult annual survival showed little year-to-year variation (Fig. 2). Survival of female Snow Petrels showed high year-to-year variations because the model $\{\phi_t\ p_{t+m}\}$ had the lowest AIC$_c$ (Fig. 2). For female Emperor Penguins, in contrast, the model $\{\phi_.\ p_{t+m}\}$ had the lowest AIC$_c$.

Survival estimates for males (subscript M) and females (F) from models $\{\phi_.\ p_{t+m}\}$ and the process variance from best models (Table 4) were $\phi_M = 0.950$, $\tau_M^2 = 4 \times 10^{-7}$, and $\phi_F = 0.940$, $\tau_F^2 = 0.003$ for the Snow Petrel, and $\phi_M = 0.791$, $\tau_M^2 = 0.002$, and $\phi_F = 0.820$, $\tau_F^2 = 3 \times 10^{-5}$ for the Emperor Penguin.

To test for the effect of sex on adult survival, we used a general procedure for the comparison of several survival estimates that incorporates associated variance using the software CONTRAST (Hines and Sauer

TABLE 2. Extended.

	Emperor Penguin			
N	BS	S_0	P_b	P_{b6+}
0.45*	−0.42†			
−0.08	−0.03			
−0.08	−0.40†			
0.40*	−0.08		−0.07	0.50
0.15	0.04		**0.62***	**0.55†**
0.06	0.02		**0.18**	**0.24**
−0.09	0.02	0.14	0.23	0.25
0.09	−0.11	0.89**	**−0.55***	**−0.02**
−0.18	−0.16	0.60*	**−0.15**	**−0.30**
		0.15		
0.38*	0.40*	−0.08	0.36	0.39

1989). Adult survival differed significantly between sexes for both species (for Snow Petrels, $\chi_1^2 = 4$, $P = 0.0455$; for Emperor Penguins, $\chi_1^2 = 3.85$, $P = 0.0498$). Male Snow Petrels survived better than females, whereas female Emperor Penguins survived better than males.

There was no effect of covariates on adult survival for Snow Petrels (Table 4; $\Delta AIC_c < 2$, $R^2 < 10\%$), whereas Emperor Penguin survival was strongly affected by covariates. The survival of male Emperor Penguins was negatively related to the number of breeding pairs ($\Delta AIC_c > 2$, $R_M^2 = 22\%$). Air temperature during summer and winter, respectively, accounted for 35% and 18% for male and 21% and 15% for female Emperor Penguin yearly variation in survival (Table 4). Adult Emperor Penguins survived better when air temperature was lower. Sea ice concentration during summer, autumn, and winter had a strong positive influence on male Emperor Penguin survival (R^2: 27%, 72%, and 50%, respectively).

To correct Emperor Penguin survival for tag loss, we fitted a model with an age effect for a cohort of birds marked with two tags or one tag. We compared adult survival between groups of birds that were double or single marked, for two different age classes. During the first year after marking (first age class), the difference between groups indicated an important tag loss of 44.6%. For 2–5 years after marking, we estimated a mark loss of 5.8%. Because we had already suppressed the two first captures, the effect of tag loss remained low, but not negligible. We thus corrected our adult survival estimate for matrix modeling by a factor $1/\tau$, where τ is the probability of retaining the tag ($1 − 0.058$).

Matrix analyses

For the prospective analysis, we focused on the period between 1962 and 1974 to study Emperor Penguin population dynamics, i.e., when the population was stable (Fig. 2). We used the overall period for the Snow Petrel. The population projection matrix gave an annual growth rate of $\lambda = 0.9999$ for the Snow Petrel and $\lambda = 0.9978$ for the Emperor Penguin. These values agree well with the observed population stability for both species over the period considered (0.9986 and 0.9990, respectively).

Prospective analysis.—For Snow Petrels, the largest elasticities were found for the transition corresponding to the immatures staying in the same "breeding at age 6+ years" state (a_{55}, Table 5). The transitions between the breeding and nonbreeding states (a_{67} and a_{76}), for nonbreeders and breeders staying in the same states (a_{66} and a_{77}) were high and showed almost equal elasticity for the Snow Petrel, whereas the transition for breeders staying in the same state had by far the largest elasticity for the Emperor Penguin.

The sensitivity analysis of λ to changes in the lower-level demographic parameters showed that the growth rate is mainly sensitive to adult survival for both species at both scales (Table 6). Survival during the first year at sea, breeding success, the proportion of birds attempting to breed for the first time, the proportion of breeders, and the proportion of immigrants had lower elasticities.

Retrospective analyses.—The transitions between the breeder and nonbreeder state, for breeders or nonbreeders staying in the same state transition (a_{67}, a_{76}, a_{77}, and a_{66}, respectively) showed the most important variation and contribution to the variance of the growth rate ($V(\lambda)$) for the Snow Petrel (Table 5). Fecundity was also variable, but made no contribution to $V(\lambda)$. Emperor Penguins showed the opposite pattern, with a strongly variable fecundity that made the most important contribution to $V(\lambda)$, and slightly variable transitions a_{67}, a_{76}, a_{77}, and a_{66} that made a lower contribution

TABLE 3. Modeling capture and survival probabilities for adult Snow Petrels (1968–2001) and Emperor Penguins (1971–2002).

Model	Male			Female		
	ΔAIC_c	k	DEV	ΔAIC_c	k	DEV
Snow Petrel						
$\phi_{\cdot}\, p_{t+m}$	0.00	36	2865.97	0.00	36	2877.95
$\phi_t\, p_{t+m}$	0.04	67	2802.29	−56.46	62	2767.92
$\phi_{t+c}\, p_{t+m}$	3.14	69	2801.26	−53.38	64	2766.83
$\phi_{t*c}\, p_{t+m+c}$	20.15	112	2728.08	−28.22	110	2694.98
$\phi_{t*c}\, p_{t+m}$	21.58	109	2735.87	−30.66	105	2703.22
$\phi_{t*c}\, p_{t+m*c}$	44.49	173	2620.87	−20.29	167	2578.78
$\phi_{t*c}\, p_{t+c}$	130.78	109	2845.07	37.42	106	2769.16
$\phi_{t*c}\, p_{t*m*c}$	218.64	294	2520.81	159.77	294	2465.60
$\phi_{t*c}\, p_m$	657.68	104	3382.55	588.92	104	3324.93
Emperor Penguin						
$\phi_t\, p_{t*m}$	0.00	87	1313.93	0.00	117	1631.74
$\phi_{\cdot}\, p_{t+m}$	49.80	32	1487.77	−47.66	32	1772.86
$\phi_t\, p_{t+m}$	51.15	57	1434.47	−38.55	59	1724.45
$\phi_t\, p_t$	137.60	59	1516.42	76.66	59	1839.66
$\phi_t\, p_m$	147.44	33	1603.74	193.38	33	2011.81

Notes: The difference between the best model selected for males (lowest Akaike Information Criterion, AIC_c) and other models is specified (ΔAIC_c). The models are sorted according to the best model for males. Therefore, a negative ΔAIC_c for females means that the model is better than the model with $\Delta AIC_c = 0$ (i.e., the better model for males). For the other column headigs, k refers to the number of parameters estimated, and DEV to the deviance of the model. Explanation of model notation: $\phi_t\, p_t$ is the CJS model where survival probability (ϕ) and capture probability (p) varied with time (t), $\phi_t\, p_{t*m}$ is the trap-dependent model where capture probability varied over time and differed between animals captured at the previous occasion and those not captured then; subscript c denotes the colony effect.

to $V(\lambda)$. However, transitions a_{67} and a_{77} showed more variation and contribution to $V(\lambda)$ than the other transitions a_{76} and a_{66}. The transition of birds attempting to breed for the first time at ≥6 years old showed little variability and made no contribution to $V(\lambda)$ for either species.

Focusing on the lower-level parameters, the largest contribution came from the variability of adult survival, although adult survival varied little for both species (Table 6). Breeding success and survival during the first year at sea were the most variable demographic parameters for both species. However, their variability made no contribution to $V(\lambda)$ for Snow Petrels. For Emperor Penguins, in contrast, the contribution of breeding success was very high (the same value as adult survival), and survival during the first year at sea was the next demographic parameter that most contributed to the variability of population growth rate. The proportion of breeders showed a more important contribution to $V(\lambda)$ for the Snow Petrel than for the Emperor Penguin (next most important contribution for Snow Petrel among the other demographic parameters). The proportion of birds attempting to breed for the first time at ≥6 years old did not vary much and made no contribution to $V(\lambda)$ for either species.

DISCUSSION

Emperor Penguins and Snow Petrels live all year long in a harsh, unpredictable environment in terms of weather, sea ice, food, and breeding site availability. These highly ice-associated species are affected by sea ice variability through an impact on food availability and/or habitat (Barbraud et al. 2000, Barbraud et Weimerskirch 2001a, b). The variability of sea ice is linked to local, direct factors, such as temperature and wind, as well as to remote, indirect factors that may be related to or affected by the Southern Oscillation (White and Peterson 1996). The impact of environmental variability on population dynamics through its effect on demographic parameters is complex, because it involves direct or indirect ecological mechanisms. In this study, we have highlighted our finding that Emperor Penguin and Snow Petrel populations show different demographic responses to climate variability, according to their demographic strategies.

The number of Snow Petrel breeding pairs varied greatly from year-to-year, whereas it showed a strong decrease during the mid 1970s for the Emperor Penguin. In Terre Adélie, the number of Southern Fulmars (*Fulmarus glacialoïdes*) also showed strong interannual variations and decadal fluctuations similar to those observed for the Snow Petrel (Jenouvrier et al. 2005b). The differences in year-to-year variations in breeding numbers are related to differences in demographic strategies between petrels and penguins. Emperor Penguins are shorter lived species than Snow Petrels. In theory, long-lived species are more likely to refrain from breeding than shorter lived species during unfavorable years (Stearns 1992). Indeed, one of the most striking feature of the Snow Petrel demography is a low breeding frequency, with birds breeding in only half of the years, on average (Chastel et al. 1993).

TABLE 4. Modeling the effect of covariates on capture and survival probabilities for adult Snow Petrels (1968–2001) and Emperor Penguins (1971–2001).

Models	Males					Females				
	ΔAIC_c	k	DEV	R^2	Slope	ΔAIC_c	k	DEV	R^2	Slope
Snow Petrel, 1968–2001										
$\phi_{Tautumn}\, p_{t+m}$	−0.92	37	2549.67	0.05		59.47	37	2543.94		
$\phi_{Tsummer}\, p_{t+m}$	−0.78	37	2549.8	0.04		48.56	37	2533.02		
$\phi_{.}\, p_{t+m}$	0	36	2552.62			58.51	36	2545.02		
$\phi_{t}\, p_{t+m}$	0.04	67	2488.96			0	61	2435.01		
$\phi_{Twinter}\, p_{t+m}$	1.71	37	2552.3			59.92	37	2544.38		
$\phi_{N}\, p_{t+m}$	1.8	37	2552.39			49.77	37	2534.23		
$\phi_{Tspring}\, p_{t+m}$	1.91	37	2552.49			60.5	37	2544.96		
Snow Petrel, 1972–2001										
$\phi_{SIEsummer}\, p_{t+m}$	−0.62	32	2417.19	0.09		61.47	32	2372.76		
$\phi_{t}\, p_{t+m}$	0	57	2366.53			0	52	2270.16		
$\phi_{.}\, p_{t+m}$	2.15	31	2421.99			59.56	31	2372.89		
Emperor Penguin, 1971–2002										
$\phi_{Tsummer}\, p_{t+m}$	−16.44	33	1469.20	0.35	−	−14.92	34	1762.87	0.21	−
$\phi_{N}\, p_{t+m}$	−7.46	34	1476.03	0.22	−	−6.07	34	1771.72		
$\phi_{Tspring}\, p_{t+m}$	−7.19	33	1478.44	0.17		−5.93	34	1771.86		
$\phi_{Twinter}\, p_{t+m}$	−5.53	34	1477.96	0.18	−	−12.13	34	1765.65	0.15	−
$\phi_{Tautumn}\, p_{t+m}$	−4.41	34	1479.09	0.16		−5.80	34	1771.99		
$\phi_{SIEwinter}\, p_{t+m}$	−0.92	35	1480.43	0.14		−3.69	35	1772.00		
$\phi_{SIEautumn}\, p_{t+m}$	−0.70	35	1480.65	0.13		−3.87	35	1771.82		
$\phi_{SIEspring}\, p_{t+m}$	−0.21	35	1481.15	0.12		−4.39	35	1771.30		
$\phi_{.}\, p_{t+m}$	0.00	32	1487.77			−9.11	32	1772.86		
$\phi_{SIEsummer}\, p_{t+m}$	0.13	35	1481.48	0.12		−3.99	35	1771.70		
$\phi_{t}\, p_{t+m}$	1.35	57	1434.47			0.00	59	1724.45		
Emperor Penguin, 1981–2002										
$\phi_{SICautumn}\, p_{t+m}$	−15.54	21	479.45	0.72	+	4.02	24	847.05		
$\phi_{SICwinter}\, p_{t+m}$	−9.53	21	485.45	0.50	+	3.61	24	846.64		
$\phi_{SICsummer}\, p_{t+m}$	−3.07	21	491.91	0.27	+	3.77	24	846.80		
$\phi_{SSTspring}\, p_{t+m}$	−2.09	21	492.89	0.23		2.80	24	845.84	0.05	
$\phi_{SSTwinter}\, p_{t+m}$	−1.38	21	493.60	0.21		3.56	24	846.60		
$\phi_{.}\, p_{t+m}$	0.00	19	499.41			0.00	22	847.30		
$\phi_{SSTautumn}\, p_{t+m}$	0.64	21	495.62	0.14		2.50	24	845.54	0.06	
$\phi_{SSTsummer}\, p_{t+m}$	1.42	21	496.40	0.11		0.36	24	843.39	0.14	
$\phi_{SICspring}\, p_{t+m}$	1.85	21	496.83			4.02	24	847.06		
$\phi_{t}\, p_{t+m}$	8.97	35	471.60			9.39	39	819.66		

Notes: Only the covariates that have a significant impact are represented ($\Delta AIC_c < 2$). R^2 refers to the proportion of explained variation in survival or capture probabilities accounted by covariates. Abbreviations of model factors are as in Table 2. Significant slopes at $P < 0.05$ are indicated; negative slopes are designated "−."

Emperor Penguins, however, breed almost annually, but their adult survival is sensitive to unfavorable oceanographic conditions (Barbraud and Weimerskirch 2001*a*).

Adult survival, a key demographic parameter for both species

As predicted by a slow–fast continuum in avian life histories for species that lay only a single egg and have deferred breeding and high adult survival rates (Sæther and Bakke 2000), the sensitivity of population growth rate to adult survival was very high, and the adult survival variability was weak for both species in our study. A decrease in the variation of a trait with increasing sensitivity may be a common pattern (Sæther and Bakke 2000, Gaillard and Yoccoz 2003, Morris and Doak 2004), suggesting that a reduction in the variance of sensitive traits is favored through selection. However, our results indicate that adult survival variability made the largest contribution to the variance of the popu-

lation growth rates. Adult survival is thus a key demographic parameter for the population dynamics of both species, from a prospective and a retrospective point of view (Caswell 2001).

For both species, the difference in adult survival between sexes increased during unfavorable years, indicating that the sex with higher mortality was more strongly affected. Male Snow Petrels survived better than females, whereas male Emperor Penguins survived less than females. These differences may be explained by the different investment in breeding. The Snow Petrel is one of the most sexually dimorphic species of petrels, males being much larger (nearly 8%), and heavier (20.5%) than females (Barbraud and Jouventin 1998). A previous study (Barbraud et Chastel 1999) showed that the body condition of females, but not of males, had a significant effect on hatching success. Being structurally smaller, females have a lower fasting capacity, and the higher breeding effort of females may reduce their survival. In Emperor Penguins,

TABLE 5. Elasticity of the population growth rate to changes in the matrix entries of **A** (Fig. 1), variability (V) of matrix entries of **A**, and their contribution (Cont) to the variance of the population growth rate for two different time periods when variability of demographic parameter could be estimated (see Fig. 2).

Matrix entries	Snow Petrel					Emperor Penguin				
		1968–1984		1979–2000			1971–1977		1976–1986	
	Elasticity	V	Cont	V	Cont	Elasticity	V	Cont	V	Cont
a_{17}	0.0289	0.0134	0.0003			0.0633	0.98968	0.0746		
a_{77}	0.1734	0.0221	0.0029	0.0221	0.0029	0.3831	0.0030	0.0009	0.0075	0.0023
a_{66}	0.1441	0.0210	0.0019	0.0203	0.0018	0.0211	0.0035	0.00003	0.0117	0.0001
a_{76}	0.1581	0.0221	0.0024	0.0221	0.0024	0.0898	0.0030	0.00003	0.0075	0.00008
a_{67}	0.1581	0.0210	0.0023	0.0203	0.0022	0.0898	0.0035	0.0008	0.0117	0.0027
a_{55}	0.1929			0.0019	0.00009	0.1015			0.0068	0.0001
a_{75}	0.0289			0.0013	0.0002	0.0260			0.0034	0.0002
a_{54}	0.0289					0.0260				
a_{43}	0.0289					0.0415				
a_{32}	0.0289					0.0572				
a_{21}	0.0289					0.0633				
a_{74}						0.0155				
a_{73}						0.0156				
a_{72}						0.0061				

males are larger than females, and undertake the entire incubation in a single 60–70 day shift, during which they fast. Consequently, their survival will be much more dependent on environmental conditions during winter than that of females. Indeed, Emperor Penguin adult survival was affected by air temperature for both sexes and by sea ice concentration for males, whereas there was no effect of environmental covariates on Snow Petrel adult survival.

Barbraud and Weimerskirch (2001*a*) have suggested that the population of Emperor Penguins has declined by 50% because of a decrease in adult survival during the late 1970s related to reduced winter sea ice extent. Our retrospective analysis confirms that the variation in adult survival makes the strongest contribution to the variability of Emperor Penguin population growth rate. During the late 1970s, a regime shift probably occurred in the Southern Indian Ocean (Weimerskirch et al. 2003, Jenouvrier et al. 2005*b*), with an important warm event affecting the marine ecosystem. The dramatic decrease in the Emperor Penguin population during this regime shift suggests that this species may be very susceptible to environmental variability, and particularly to sudden changes in the environment. Snow Petrels showed their lowest number during this period, but being able to skip reproduction, they seem to be less sensitive to major changes in their environment.

How oceanographic conditions affect two contrasting breeding strategies

The proportion of breeders was demographic parameter making the second greatest contribution to the variance of the Snow Petrel population growth rate, whereas it showed a weak contribution to the variance of the Emperor Penguin population growth rate. For Emperor Penguins, breeding success showed a similar contribution to that of adult survival, and survival during the first year at sea was the second-ranked demographic

TABLE 6. Sensitivity of population growth rate to changes in demographic parameters for Snow Petrel (SP) and Emperor Penguin (EP), relative variability of demographic parameters (corrected cv as a fraction of maximum value), and their contribution to variance of the population growth rate.

Demographic parameter	Sensitivity						cv, corrected†		Contribution	
	Mean value		Log scale		Sin^{-1} scale					
	SP	EP	SP	EP	SP	EP	SP	EP	SP	EP
S_a	0.94	0.86	0.976	0.929	0.236	0.390	0.11	0.06	0.0008	0.0008
S_0	0.34	0.43	0.029	0.071	0.035	0.077	0.35	0.58	0.0001	0.0002
BS	0.50	0.56	0.029	0.071	0.029	0.065	0.38	0.46	0.0001	0.0008
P_b	0.48	0.79	0.041	0.057	0.042	0.027	0.31	0.24	0.0002	0.00004
P_{b6+}	0.05	0.12	0.015	0.013	0.053	0.034	0.17	0.30	0.00006	0.00005
P_{b5}		0.24		0.007		0.013				
P_{b4}		0.18		0.007		0.014				
P_{b3}		0.06		0.003		0.010				
P_{imm}‡	0.05		0.017		0.075					

† cv corrected by its maximum possible value, given the mean (Morris and Doak 2004).

‡ Proportion of immigrants.

parameter in contribution to the variance of the population growth rate. Moreover, the retrospective analysis of the projection population matrix entries demonstrated that breeding abstention played a critical role in Snow Petrel population dynamics, whereas the fecundity of birds attempting to breed contributed most to the Emperor Penguin population dynamics. In fact, fecundity was the most variable matrix entry that showed the largest contribution to the variance of the Emperor Penguin population growth rate. The transition from nonbreeder to breeder state, and for breeders staying in the same state also contributed to the variance of the Emperor Penguin population growth rate, but not the transition from the breeder to nonbreeder state or nonbreeders staying in the same state. On the other hand, the lower variability of Snow Petrel fecundity made no contribution to the variance of the population growth rate. The transition between the breeder and nonbreeder state, and high elasticities for breeders and nonbreeders staying in the same state, showed the strongest variations and made the most important contributions to variance in the Snow Petrel population growth rate. These results highlight the important role of breeders and nonbreeders in the Snow Petrel population dynamics, while nonbreeders did not contribute to the Emperor Penguin population dynamics. Therefore the demographic strategy of Snow Petrels, but not Emperor Penguins, is characterized by breeding abstention.

Birds of the order Procellariiformes are very long-lived 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 (Stearns 1992). Weimerskirch (1999) showed the important role of body condition in allocation decisions for foraging and breeding albatrosses and petrels. Breeding abstention among long-lived species may be a response to poor feeding conditions early in the breeding season (Chastel et al. 1993). When facing food shortage, individuals may not reach a threshold value of early body condition. Indeed, Southern Fulmars and Snow Petrels are able to skip reproduction when environmental conditions are poor (Chastel et al. 1993, Jenouvrier et al. 2003). Snow Petrels do not breed when severe physical conditions (snow, ice) make nest attendance and laying impossible, or when food is not available (Chastel et al. 1993).

Our study supports these findings because the proportion of Snow Petrels attempting to breed increased with air temperature during spring. Breeding success was also positively related to air temperature during spring. Chastel et al. (1993) highlighted a negative relationship between breeding success and average snowfall during spring. Indeed, breeding failure was mostly due to incubation failure because Snow Petrels nest in crevices, which could be obstructed with snow and ice, making laying impossible. Therefore, when air temperature during spring increased, the availability of

nests without ice probably increased, and more Snow Petrels attempted to breed.

We also showed that fewer Snow Petrels attempted to breed when sea ice concentration was lower in autumn preceding the breeding season. Sea ice influences the distribution and abundance of food supplies. Indeed, decreased frequency of krill recruitment associated with a decreased sea ice extent may be responsible for low population sizes of krill (Loeb et al. 1997, Brierley et al. 2002), and lower krill abundance is associated with areas with lower winter cover of sea ice (Nicol et al. 2000). In years with low sea ice concentration during autumn, Snow Petrels may have difficulty in finding food, and may not reach the threshold value of early body condition necessary for breeding.

Similarly to Snow Petrels, but to a larger extent, Emperor Penguins are able to store energetic reserves (Prévost 1961). The proportion of breeding Emperor Penguins was almost twice as high as for the Snow Petrel, and showed less contribution to the variance of the population growth rate. Nevertheless, the proportion of birds attempting to breed increased when sea ice extent increased and air temperature decreased in the previous autumn. Like Snow Petrels, in years with low sea ice extent and high air temperature during autumn, Emperor Penguins may have difficulty in finding food, and may not reach the body condition necessary for breeding.

However, is it fecundity, and especially breeding success, that contributes most to the variance of the Emperor Penguin population growth rate. Emperor Penguin breeding success decreased continually from a maximum in the early 1960s to a minimum in the mid 1990s, and this decrease probably explains why the Emperor Penguin population did not recover to the levels prior to the 50% population decrease. Emperor Penguin breeding success was positively related to the Southern Oscillation Index. In years with a negative SOI (warm sea surface temperature and lower sea ice extent), Emperor Penguins may have difficulties in finding food to rear their chicks until fledging.

The number of breeding pairs of Snow Petrels was most strongly affected by variability in adult survival and the proportion of birds attempting to breed. None of the environmental covariables examined influenced adult survival, whereas the proportion of breeders was mostly positively correlated with sea ice concentration during autumn. Therefore, sea ice concentration during autumn had the greatest effect (of the environmental variables examined) on the number of breeding pairs. For Emperor Penguins, on the other hand, the number of breeding pairs was mostly influenced by the variability in adult survival and breeding success. Adult survival of males was highly affected by sea ice concentration between autumn and summer, and survival of both sexes was negatively related to air temperature during summer. In addition, breeding success increased when the SOI increased. Thus, the number of breeding

pairs of Emperor Penguins was affected by sea ice concentration and sea ice extent during autumn and the SOI.

CONCLUSIONS

Snow Petrels and Southern Fulmars, with their high and little-varying adult survival (despite a small body size) and low and highly variable breeding frequency and breeding success (Jenouvrier et al. 2003), can be placed at the extreme end of a ''slow–fast continuum'' of avian life histories (Sæther and Bakke 2000). The important role of nonbreeders in the population dynamics of these two petrel species (Jenouvrier et al. 2005a) highlights the need to understand the effects of environmental variation on the propensity of birds to skip breeding. This extreme feature allows these species to spread their breeding attempts over a long lifetime, whereas individuals of species such as the Emperor Penguin attempt to breed more often, but have lower adult survival.

This study, and our previous study of the Southern Fulmar, show that the breeding population sizes of these three Antarctic species are positively influenced by sea ice. Sea ice has strong influences on key demographic parameters through its impact on food web processes (Loeb et al. 1997), on the distribution and abundance of food supplies (Loeb et al. 1997, Nicol et al. 2000, Brierley et al. 2002), and on the nature and extent of breeding and feeding habitats (Chastel et al. 1993, Barbraud et Weimerskirch 2001a).

Therefore, we can predict that the population sizes of these three species probably will be negatively affected by reduced sea ice in the context of a global warming (Curran et al. 2003). Moreover, Emperor Penguin populations are more susceptible to environmental variations than Snow Petrel and Southern Fulmar populations because petrels can avoid the important costs of reproduction by skipping reproduction during unfavorable years.

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APPENDIX A

Figures showing recruitment are available in ESA's Electronic Data Archive: *Ecological Archives* E086-157-A1.

APPENDIX B

A table showing goodness-of-fit tests is available in ESA's Electronic Data Archive: *Ecological Archives* E086-157-A2.

APPENDIX A: Recruitment

Most snow petrel came back for the first time at the colony and bred around nine years of age (modal values for age at first return and first breeding are nine years; Fig. 1), whereas most emperor penguins returned for the first time at the colony around four years of age, and bred one year later (modal values for age at first return and first breeding are four and five years respectively).

SNOW PETREL   EMPEROR PENGUIN
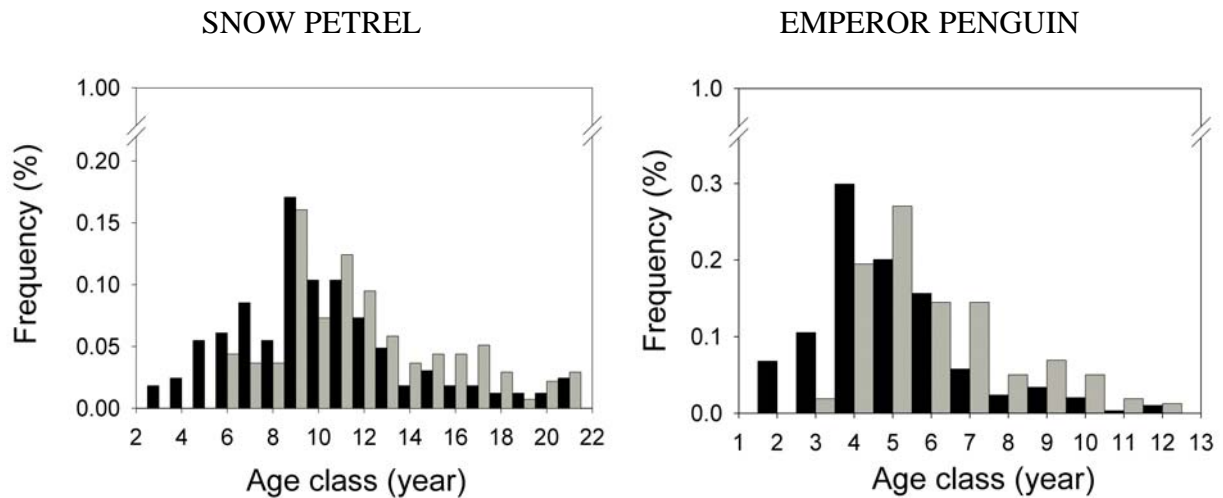
Fig. 1. Proportion of adults marked as chicks that came back for the first time at the colony (black bars) or that were breeding for the first time at the colony (grey bars) as a function of age, for snow petrels (left panel) and emperor penguins (right panels).

The proportions of adults marked as chicks that came back or bred for the first time at the colony in each age class were calculated as the number of birds in each age class on the total number of birds that came back or bred for the first time at the colony. Therefore, these proportions did not account for mortality. The proportions of birds attempting to breed for the first time used in the matrix models were based on the log normal regression of the proportion of adults marked as chicks that breed for the first time at the colony. Emperor penguins can breed when three years old, and age specific probabilities of first time breeding were: $P_{b3}=0.06$, $P_{b4}=0.18$ and $P_{b5}=0.24$. All birds can breed after six years old for both species with
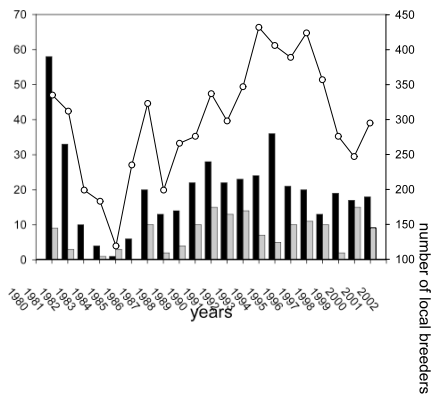
a probability (P_{b6}^+) calculated according to the distribution of age at first breeding (Fig. 1).

For the snow petrel: $P_{b6}^+=0.91/13=0.07$, because 91% of birds bred for the first time before 17

years old, and for the emperor penguin $P_{b6}^+=\dfrac{0.97-\sum_{i=3}^{5}Pb_i}{4}=0.12$, where Pb_i are the

probabilities of first time breeding at age i, and because 97% of birds bred for the first time

before nine years old.

Fig. 2. Annual variation of the number of local breeders (black line), the number of immigrants (black bar) and the number of local recruits (grey bar) for snow petrels between 1981 and 2001. The number of local breeders represents the birds that bred at least one time before. The sum of local recruits (adults marked as chicks that bred for the first time at the colony) and immigrants (adults found breeding for the first time and not banded as chicks in the colony) represents the recruitment. The number of local breeders, local recruits and immigrants is calculated from 1981 since more than 90% of the birds at 17 years old have bred at least once (Fig. 1). The number of local breeders, the number of immigrants and the number of local recruits showed similar inter-annual variations (Spearman correlation coefficient: local breeders- immigrants: $r_s=0.75$, $p<0.05$, local breeders- local recruits: $r_s=0.55$, $p<0.05$, and immigrants-local recruits: $r_s=0.52$, $p<0.05$)

Table 1. Goodness of fit tests for the modeling of capture and survival probabilities for adult snow petrels (1968-2001) and emperor penguins (1971-2002) at Dumont d'Urville. $\phi_t\ p_t$ is the CJS model where survival probability (ϕ) and capture probability (p) varied with time (t). $\phi_t\ p_{t*m}$ is the trap dependent model where capture probability varied over time and differed between animal captured at the previous occasion and those not captured then. $\phi_{a2*t}\ p_t$ is the transient model where survival probability varied over time and differed between newly marked and previously marked animals.

SNOW PETREL

	Male							Female						
GOF	3SR	3SM	**2CT**	2CL	$\phi_t\ p_t$	$\phi_t\ p_{t*m}$	$\phi_{a2*t}\ p_t$	3SR	3SM	2CT	2CL	$\phi_t\ p_t$	$\phi_t\ p_{t*m}$	$\phi_{a2*t}\ p_t$
DAMIER COLONY														
Df	20	26	**28**	22	96	68	76	19	24	28	22	93	65	74
χ^2	32	15	**48**	19	114	66	82	11	9.5	39	16	75.5	36.5	64.5
P	0.04	0.95	**0.01**	0.65	0.10	0.556	0.299	0.91	0.99	0.09	0.82	0.907	0.998	0.777
HYBRIDE COLONY														
Df	25	29	**30**	29	113	83	88	27	31	32	31	121	89	94
χ^2	13	9	**58**	20	100	42	87	9	21	60	13	103	43	94
p	0.98	0.99	**0.001**	0.9	0.804	1.000	0.510	0.99	0.91	0.002	0.99	0.88	1	0.481
PYLONE COLONY														
Df	32	31	**32**	32	127	95	95	30	33	32	34	129	97	99
χ^2	10	35	**93**	51	189	96	179	21	42	68	27	158	90	137
p	0.99	0.29	**<0.001**	0.02	<0.001	0.452	<0.001	0.87	0.13	<0.001	0.81	0.04	0.666	0.007
SUM OVER GROUPS														
Df					336	246	259					343	251	267
χ^2					403	204	348					337	170	295.5
p					0.007	0.976	0.000					0.581	1	0.111

EMPEROR PENGUIN

	Male							Female						
GOF	3SR	3SM	**2CT**	2CL	$\phi_t\ p_t$	$\phi_t\ p_{t*m}$	$\phi_{a2*t}\ p_t$	3SR	3SM	2CT	2CL	$\phi_t\ p_t$	$\phi_t\ p_{t*m}$	$\phi_{a2*t}\ p_t$
Df	23	18	27	22	90	63	67	22	14	27	17	80	53	58
χ^2	19	14	112	40	185	73	167	22	9	148	24	204	56	182
p	0.714	0.721	<0.001	0.010	<0.001	0.182	<0.001	0.449	0.799	<0.001	0.116	<0.001	0.370	<0.001