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Sea ice affects the population dynamics of Adélie penguins in Terre Adélie

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Abstract Overall Adélie penguin population size in Pointe Géologie Archipelago increased between 1984 and 2003 at a rate of 1.77% per year, and averaged $33,726 \pm 5,867$ pairs. As predicted by the optimum model proposed by Smith et al. (Bioscience 49:393–404, 1999). Adélie penguin population size increased when sea ice extent and concentration (SIE and SIC) decreased six years earlier, indicating that the conditions around reproduction or first years at sea, were determinant. The breeding success averaged $85.2 \pm 35.45\%$ and was not related to environmental variables. Adult survival probability varied between years from 0.64 to 0.82. Southern oscillation index (SOI) had a strong negative effect on adult annual survival. Adult survival of Adélie penguins increased during warmer events, especially during winter and spring at the beginning of reproduction. Therefore, we speculate that the rapid decreases in 1988–1991 and 1996 of the breeding population size were related to a decrease in adult mortality. However, adult survival varied little, and could not explain the strong increasing population trend. The sea ice conditions during breeding or during the first year at sea appeared determinant and influenced the population dynamics through cohort effects, probably related to the availability of productive feeding habitats.

critical role in global climate changes, and several studies have highlighted an important warming in Antarctica (Houghton et al. 2001; Curran et al. 2003), especially in the Antarctic Peninsula (Vaughan et al. 2001). In Antarctic ecosystems, environmental conditions have been shown to affect population dynamics of top predators, such as seabirds (Croxall et al. 2002). Changes in sea surface temperature (SST) and sea ice conditions have profound and contrasted effects on species and populations, decrease in sea ice extent (SIE) having for example a positive impact on some species and populations, and negative on others (Fraser 1992; Smith et al. 1999; Croxall et al. 2002; Ainley et al. 2003). Understanding these contrasted responses to climate fluctuations is crucial to understand the effect of global warming on Antarctic ecosystems.

The population dynamics of the Adélie penguin (*Pygoscelis adeliae*) is sensitive to Antarctic climate variations (Baroni and Orombelli 1994; Wilson et al. 2001; Emslie and Mc Daniel 2002). It has long been known that Adélie penguins are closely associated with pack ice in the Southern Ocean (Prévost and Sapin-Jaloustre 1965). Paleological records indicate fluctuations in their appearance and disappearance in close conjunction with ice cover (Smith et al. 1999). Pack-ice conditions (especially ice cover) can affect the reproductive success (Ainley 2002), the breeding population size (Fraser et al. 1992; Wilson et al. 2001) and the viability of this species in contrasted ways (Smith et al. 1999).

Indeed, recent studies show strong and contrasted regional responses of Adélie penguin populations to the inter-annual variations in SIE. The western Peninsula region has experienced the largest coastal climate change over the last four decades in the Southern Ocean (Vaughan et al. 2001), a decrease in winter and spring SIE that has supposedly led to a decrease in populations of Adélie penguin since the 1980s (Smith et al. 1999). In the Ross Sea, Adélie penguins face a very different situation and populations showed a high increase in the 1970s. Using sea ice data available from satellites

Introduction

Ecological and population processes are affected by climatic fluctuations (Stenseth et al. 2002, 2004). Antarctica and the surrounding Southern Ocean play a

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beginning in 1979, Wilson et al. (2001) found that population trends have been inversely related to the maximum extent of winter sea-ice five years earlier, indicating that juvenile survival, expressed in terms of recruitment to the breeding population at an average age of 5 to 6 years, was crucial to explain the population dynamics there. Ainley et al. (2005) also highlighted that annual growth rate of Adélie penguin populations on Ross Island appear to be sensitive to the size (and rate of seasonal growth) of the Ross Sea Polynya. The western side of Antarctica (i.e. the Antarctic Peninsula and its neighbouring islands) and the Ross Sea showed contrasted population trends and converse relationships with sea ice conditions. Smith et al. (1999) suggested that in western Antarctica, SIE has been reduced beyond an optimum condition for the growth of Adélie penguins populations, and that good conditions are attained only in years of large, northward extent of ice. By contrast, in the Ross Sea region, SIE conditions were probably above the optimum sea ice condition, and good conditions for Adélie penguins are attained only in years of lower SIE (Wilson et al. 2001), conditions that became more frequent during the last decade (Smith et al. 1999).

Apart from these two regions, no information is available on the effect of sea ice conditions on Adélie penguin population dynamics. In this study we estimate the interannual variations of the overall Adélie penguin population size in Pointe Géologie Archipelago and explore the effect of Antarctic environmental variability on population dynamics. Pointe Géologie Archipelago is located in Eastern Antarctica, about 30° west of the Ross Sea region. Therefore, according to the optimum model proposed by Smith et al. (1999) we predicted that an increase in SIE should be associated with a decrease in penguin population size, either by an instantaneous impact of SIE or by a delayed effect with a 5–6 years lag when most birds return at the colony to breed for the first time.

In addition, although it is well established that the prolonged presence of sea ice close to penguin breeding sites may delay the start of breeding, reduced clutch size or breeding success (Ainley 2002), few studies have estimated adult survival, and to our knowledge, none has explored the influence of sea ice on adult survival. We thus investigate the effect of environmental conditions on breeding success and on adult survival.

The variability in SIE in Antarctica is linked to remote, indirect factors, that may be related to the Southern Oscillation (SO) (Park et al. 2004; Liu et al. 2002; Kwok and Comiso 2002). Significant relationships between changes in Adélie population size and the El Niño Southern Oscillation (ENSO) index have been demonstrated in the Ross Sea (Wilson et al. 2001). Therefore, we studied the influence of sea ice conditions (SIE, sea ice concentration), SST and the Southern Oscillation Index (SOI) on the demography of Adélie penguins of Pointe Géologie Archipelago.

Materials and methods

Study site and monitoring

The coast of Adélie Land stretches from 136°E to 142°E near the Antarctic polar circle. Adélie penguins breed in colonies on nearly all the islands and islets free of ice of Pointe Géologie Archipelago (Micol and Jouventin 2001; Fig. 1, 66°40'S, 140°01'E). They forage over the continental shelf or the shelf break (Wienecke et al. 2000), and have a generalist diet that varies spatially and temporally (Ainley 2002).

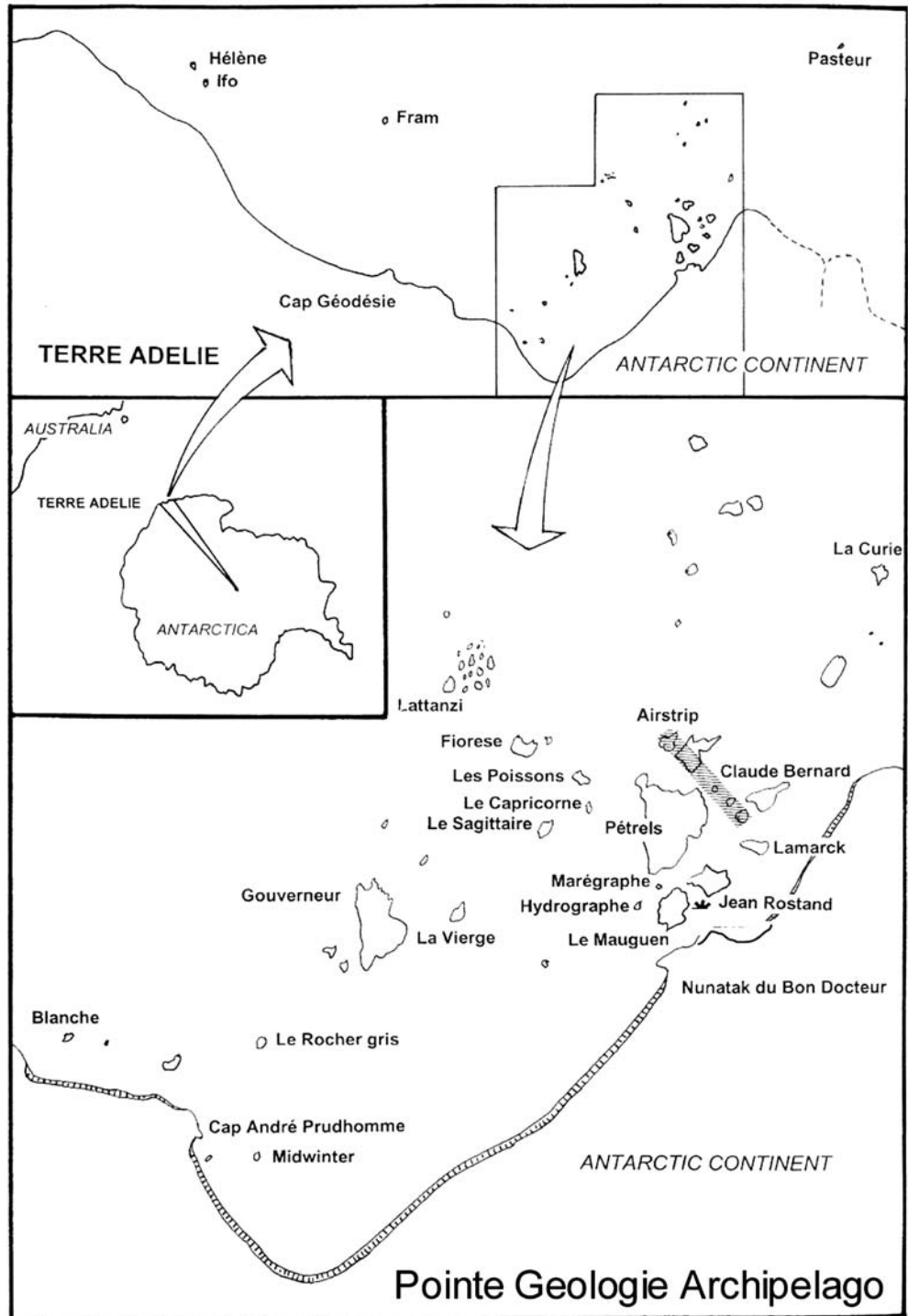
All the breeding pairs of the Archipelago were counted visually. Large colonies (> 100 pairs) were divided into sectors using geological natural features and numbers from all sectors in the colony were summed to derive a total colony estimate. In smaller colonies (< 100 pairs) pairs were individually counted. The first counts were carried out in 1958 and the first complete census of Pointe Géologie Archipelago was made in 1984/1985. From 1988/1989 to 2003/2004 (except for some islands in 1992/1993), all breeding pairs of the Archipelago were counted visually between 15 and 18 November during the laying period. Live chicks were counted just before fledging between 3 and 6 February from 1992/1993 for main islands.

Description of environmental variables

In our analysis, we used environmental covariates obtained from different spatial sectors. Indeed, satellite tracking during summer (Wienecke et al. 2000) indicates that Adélie penguins from Terre Adélie forage during breeding in a sector between 137.5°–142.5°E and 66.5°–65.5°S. However, because the exact winter distribution of the population from Terre Adélie is unknown, we used a sector between 130–150°E based on the distance travelled by an Adélie penguin in the Ross Sea sector during its over-winter migration (Davis et al. 2001).

The monthly sea surface temperature (SST) and sea ice concentration (SIC) were available from the Internet on-line information maintained by the International Research Institute for Climate Prediction (<http://ingrid.lidgo.columbia.edu/>). They were obtained on a 1° scale, and thus averaged over 5° of latitude above the northern limit of the pack ice edge for SST, and over the sea ice extent sector for the SIC. In fact, SST north of the pack ice zone is involved with the Antarctic Oscillation (AAO, Gong and Wang 1999; Fyfe et al. 1999) and Antarctic Dipole (Yuan and Martinson 2001; Liu et al. 2002; 2004) phenomena and would affect the coastal wind patterns, i.e. a decrease or increase in the temperature difference between northern latitudes and the continent would then affect atmospheric pressure differential and winds. More wind leads to more pack ice and vice versa, and more wind results in more extensive polynyas inside the ice pack, with an immediate benefit to penguins, as suggested by Ainley et al. (2005).

Fig. 1 Pointe Géologie Archipelago in Terre Adélie, Antarctica. Adélie penguins nest on 20 islands



The SIE was obtained using the sea ice data available from the Antarctic CRC and Australian Antarctic Division Climate Data Sets (http://www.ant-crc.utas.edu.au/~jacka/seoice_C_html). Finally, we used the Southern Oscillation Index (SOI), available from the Climatic Research Unit (<http://www.cru.uea.ac.uk/cru/data/soi.htm>) because evidence of ENSO teleconnections in southern high-latitude climate have been identified (Liu et al. 2002). The SOI was considered as a

proxy for the overall climate conditions (Stenseth et al. 2003).

To study the effect of environmental fluctuations on the number of breeding pairs and breeding success we calculated Spearman correlation coefficients between the number of breeding pairs, breeding success and monthly SST, SIC, SIE and SOI. To study the effect of environmental fluctuations on the yearly variation in adult survival, we considered the averaged values of environ-

mental variables over seasonal time periods of a calendar year. Summer corresponds to the chick rearing period (January to March), autumn and winter to the non-breeding period (April to September), and spring to the laying and incubation periods (October to December). We also used the previous spring that corresponds to the same breeding period than the summer period, and the previous winter, since winter sea ice affects the abundance of krill the next summer (Loeb et al. 1997), a major prey for Adélie penguin (Ainley 2002). To reduce the number of environmental variables to a smaller number of ‘representative’ and ‘uncorrelated’ variables we used the principal components analysis (PCA). Indeed, PCA involves a mathematical procedure that transforms a number of (possibly) correlated variables into a (smaller) number of uncorrelated variables called *principal components*. The first principal component accounts for as much of the variability in the data as possible, and each succeeding component accounts for as much of the remaining variability as possible. PCA is performed on a square symmetric matrix of type correlation because the units of measurement of the variables differ.

Estimating the number of breeding pairs

To assess between-year changes in the number of pairs, we used log-linear Poisson regressions, modelling logarithms of bird counts using the software TRIM (Pannekoek et al. 2004). The data consist of annual counts made over a period of years at a series of sites. They can thus be summarised as a sites * years data matrix within which a proportion of the cells contain missing values because not all of the sites are covered every year. Such data can be represented as a simple model: $\text{Ln } \mu_{ij} = \alpha_i + \gamma_j$, with μ_{ij} the expected counts, α_i the effect for site i and γ_j the effect for time j on the log-expected counts.

We started the analysis with a model with change-points at each time-point because there was missing year count for all sites between 1985 and 1987 (Pannekoek et al. 2004). According to this switching trend model the log expected counts ($\text{Ln } \mu_{ij}$) for each site i are linear function of time j with slope β : $\text{Ln } \mu_{ij} = \alpha_i + \beta(j-1)$, with β the slope of the linear function of time j . The log expected count increases with an amount β from one time point to the next. So, the switching trend model is a more general model than the time-effects model: $\text{Ln } \mu_{ij} = \alpha_i + \gamma_j$, since it includes this last model as a special case. We took into account over-dispersion and serial correlation since they can have important effects on standard errors, although they have usually only a small effect on the parameters estimates. We used the stepwise selection procedure to identify change-points with significant changes in slope based on Wald tests (Pannekoek et al. 2004) with a significance level threshold value of 0.05 (Table 1). The stepwise procedure for selection of change-points indicated 10 significant change-points

Table 1 Wald test results for a model with change-points at each time-point

Changepoint	Wald test	df	P
1984	7.34	3	0.0618
1988	13.73	3	0.0033
1990	22.56	3	0.0000
1991	12.87	3	0.0049
1992	11.45	3	0.0095
1995	12.58	3	0.0056
1996	22.76	3	0.0000
1997	12.67	3	0.0054
1999	11.64	3	0.0087
2000	13.18	3	0.0043

(Table 1: 1984, 1988, 1990, 1991, 1992, 1995, 1996, 1997, 1999 and 2000).

Survival analyses

To study the impact of the construction of an airstrip, four cohorts of breeding adults from islands destroyed during the building of the airstrip, were marked with flipper bands between 1989 and 1992. A total of 1,001 adults were marked in 1989, 764 in 1990, 133 in 1991 and 96 in 1992. Each year, marked birds were controlled within the Archipelago three times per season to study the breeding performance (resighting during the laying, hatching and fledging period with binocular). In our survival analysis we focused on birds that came back and breed on the Archipelago.

For penguins, there is an important tag loss, and the bands apparently may cause some mortality (Ainley 2002). Mortality of Adélie penguins with flipper bands may result from complications arising when the wings swells during moult and the band constricts blood flow (Ainley 2002). Tag loss arises when the flipper band is slack after the moult, probably mostly after the first moult. Therefore, we removed the first capture to limit the effect of tag loss and heterogeneity amongst individuals.

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. We first started with CJS model with time dependent survival (ϕ_t) and capture probabilities (p_t), and tested if it fitted the data, using the U-CARE software (Choquet et al. 2002). To test the main effects of different factors and their interactions we used the MARK software (White and Burnham 1999).

To select the most appropriate model we used the Akaike Information Criterion (AICc) corrected for the effective sample size (Lebreton et al. 1992): $\text{AICc} = \text{DEV} + 2k + 2k(n/(n-k-1))$, 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. The models are ranked using the difference between the AICc of the model and

the AICc of the best model (noted ΔAICc). ΔAICc can easily be interpreted following this scale (Burnham and Anderson 2001): models having $\Delta\text{AICc} \leq 2$ are strongly plausible, those where $4 \leq \Delta\text{AICc} \leq 7$ are considerably less plausible whereas models having $\Delta\text{AICc} \geq 10$ are improbable. It can be also convenient to normalise the ΔAICc values such that they sum to 1 in calculating the Akaike weight. The Akaike weight allows us to know the probability that a model is the best among the others. If more than one model are strongly plausible, model averaging must be applied (see Burnham and Anderson (1998) for more details).

To assess the effects of the covariates, we compared constant and time-dependent survival models (Barbraud et al. 2000; Gaillard et al. 1997). The amount of variation accounted by covariates was calculated as $[\text{DEV}(\phi_{\text{covariate}}) - \text{DEV}(\phi_{\cdot})] / [\text{DEV}(\phi_{\cdot}) - \text{DEV}(\phi_{\cdot})]$, where DEV was the deviance for survival models with covariate, constant, and time effects, respectively. This corresponds to the proportion of explained variation and is comparable to a squared correlation coefficient (Schemper 1990). Survival and recapture probability estimates are given ± 1 SE.

Results

Population size and breeding success

The total number of pairs for the Pointe Géologie Archipelago averaged $33,726 \pm 5,867$ between 1984 and 2003. It increased during this period at a rate of 1.77% per year (overall slope 1.0177 ± 0.0029 , $\text{IC}_{95\%} = [1.0097; 1.0257]$), but showed marked changes of trend around 1990, 1996 and 2000 (Fig. 2). Before 1991 it fluctuated between 24,000 and 30,000 pairs with an important decrease in 1990. Then the number of pairs doubled between 1990 and 1992, varying around 40,000 pairs with a strong decrease in 1996. Finally, it decreased between 1999 and 2000, and remained stable until today around 33,000 pairs. Almost all the islands showed the same dynamics, except islands where the number of pairs was very small (Fig. 3). Indeed, islands with less than 100 pairs remained stable during all the study period.

We focused on the number of pairs and breeding performance of birds breeding on Péterls Island because the census effort was very high and the island was not affected by airstrip construction. Moreover, the number of pairs on Péterls Island averaged $12,396 \pm 2,577$ and represented 37% of the total number of pairs of the Pointe Géologie Archipelago. The number of pairs on Péterls Island was correlated with SIC and SIE during almost all months six years before the breeding season (Fig. 4b and c), whereas no correlation pattern emerged with SST (Fig. 4a) and SOI. It decreased when SIC or SIE increased six years before the breeding season. The breeding success showed high inter-annual variability (Fig. 5), and averaged $85.2 \pm 35.4\%$. There was no

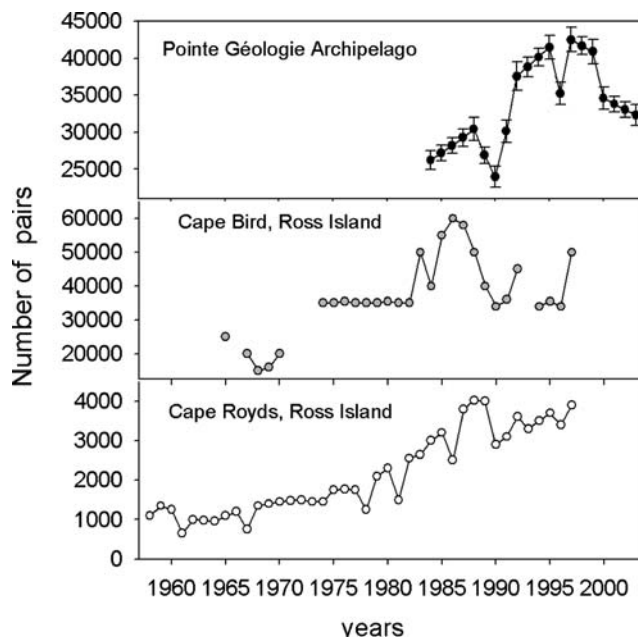


Fig. 2 Number of breeding pairs of Adélie penguins at Pointe Géologie Archipelago between 1984 and 2003 ($66^{\circ}40'S$, $140^{\circ}01'E$), and at Cape Birds ($77^{\circ}13'S$, $166^{\circ}28'E$) and Cape Royds ($77^{\circ}34'S$, $166^{\circ}11'E$) on Ross Island from 1959 to 1997 (reproduction of Fig. 2 of Wilson et al. 2001). Estimates of the total number of pairs at Pointe Géologie Archipelago were computed from a model with 10 changepoints using program TRIM (see methods). *Errors bar* indicate \pm standard errors

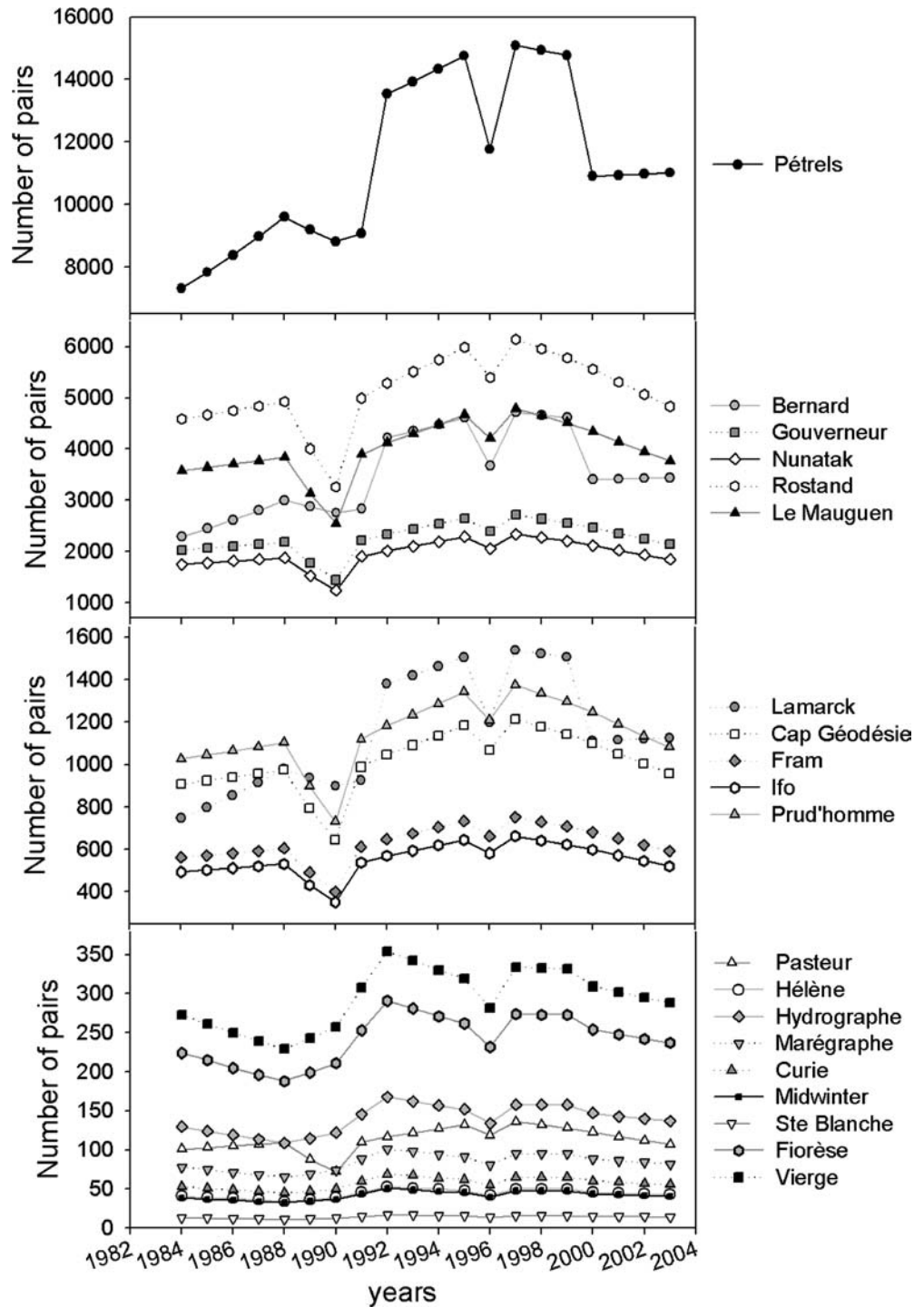
relationship between breeding success and the environmental variables.

Principal component analysis

The first principal component of the PCA corresponding to the largest eigenvalue accounts for approximately more than 70% of the total variance of the data for all seasons (Table 2). When analysing correlation matrices, the sum of the eigenvalues is equal to the number of variables (3) from which the principal components were computed, and the “average expected” eigenvalue is equal to 1.0. Many criteria are used in practice for selecting the appropriate number of principal components for interpretation; the simplest is to use as many principal components as the number of eigenvalues that are greater than 1. The eigenvalues of the first principal component are greater than 2 for all seasons (Table 2). We used therefore only this principal component in further analysis.

The first principal component is strongly negatively correlated with all the environmental variables (Table 3). Sea ice conditions (SIE and SIC) contribute more to the variance of the first principal component than SST, especially for the summer season (Table 3). However, the contributions of SST were higher than 20% for all seasons. When SST, SIC and SIE increased the first principal component decreased. The positive relationships between SST and SIE or SIC, was related to the

Fig. 3 Estimates of the number of pairs between 1984 and 2003 for each islands of Pointe Géologie Archipelago. Estimates were computed from a model with 10 changepoints using program TRIM (see Methods)

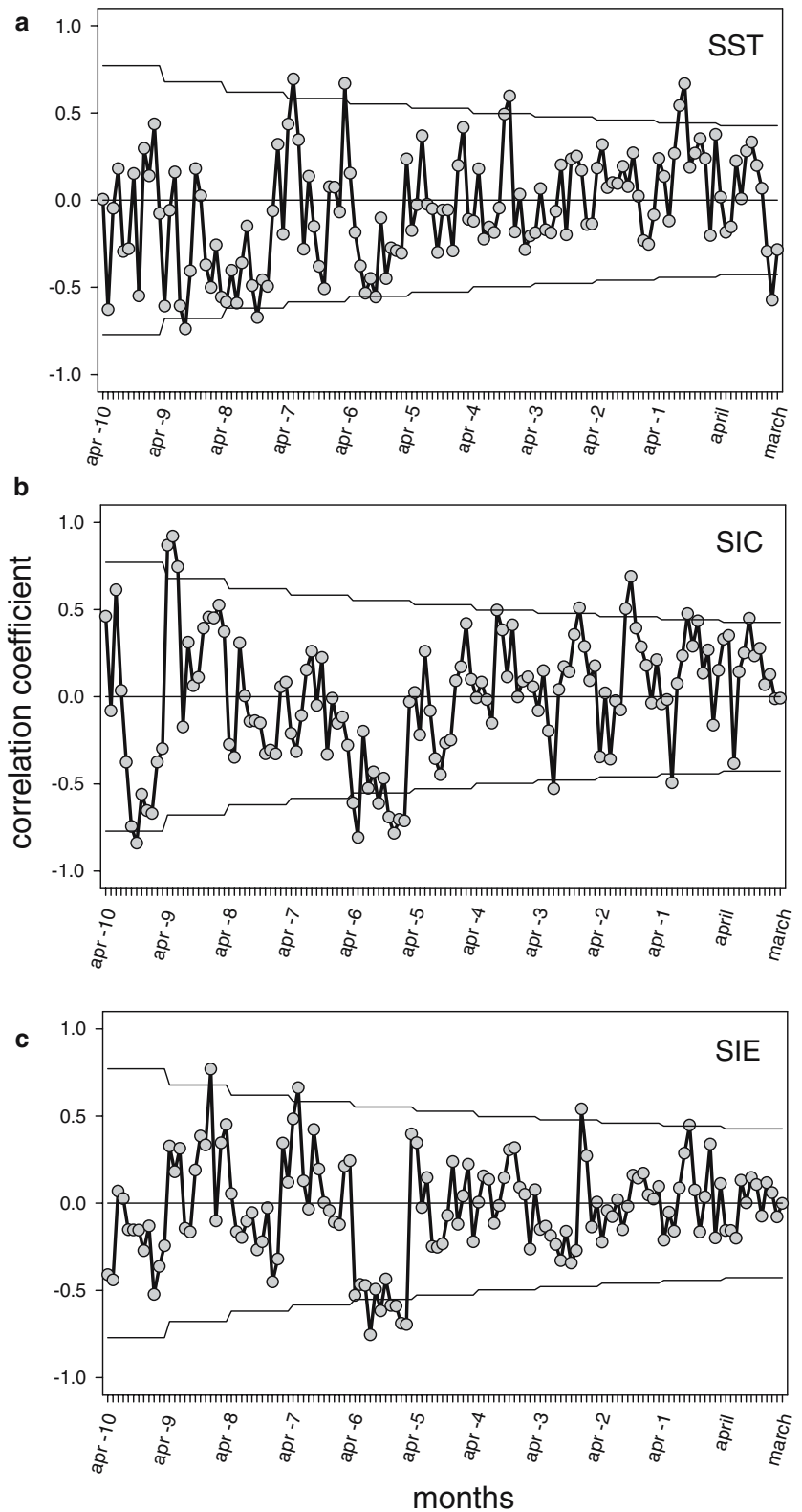


fact that these variables were calculated over different spatial sectors. Indeed, SST was computed over a sector of 5° of latitude above the maximum SIE. Therefore, when maximum SIE decreased, SST was calculated over a sector of decreasing latitude and cooler water. SOI was not related to the first principal component for all season (Pearson correlation coefficient: PCsummer $r=0.23$, $P=0.47$; PCautumn $r=-0.38$, $P=0.22$; PCwinter $r=-0.05$, $P=0.87$; PCSpring $r=0.06$, $P=0.86$)

Adult survival analysis

We removed the first capture to limit heterogeneity amongst individuals and take into account band loss that occurred mostly during the first year, and thus worked a total of 1,135 capture histories of banded adults breeding throughout the Archipelago (666 individuals in 1989, 335 in 1990, 78 in 1991 and 56 in 1992). We fitted the data to the CJS model $\{\phi_t, p_t\}$, where both

Fig. 4 Variation in Spearman correlation coefficients calculated between the number of pairs of Adélie penguins breeding on Pétrels Island and (a) SST; (b) SIC and (c) SIE for each month with different year lags (until 10 years, from April (end of the previous breeding season) to March of the following breeding season. Upper and lower limits of Spearman correlation coefficient at 5% level are indicated by the *hair lines*



the survival (ϕ) and recapture probability (p) are time dependent (t). The CJS model fitted the data poorly (Test 2 + Test 3, $\chi^2_{35} = 66$, $P = 0.0012$). The CJS is the most restrictive model because it does not permit survival to differ between newly and previously marked

animals contrary to the transient model $\{\phi_{a2*t} p_{tj}\}$, nor capture to differ between animals captured at the previous occasion and those captured then, contrary to the trap-dependent model $\{\phi_t p_{t*m}\}$. The trap dependent and transient models also fitted the data poorly ($\chi^2_{29} = 47$,

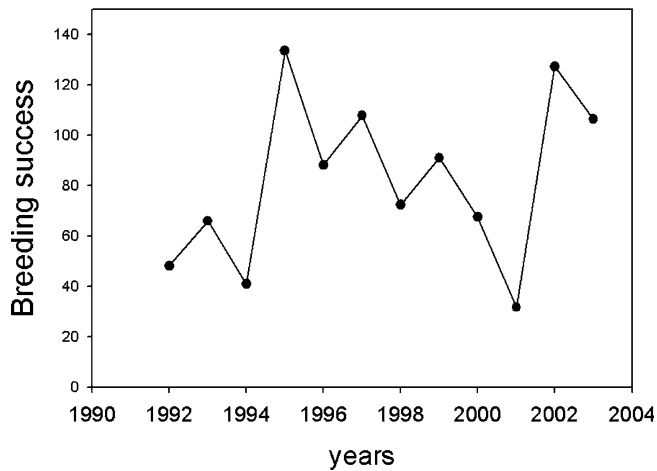


Fig. 5 Breeding success for Adélie penguins breeding at Pétréls Island between 1992 and 2003

$P=0.0204$ and $\chi^2_{23}=44$, $P=0.0055$, respectively). However, a model taking into account both trap dependence and transience effects fitted the data ($\chi^2_{17}=25$, $P=0.11$). Consequently, we numerically fitted model $\{\phi_{a2*t} p_{t*m}\}$.

Capture probabilities were time dependent, and the trap effect was not additive (Table 4, Fig. 6). Therefore, model $\{\phi_{a2*t} p_{t*m}\}$ was used for modelling survival probabilities. The transient effect was additive, but the best model $\{\phi_{a1} . . a2 t p_{t*m}\}$ assumed that adult survival for the first age class did not varied over time contrary to adult survival for the second age class (Table 4). The adult survival varied from a 64% to 82%, the mean value was 76% and the process standard error 4.5%. Among the covariates, SOI accounted for 92% of the yearly variation in adult survival and was the best model (AICc weights =87%, Table 4). The first principal component for previous winter and previous spring

season explained 42 and 32% of the survival variations respectively, and these models did not significantly differ from the model $\{\phi_{a1} . . a2 t p_{t*m}\}$. The slopes of these models were significant. Adult Adélie penguins survival increased when SOI, SST, SIC and SIE decreased during the previous winter and previous spring. All the signs of the slope of the models accounting for an environmental covariate were coherent, indicating that Adélie penguins survived better during warmer events (Table 4). Moreover, the sum of Akaike weights of the models accounting for an environmental covariate was 95% (Table 4), highlighting a strong effect of environmental fluctuations on Adélie penguin adult survival.

Discussion

This study confirms the predictions of the optimality model proposed by Smith et al. (1999). The Adélie penguin population at Pointe Géologie Archipelago increased between 1984 and 2003 and showed similar fluctuations than Adélie populations on Ross Island between 1959 and 1997 (Fig. 2, Smith et al. 1999; Wilson et al. 2001). The increase of the Pointe Géologie Archipelago population through the 1980s and 1990s could not be only related to dislocated birds from the islands destroyed for the construction of the airstrip between 1984 and 1992. Indeed, nests of 2,964 Adélie penguins were destroyed, i.e. around 10% of the Archipelago's nesting sites (Micol and Jouventin 2001), whereas the population increased from around 30,000 pairs at the beginning of 1980s to around 40,000 through the 1990s. The fact that the Ross Sea and Pointe Géologie Archipelago Adélie penguin populations share similar dynamical features, suggests that a strong environmental forcing influences the dynamics of both populations. Indeed, like in the Ross Sea (Wilson et al.

Table 2 Eigenvalues (λ) and percent of total variance of the data explained by the principal component (% var) for PCA conducted on each season between 1989 and 2000. The eigenvalues are arranged in decreasing order, indicating the importance of the respective principal component in explaining the variation of the data

Principal component	Summer		Autumn		Winter		Spring	
	λ	% var	λ	% var	λ	% var	λ	% var
1	2.10	70	2.19	73	2.42	81	2.16	72
2	0.73	24	0.72	24	0.51	17	0.60	20
3	0.17	6	0.09	3	0.07	2	0.24	8

Table 3 First principal component coordinates of the variables and the relative contribution of the variable to the variance of the first principal component. Because the current analysis is based on the

correlation matrix, the principal component coordinates of the variables can be interpreted as the correlations of the respective variables with the first principal component

Environmental variables	Summer		Autumn		Winter		Spring	
	Coord	Cont (%)	Coord	Cont (%)	Coord	Cont (%)	Coord	Cont (%)
SST	-0.647	20	-0.695	22	-0.827	28	-0.774	28
SIC	-0.912	40	-0.877	35	-0.881	32	-0.920	39
SIE	-0.923	40	-0.969	43	-0.977	40	-0.844	33

Table 4 Modeling capture and adult survival probabilities for Adélie penguins between 1990 and 1998, and the effect of covariates on adult survival

Model	$\Delta AICc$	AICc weights	K	Dev	R^2	Slope	SE
ϕ a1 . . , a2 SOI P_{t^*m}	0.00	0.87	18	3364.37	0.92	-0.49*	0.13
ϕ a1 . . , a2 PC previous winter P_{t^*m}	6.39	0.04	18	3370.76	0.42	0.22*	0.11
ϕ a1 . . , a2 t P_{t^*m}	7.12	0.02	22	3363.36			
ϕ a1 . . , a2 PC previous spring P_{t^*m}	7.60	0.02	18	3371.98	0.32	0.22*	0.11
ϕ a1 . . , a2 PC autumn P_{t^*m}	8.41	0.01	18	3372.78	0.26	0.36	0.20
ϕ a1 . . , a2 PC winter P_{t^*m}	9.62	0.01	18	3373.99	0.16	0.19	0.14
ϕ a2 P_{t^*m}	9.67	0.01	17	3376.07	0.00		
ϕ a1 . . , a2 PC spring P_{t^*m}	10.54	0.00	18	3374.91	0.09	0.20	0.19
ϕ a2+ t P_{t^*m}	11.06	0.00	23	3365.27			
ϕ a1 . . , a2 PC summer P_{t^*m}	11.68	0.00	18	3376.05	0.00	0.01	0.13
ϕ a2* t P_{t^*m}	12.90	0.00	28	3356.89			
ϕ a1 t . , a2. P_{t^*m}	15.40	0.00	23	3369.60			
ϕ a2* t P_{t+m}	15.46	0.00	22	3371.70			
ϕ a2* t P_m	94.69	0.00	17	3461.09			

The model with the lowest Akaike Information Criterion (AICc) is in bold characters. k refers to the number of parameters estimated, DEV to the deviance of model. R^2 stands for the proportion of variance explained by the model, and SE indicates the standard error of the covariate slope estimate

*indicates significant slope at the 5% level

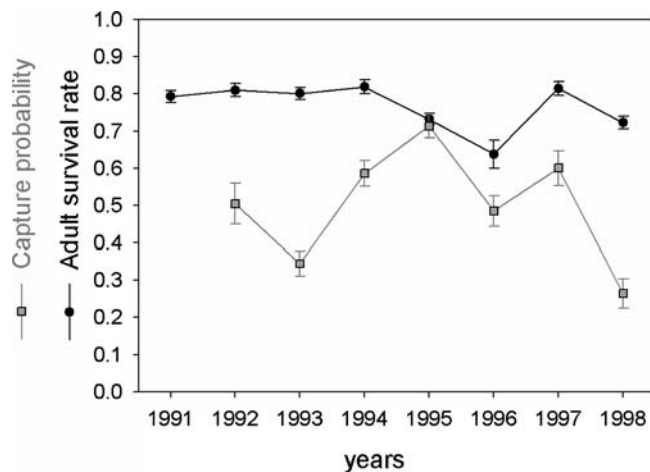


Fig. 6 Annual capture probability (square and gray line) and adult survival (circle and black line) of Adélie penguins at Pointe Géologie Archipelago between 1991 and 1998. Capture and adult survival probabilities were estimated from the best model (Table 4), and error bars represent standard errors calculated with profile deviance methods

2001), the number of breeding pairs on Pointe Géologie Archipelago was negatively related to sea ice conditions with delayed effects. Adélie penguin population size increased when sea ice extent and concentration was reduced six years earlier. Almost all birds return to breed for their first time between 5 and 6 years of age (Ainley 2002). Therefore, the sea ice conditions around breeding or during the first year at sea appeared determinant and influenced the population dynamics through cohort effects.

Wilson et al. (2001) suggested that greater sea ice extent produced several problems for young, inexperienced Adélie penguins in the Ross Sea. First, more extensive (increased SIE) and consolidated ice (increased SIC) provide fewer areas of open water for feeding. Second, more northerly ice extent may force Adélies to

forage in areas outside the food-rich waters just south of the Antarctic circumpolar current (ACC, Tynan 1998). Indeed, correlations with SIE may actually be related to the amount of habitat available between the outer edge of the consolidated ice pack and the southern boundary of the ACC (which does not vary much in position). Alternatively or in addition, the distribution of their main predator, the leopard seal *Hydrurga leptonyx*, would also be shifted north. Finally, reduced sea ice extent negatively affects the abundance of krill (Loeb et al. 1997), and during years of low krill and/or fish abundance, the seals might turn more to penguins as a food resource, especially young, inexperienced birds (Wilson et al. 2001; Ainley and DeMaster 1980).

Adult survival probability of Adélie penguins in Pointe Géologie Archipelago varied between 64 and 82% an estimation that is in agreement with previous studies that took into account band loss. At Cape Crozier, Ross Island, adult survival for individuals of six years and older varied from 57 to 92%, with strong differences between two periods (1968/69 to 1969/70 and 1974/75 to 1975/76; Ainley and DeMaster 1980). Ainley and DeMaster (1980) suggested that these differences were probably related to environmental conditions. In this study, we have highlighted that environmental fluctuations influenced Adélie penguin adult survival. During warm events, especially during low SOI years and during warm winter and spring preceding the breeding period, Adélie penguins survived better. These results were in accordance with the previous assumptions of the impact of environmental condition on juvenile or adult survival (Ainley and DeMaster 1980; Wilson et al. 2001).

The Adélie penguin is a long-lived species, and a general result from population modelling is that the population growth rate of such species is very sensitive to adult survival (Clobert and Lebreton 1991; Wilson et al. 2001). Adult survival of Adélie penguins in Terre Adélie showed a strong decrease in 1996, down to 64%,

related to a cooling event (higher SOI value). This strong decrease probably explains the important population size decrease during this year. Moreover, Ainley et al. (2005) speculated that the decrease in Adélie penguin populations in the Ross Sea and at Pointe Géologie Archipelago during 1988–1991 was also due to adult mortality related to an unusually strong positive excursion of the Antarctic Oscillation (AAO, Gong and Wang 1999; Fyfe et al. 1999). As discussed by Ainley et al. (2005), SOI correlates to and likely affects the wind patterns of coastal Antarctica, which are indexed by the Antarctic Oscillation. In 1988 and 1989, the SOI was also positive, but strongly decrease between 1990 and 1995 indicating an unusual warm event (but see Jenouvrier et al. 2005 for more details). Therefore, strong and Antarctic wide decline in Adélie penguin populations could be related to an increase in mortality related to large-scale environmental fluctuations, and especially cooler events. Indeed, the Antarctic Dipole refers to the see-sawing behaviour of sea ice extent, and sea level pressure, surface air temperature, winds between the Victoria Land (Ross Sea)/Terre Adélie sector of Antarctica and the western Weddell Sea/northern Antarctic Peninsula (Yuan and Martinson 2001; Liu et al. 2002, 2004). The strong implied correlation between Terre Adélie penguin populations and the Ross Sea populations, as shown in this paper, support this relationship relative to the penguin patterns of the Antarctic Peninsula.

However, annual adult survival varied little. Several studies have highlighted a negative relationship between the sensitivity of population growth rate to a vital rate and their variability. Therefore, long-lived species survival variations are probably buffered against environmental variability and fecundity probably mostly contributes to the fluctuations of populations than survival (Saether and Bakke 2000; Gaillard et Yoccoz 2003). A matrix population model of the Ross Sea population showed that a decrease of 1.2% in adult survival, but of 11.4% in breeding success and in the 1st, 2nd and 3rd years of immature survival, will produce a similar decrease in population growth rate from 1 to 0.99 (Wilson et al. 2001). According to these results and life history theory, the fecundity and/or immature survival probably contribute highly to the strong fluctuations of Adélie penguin population size, whereas the contribution of adult survival to the population growth rate variations should be limited. The Adélie penguin population at Pointe Géologie Archipelago was probably strongly affected by environmental factors through recruitment. The strong fluctuations of population size, and especially the high increase at the beginning of 1990s, could be explained by a strong recruitment due to an increase in fecundity and/or immature survival 5–6 years earlier. Indeed, like adult survival, immature survival could be enhanced during warm events that probably produce more productive habitat available for Adélie penguins.

Curran et al. (2003) showed that there has been a 20% decline in SIE in eastern Antarctica since about 1950. Population sizes of Adélie penguins at Pointe Géologie Archipelago and on Ross Island have dramatically increased these past decades possibly due to this important sea ice retreat as suggested by our results and previous studies. Indeed, the number of pairs is negatively related to SIE with a delayed effect highlighting that the recruitment was strongly affected by SIE. Moreover, our study provided some evidence that adult survival was enhanced during years of lower SOI and reduced SIE. In the light of these results and in the context of a global warming, population sizes of Adélie penguins at Pointe Géologie and on Ross Island would probably be positively affected by reduced sea ice on a short time scale, although the indirect impact of reduced sea ice (i.e. the probable decrease in available productive habitats) remains unknown. When SIE will be reduced beyond optimal conditions for the growth of Adélie penguin populations (Smith et al. 1999), like in the Antarctic Peninsula, Adélie penguin populations will probably decrease. The reduction of the growth of Adélie penguin populations could accelerate if changes in sea ice cover occur over the continental slope off Terre Adélie because the abundance of the Antarctic krill, one of the main prey for Adélie penguin (Ainley 2002), is negatively affected by SIE (Loeb et al. 1997). However, these phenomena are complex, owing to varying lags in demographic processes and to the indirect effect of sea ice that could affect both the productive habitat and prey availability. Ultimately, a simulation model of demography for the Adélie penguins that take into account the effect of environmental variation, and especially sea ice, will be required.

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