

# Nonlinear effects of winter sea ice on the survival probabilities of Adélie penguins

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**Abstract** The population dynamics of Antarctic seabirds are influenced by variations in winter sea ice extent and persistence; however, the type of relationship differs according to the region and the demographic parameter considered. We used annual presence/absence data obtained from 1,138 individually marked birds to study the influence of environmental and individual characteristics on the survival of Adélie penguins *Pygoscelis adeliae* at Edmonson Point (Ross Sea, Antarctica) between 1994 and 2005. About 25% of 600 birds marked as chicks were re-observed at the natal colony. The capture and survival rates of Adélie penguins at this colony increased with the age of individuals, and five age classes were identified for both parameters. Mean adult survival was 0.85 (SE = 0.01), and no effect of sex on survival was evident. Breeding propensity, as measured by adult capture rates, was close to one, indicating a constant breeding effort through time. Temporal variations in survival were best explained by a quadratic relationship with winter sea ice extent anomalies in the Ross Sea, suggesting that for this region optimal

conditions are intermediate between too much and too little winter sea ice. This is likely the result of a balance between suitable wintering habitat and food availability. Survival rates were not correlated with the Southern Oscillation Index. Low adult survival after a season characterized by severe environmental conditions at breeding but favorable conditions during winter suggested an additional mortality mediated by the reproductive effort. Adélie penguins are sensitive indicators of environmental changes in the Antarctic, and the results from this study provide insights into regional responses of this species to variability in winter sea ice habitat.

**Keywords** Age dependence · Capture–mark–recapture · Life history · Population dynamics · Southern Oscillation Index

## Introduction

Variability in the population dynamics of seabird populations in the Southern Ocean is known to be an indicator that integrates the effects of changes that occur in the marine ecosystem (Croxall et al. 2002; Croxall and Nicol 2004; Ainley et al. 2007; IPCC 2007). The responses of seabirds to environmental change manifest themselves through demographic parameters, such as adult survival (Barbraud and Weimerskirch 2001), breeding proportion (Jenouvrier et al. 2005a), and recruitment rate (Wilson et al. 2001; Hinke et al. 2007), which determine variations in population size and composition. Ecological studies of marine top predators (e.g., Testa et al. 1991; Ainley et al. 2005; Jenouvrier et al. 2005b) suggest that oceanographic responses to large-scale climate signals, such the El Niño–Southern Oscillation (ENSO), are directly related to the

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variability observed in these populations. In particular, the ENSO phases are correlated with changes in seasonal sea ice extent (SIE) (Kwok and Comiso 2002), a key environmental factor in the polar ecosystem (Ferreira et al. 2004). Seabirds show different degrees of association with sea ice (Ribic et al. 2008) and respond in contrasting ways to changes in SIE according to their ecological characteristics, demographic strategies and regional distribution (Croxall et al. 2002; Jenouvrier et al. 2005b; Forcada et al. 2006). For example, reduced winter SIE negatively affects breeding propensity and adult survival in some species, but is positively correlated to breeding performance in others (Barbraud and Weimerskirch 2001; Jenouvrier et al. 2005a).

Sea ice is known to affect Adélie penguin (*Pygoscelis adeliae*) population dynamics (Wilson et al. 2001; Kato et al. 2002; Jenouvrier et al. 2006; Forcada et al. 2006) through changes in survival (Jenouvrier et al. 2006), breeding success (Ainley 2002; Emmerson and Southwell 2008) and recruitment (Hinke et al. 2007). Its effects on Adélie penguin populations have been investigated in the Antarctic Peninsula region (Smith et al. 1999; Forcada et al. 2006; Hinke et al. 2007), in East Antarctica (Kato et al. 2002; Jenouvrier et al. 2006; Emmerson and Southwell 2008), and in the southern Ross Sea (Wilson et al. 2001). Adélie penguins are obligate associates of the pack ice habitat outside the breeding season. Their winter distribution ranges from the north of the consolidated pack ice (>80% ice cover) to the south of the unstable ice edge (<15% ice cover; Ainley 2002). Fraser and Trivelpiece (1996) hypothesized that optimal conditions for population growth during winter result from the juxtaposition of several factors, such as the type of sea ice, the bottom topography, the availability of prey, and a minimum amount of hours of daylight during which to feed (“optimum habitat hypothesis,” see also Smith et al. 1999; Ainley 2002). According to the “optimum habitat hypothesis,” both extremely high and extremely low SIE negatively affect Adélie penguin population growth. The difference in position of the ice edge, determined by the total SIE, could indeed affect the overwinter survival of Adélie penguins by displacing them into a better or worse winter habitat (Wilson et al. 2001).

Sea ice extent and duration have markedly decreased in some regions of the Antarctic, such as the Western Antarctic Peninsula (cf. Smith et al. 1999; Parkinson 2002). This reduction in SIE has been suggested as a factor contributing to the decrease in the breeding populations of ice-associated Adélie penguins along the Western Antarctic Peninsula and the partial replacement of these populations by open water *Pygoscelis* species (Smith et al. 1999; Forcada et al. 2006; Hinke et al. 2007). In contrast, SIE in the Ross Sea region of the Antarctic has increased since the

late 1970s (Parkinson 2002; Zwally et al. 2002), and Adélie penguin populations in this region have increased since the 1960s (Ainley et al. 2005; Jenouvrier et al. 2006). However, in spite of this increasing trend in the Ross Sea, there is evidence that high winter SIE can negatively affect the sizes of Adélie penguin colonies in both the southern Ross Sea and in East Antarctica (Wilson et al. 2001; Jenouvrier et al. 2006). Studies of Ross Sea Adélie penguin populations (Wilson et al. 2001; Jenouvrier et al. 2006) showed a negative correlation between increased winter SIE five years earlier and population growth, suggesting that juvenile survival, expressed in terms of recruitment to the breeding population at an average age of 5–6 years, is crucial in explaining population dynamics. Also, adult survival rates were lower after winters with higher SIE (Jenouvrier et al. 2006).

In this study, data from an 11-year mark–recapture study were used to derive relationships between winter environmental conditions and adult and juvenile survival of Adélie penguins breeding in Central Victoria Land, Ross Sea, which is in the middle of a latitudinal gradient between the southernmost colonies in the Ross Sea (Ainley et al. 2005) and the colonies in East Antarctica (Jenouvrier et al. 2006). Annual presence–absence data for known-age birds and for adult birds of unknown age were analyzed using mark–recapture models (Lebreton et al. 1992) to estimate age-dependent survival, detection probability and breeding propensity. Temporal variations in survival rates were then modeled as a function of winter sea ice extent anomalies (SIEA) in the Ross Sea and as a function of the winter Southern Oscillation Index (SOI). The SIEA provide comparisons of winter conditions in individual years with long-term average conditions. The SOI provides a measure of large-scale climate variability that is correlated with the survival of Adélie penguins in Eastern Antarctica and to changes in population size in the Southern Ross Sea (Jenouvrier et al. 2006; Wilson et al. 2001). Survival probabilities of Adélie penguins from Edmonson Point were modeled as a function of SIEA and SOI using linear and nonlinear models.

## Methods

### Study colony and sample size

The Adélie penguin colony at Edmonson Point (74°20'S, 165°08'E) is an ice-free area of about 6 km<sup>2</sup> along the Victoria Land coast (Ross Sea, Antarctica). The colony consists of about 2,100 pairs distributed in a dozen breeding groups (Pezzo et al. 2007). In 1994, the northern part of the colony, about 30% of the whole population, was enclosed with wire netting fences, and

an automatic penguin monitoring system (APMS) (Kerry et al. 1993) was installed across the pathway that provides colony access (Olmastromi et al. 2000). During the 1994–2002 breeding seasons, 538 adult breeders (273 males and 265 females sexed according to Sladen 1978) and 600 chicks at the crèche stage were marked with subcutaneously implanted passive transponders (Olmastromi et al. 2000). This allowed their presence at the colony in subsequent years to be recorded by the APMS. For subsequent mark–recapture analyses, the Adélie penguins were sorted into three groups: adult male breeders ( $\geq 4$  years old), adult female breeders ( $\geq 4$  years old), and birds of unknown sex but known age that were marked as chicks.

### Goodness of fit

Analysis of the mark–recapture data obtained from the Edmondson Point Adélie penguins started with the identification of a general model that adequately fitted the data. This general model was then used as the basis for selecting simpler model structures (e.g., Lebreton et al. 1992). In this first model, both recapture ( $p$ ) and survival probability ( $\Phi$ ) were fully time and group dependent, and the model represents an extension of the Cormack–Jolly–Seber model (CJS, Lebreton et al. 1992) to multiple groups. The goodness of fit (GOF) test for the CJS model is based on contingency tables that verify the assumptions of parameter homogeneity across individuals of the same group (Lebreton et al. 1992). Specific directional Z-tests are available to detect departures from these assumptions (see Appendix I in Tavecchia et al. 2008). The GOF test for the general model was assessed using the software U-CARE (Choquet et al. 2005b). With three groups in the initial data set, U-CARE provided statistics for each group separately that were subsequently combined to create a global GOF test for the entire data set. This global test was significant ( $\chi^2_{61} = 464.55$ ;  $p = 0.000$ ) and suggested that the CJS model was not capturing all of the variation in the data, or at least not in all groups. Inspection of the test components suggested that much of the lack of fit was due to differences in survival between newly marked and previously marked birds in the breeding males group ( $\chi^2_9 = 41.96$ ,  $p < 0.001$ ;  $Z = 2.39$ ,  $p < 0.05$ ) and in the group of birds marked as chicks ( $\chi^2_8 = 166.99$ ,  $p = 0.000$ ;  $Z = 8.12$ ,  $p < 0.01$ ). To correct for this effect, typically called the “transient effect,” parameters were included in the general model to differentiate the first survival after marking (Pradel et al. 1997) for the adult male breeders and the birds marked as chicks, and the global GOF test was recalculated. The second GOF test was still significant ( $\chi^2_{43} = 72.54$ ,  $p = 0.003$ ), and so the remaining lack of fit was accounted for by scaling the deviance of successive

models by a variance inflator factor ( $\hat{c}$ ) calculated as the ratio of the global  $\chi^2$  statistic to its degrees of freedom ( $\hat{c} = \sum \chi^2 / \sum df = 1.69$ ; Lebreton et al. 1992). The structure of this model was further modified to include ten age classes in both recapture and survival for the birds of known age ( $\Phi_{\text{breeders}}$  transient in males + sex + time,  $\Phi_{\text{known-age birds}}$  10 age classes + time;  $p_{\text{breeders}}$  sex + time,  $p_{\text{known-age birds}}$  10 age classes + time). This allowed the analysis of age-related variations in capture and survival probabilities.

### Modeling recapture and survival processes

Model selection followed a multistep descendent strategy in which the structures of capture and survival probabilities were first modeled separately and the best structures of the two parameters were then combined and considered simultaneously in a series of “consensual models” (Grosbois and Tavecchia 2003). The consensual models included the effects of capture and survival obtained from the separate models, thereby providing a more parsimonious environment in which the effects not retained in the early steps of the analysis could be re-examined. In both recapture and survival, sex differences between the male and female groups were modeled first. The effect of age on the group of known-age birds was then modeled by progressively reducing the number of age classes. This allowed us to determine if parameters obtained for the oldest birds were similar to those of the male and female breeders of unknown age.

Competitive models were developed and fit to the data using the program M-Surge (Choquet et al. 2005a) and selected by the Akaike’s information criterion corrected for overdispersion (QAIC; Burnham and Anderson 2002). Models with  $\Delta\text{QAIC} \leq 2$  were considered mathematically equivalent to each other (Burnham and Anderson 2002). Presence–absence data were not available for the 1999–2000 breeding season, so the capture probabilities for this period were set to zero. Capture probability is conditional on the presence of marked individuals in the colony, and in seabirds adult capture probability is considered a reliable index for breeding propensity (Jenouvrier et al. 2003), which is defined as the probability that a sexually mature adult will breed in a given year. Known-age birds marked as chicks begin to return to the colony when they are two years old, so survival probabilities for the first and second years of life could only be estimated as a product. The capture probability for birds one and two years of age was set to zero and a common survival parameter was specified for these age classes. Estimates for these two parameters were obtained by calculating the probability,  $l$ , of reaching age  $j$  (i.e., the product of the age-dependent survival until age  $j$ ,  $j = 3, \dots, 10$ ) and using this cumulative

curve to back-calculate the probabilities for the first and second years of life separately.

#### Environmental covariates

Monthly measures of sea ice extent anomalies (SIEA) for the Ross Sea sector (from 150°E to 230°E) for 1994–2004 were obtained from the National Snow and Ice Data Center (<http://nsidc.org>). The SIEA were calculated as the difference between the monthly sea ice extent and the total monthly long-term average, with the ice edge defined as the location where the sea ice concentration drops below 15%. Here SIEA values from June to September for the period 1994–2004 were averaged to obtain a single winter index for each year.

Monthly values of the Southern Oscillation Index (SOI) from 1994 to 2004 were obtained from the Australian Bureau of Meteorology (<http://www.bom.gov.au>). The SOI values range from about –35 to about +35 and represent the standardized anomaly of the average difference in sea level pressure between Tahiti and Darwin (Australia) calculated over the long term. In this work, SOI values for the months from June to September for the years 1994–2004 were averaged to obtain a single winter index.

#### Covariate-dependent models

Starting from the identified age structure, temporal variations in survival were correlated with the covariates using a linear and a quadratic relationship. As in Catchpole et al. (2000), we first considered models in which the effect of the covariates was investigated for each age class separately while survival for the other age classes was allowed to vary with time. Two types of models were used to explore the functional relationship between age and climatic indexes: (1) additive models, in which the effect of the covariate was the same for all age classes, and (2) interactive models, in which the relationship between survival and the covariate was assumed to vary according to the age class considered (Coulson et al. 2001). Models were selected on the basis of the QAIC, and model weights ( $w_k$ ) were calculated as a measure of the relative importance of each model in the model set (Burnham and Anderson 2002). The fraction of deviance accounted for by the covariates was then calculated as

$$\frac{[D(\text{constant model}) - D(\text{covariate model})]}{[D(\text{constant model}) - D(\text{full-time model})]} \quad (1)$$

Here  $D$  is the deviance of the model. This statistic is equivalent to the coefficient of determination ( $R^2$ ) derived in the ANOVA (Harris et al. 2005).

## Results

### Goodness of fit and model selection

Examination of contingency tables and inspection of specific directional Z-tests indicated that the transient effect (i.e., the difference in survival probabilities between newly marked and already-marked birds) was present in the group of breeding males during the first yearly interval (1994–1995). The transient effect was not evident in successive years, and there was no support for it in subsequent model selection (Tables 2 and 3). Conversely, in the group of birds marked as chicks, the differences in survival probability between newly marked and already-marked individuals were systematically present and corresponded to age-related differences in survival (i.e., survival in the first year of life was much lower than in subsequent years). These differences were taken into account in the models. The results of the independent model selection on capture probability,  $p$ , indicated that males and females were equally present or detected in the colony (Table 1, model 4 vs. model 5;  $\Delta\text{QAIC} = 1.55$ ). In the group of known-age birds, a model with five age classes (model 1) was preferred over a model with more age classes, and the capture probability of the last age class was different from the capture probability of adult male and female breeders (Table 1, model 1 vs. model 10;  $\Delta\text{QAIC} = 25.43$ ). Results obtained for the independent model selection on survival probability,  $\Phi$ , showed that survivals of males and females were similar (Table 2, model 20 vs. model 19  $\Delta\text{QAIC} = 1.72$ ), in an analogous way to what was found for the recapture models. There was no support for the transient effect in the group of male breeders (Table 2, model 19 vs. model 18,  $\Delta\text{QAIC} = 5.48$ ). For known-age birds, model selection led to two competitive models with six and five age classes, respectively ( $\Delta\text{QAIC} < 2$ ). The model with five age classes (model 11) was arbitrarily preferred for its simpler age structure, consistent with the age structure selected for capture probability.

The structures of the best models for the capture and survival probabilities were combined in a consensual model that was used as a new starting point for model selection (Table 3). The transient effect in the group of male breeders and sex differences in survival between adult birds were retested but were not supported by the data and were not retained. Similarly, there was little support for an effect of sex on capture probability (Table 3, model 22 vs. model 23  $\Delta\text{QAIC} = 1.93$ ). Time-dependent models were preferred over time-invariant models (Table 3, model 26 vs. model 22  $\Delta\text{QAIC} = 22.27$  for survival and model 28 vs. model 22  $\Delta\text{QAIC} = 858.98$  for recapture). The best model was:  $\Phi_{\text{breeders}}$  time,  $\Phi_{\text{known-age birds}}$  5 age

**Table 1** Modelling the capture probabilities  $p$  of Adélie penguins at Edmonson Point

Model	$p$ breeders	$p$ known-age birds	$K$	DEV	QAIC	$\Delta$ QAIC
1	Time	5 age classes + time	62	3760.09	2352.86	<b>0.00</b>
2	Time	9 age classes § + time	73	3735.11	2360.05	7.19
3	Time	6 age classes + time	71	3742.26	2360.29	7.43
4	Sex + time	10 age classes + time	75	3728.83	2360.33	7.47
5	Time	10 age classes + time	74	3734.81	2361.88	9.02
6	Time	7 age classes + time	72	3742.26	2362.29	9.43
7	Time	7 age classes § + time	69	3753.58	2363.00	10.14
8	Time	8 age classes § + time	71	3748.53	2364.01	11.15
9	Time	6 age classes § + time	67	3768.56	2367.88	15.02
10	Time	5 age classes § + time	65	3792.87	2378.29	25.43

$k$ , Number of estimable model parameters;  $DEV$ , model deviance;  $QAIC$ , Akaike’s information criterion corrected for overdispersion;  $\Delta QAIC$ , difference in QAIC between each candidate model and the model with the lowest QAIC value

§, Parameter for the capture probability of the last age class in the group of known-age birds has the same value as the parameter for the capture probability in breeder birds. The structure of the survival probabilities is the same as the general model ( $\Phi_{\text{breeders}}$  transient in males + sex + time,  $\Phi_{\text{known-age birds}}$  10 age classes + time)

The  $\Delta QAIC$  of the selected model is shown in bold

**Table 2** Modeling the survival probabilities  $\Phi$  of Adélie penguins at Edmonson Point

Model	$\Phi$ breeders	$\Phi$ known-age birds	$K$	DEV	QAIC	$\Delta$ QAIC
11	Time	5 age classes § + time	53	3748.97	2328.27	<b>0.00</b>
12	Time	6 age classes § + time	54	3748.77	2330.15	1.88
13	Time	2 age classes § + time	51	3759.73	2330.65	2.38
14	Time	3 age classes § + time	51	3759.77	2330.67	2.40
15	Time	4 age classes § + time	52	3759.4	2332.45	4.18
16	Time	10 age classes § + time	58	3746.32	2336.70	8.43
17	Constant	1 age constant	46	3810.71	2350.87	22.60
18	Time	10 age classes + time	69	3736.92	2353.13	24.86
19	Transient + time	10 age classes + time	75	3725.92	2358.61	30.34
20	Transient + sex + time	10 age classes + time	75	3728.83	2360.33	32.06
21	Time	1 age classes § + time	50	3960.7	2447.78	119.51

$k$ , Number of estimable model parameters;  $DEV$ , model deviance;  $QAIC$ , Akaike’s information criterion corrected for overdispersion;  $\Delta QAIC$ , difference in QAIC between each candidate model and the model with the lowest QAIC value

§, Parameter for the survival probability of the last age class in known-age birds has the same value as the parameter for survival probability in breeder birds

The structure of the capture probabilities is the same as the general model ( $p_{\text{breeders}}$  sex + time,  $p_{\text{known-age birds}}$  10 age classes + time)

The  $\Delta QAIC$  of the selected model is shown in bold

classes + time;  $p_{\text{breeders}}$  sex + time,  $p_{\text{known-age birds}}$  5 age classes + time (Table 3, model 22).

Parameter estimates

According to the best model, the capture probability for male and female breeders was close to 1 almost every year (range: 0.98, SE = 0.01–0.99, SE = 0.01). Significant differences between the sexes occurred only in the 2001/

2002 breeding season, when both male (0.67, SE = 0.05) and female (0.80, SE = 0.05) capture probabilities were much lower than in the rest of the study period. However, these low capture rates were most likely the result of a malfunction in the remote detection system. Snow accumulated on the fences that surrounded the study area at Edmonson Point in winter 2001, collapsing them. Due to logistical constraints, the colony was not visited in 2001/2002, which prevented the removal of the snow and

**Table 3** Consensual modeling of the capture ( $p$ ) and survival probabilities ( $\Phi$ ) of Adélie penguins at Edmonson Point

Model	$\Phi$ breeders	$\Phi$ known-age birds	$p$ breeders	$p$ known-age birds	$K$	DEV	QAIC	$\Delta$ QAIC
22	Time	5 age classes § + time	Sex + time	5 age classes + time	30	3796.17	2310.25	<b>0.00</b>
23	Time	5 age classes § + time	Time	5 age classes + time	29	3802.81	2312.19	1.93
24	Transient + time	5 age classes § + time	Time	5 age classes + time	31	3799.02	2313.94	3.69
25	Sex + time	5 age classes § + time	Time	5 age classes + time	31	3799.88	2314.45	4.20
26	Constant	5 age classes § constant	Time	5 age classes + time	21	3864.10	2332.52	22.27
27	Time	5 age classes § + time	Time	5 age classes § + time	28	3848.60	2337.33	27.08
28	Time	5 age classes § + time	Constant	5 age classes constant	16	5292.51	3169.23	858.98

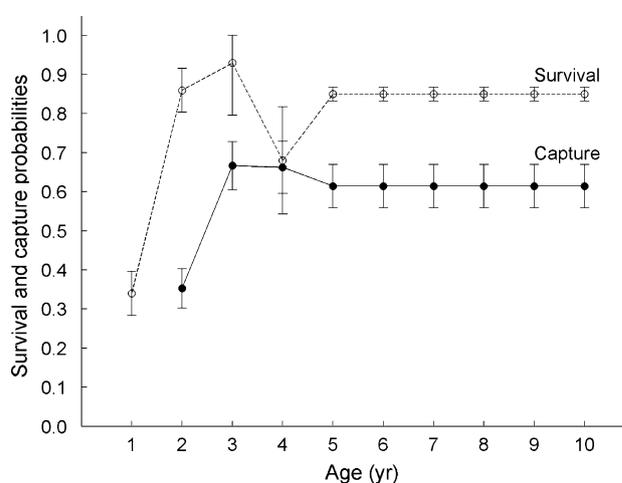
$k$ , Number of estimable model parameters;  $DEV$ , model deviance;  $QAIC$ , Akaike's information criterion corrected for overdispersion;  $\Delta QAIC$ , difference in QAIC between each candidate model and the model with the lowest QAIC value

§, The capture (or survival) probability of the last age class in known-age birds has the same value as the capture (or survival) probability in breeder birds

The  $\Delta QAIC$  of the selected model is shown in bold

realignment of the fences. Consequently, the penguins were able to enter the study area and to get to their breeding nests while avoiding the APMS.

Overall, about 25% of the chicks marked returned to their natal colony. Parameter estimates from a model with time-invariant capture probabilities (Table 3, model 28) showed that capture probability increased with age, and that full recruitment (i.e., the highest capture probability) occurred between ages 4 and 5, after which it was age invariant (Fig. 1). The capture probability of birds older than five years was 0.69 (SE = 0.09). This value was lower than the capture probability of birds marked as adults (0.98, SE = 0.01), suggesting that recruitment can be deferred to very old ages. Survival rates for breeder birds varied during the study period from a minimum value of 0.76 (SE = 0.06) in winter 1995 to a maximum of 0.94 (SE = 0.04) in winter 2001. A time-invariant survival model (model 26 Table 3) indicated a mean value of 0.85 (SE = 0.01). For the group of birds marked as chicks, a model assuming a constant survival for each included age class indicated that survival probabilities increased until the third year of life, decreased in the fourth year, and then stabilized from the fifth year onward (Fig. 1). The common survival estimate for the first two age classes was 0.54 (SE = 0.06), and separate estimates obtained from the cumulative survivorship curve were 0.34 and 0.86, respectively. Capture–recapture models do not distinguish between mortality and permanent emigration, and so part of the mortality estimated here likely corresponds to permanent pre-breeding emigration of juvenile penguins to other colonies. Overall, survival variations with age were more important than survival variations over time, and interannual variations in survival decreased with age ( $CV_{\text{first 2 years of life}} = 0.20$ ,  $CV_{\text{age 3}} = 0.03$ ,  $CV_{\text{age 4}} = 0.11$  and  $CV_{\text{age} \geq 5} = 0.06$ ).



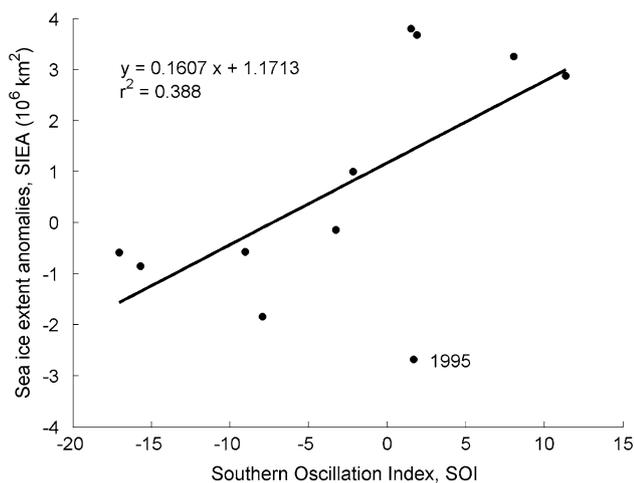
**Fig. 1** Age-specific estimates of local survival (open circle with dotted line) and capture (filled circle with straight line) probabilities ( $\pm 95\%$  CI) for Adélie penguins (*Pygoscelis adeliae*) at Edmonson Point, Antarctica, for the period 1995–2004. Survival data are from model 27 and capture data are from model 30

#### Environmental covariates

During 1993–2004 positive sea ice extent anomalies (SIEA) generally occurred in conjunction with positive values of the Southern Oscillation Index (SOI) ( $r = 0.62$ ;  $p < 0.05$ ). This means that winter SIE in the Ross Sea was usually higher during years characterized by cold “la Niña” events in the equatorial Pacific. The two indices covary positively but with different magnitudes during the years included in this study (Fig. 2).

#### Covariate-dependent models

Models that included environmental covariates were first used to consider the effect of these covariates on survival for each age class (Table 4, models 29–44). For the first



**Fig. 2** Sea ice extent anomalies (SIEA) in the Ross Sea plotted against the Southern Oscillation Index (SOI) for the period 1995–2004. The year 1995 is labeled (see “Discussion”)

three age classes, models that assumed a linear function or quadratic dependence on SIEA or SOI received the same support ( $\Delta\text{QAIC} < 2$ ). It was thus not possible to identify a single covariate that performed best in explaining the temporal variations in survival in these age classes. In contrast, the model in which survival of the adult birds was assumed to have a quadratic dependence on SIEA (model 42) received strong support (for the other models  $\text{QAIC} > 2$  and  $w_{42} = 0.95$ ). Subsequent models assumed that the relationship between survival and covariates was the same for all age classes (Table 4, additive models 45–48 and interactive models 49–52). In the set of additive models, the model with a quadratic relationship between SIEA and survival (model 46) was preferred over the others ( $\Delta\text{QAIC} \gg 2$ ) and had a model weight  $w_{46} = 1$ . This same relationship was also selected in the set of interactive models (model 50) and had a model weight  $w_{50} = 0.86$ . Considering all models, models 46 and 50 had the lowest QAIC and their model weights summed to the 71% of all model weights. It should be noted that the age class with the most data (adults) dominated the numerical relationship in these models.

The fraction of temporal deviance explained by the additive and interactive covariate models showed that the quadratic relationship between survival and SIEA (model 50) explained 95% of the temporal variability in survival rates (Table 5). Survival estimates from model 50 are in agreement with survival estimates from the fully time-dependent model (model 22) for most years, with the exception of 2002–2003 (Fig. 3). In winter 2003 the SIEA was close to zero, and according to the quadratic relationship of model 50, the adult survival rate should be 0.88 (SE = 0.04). The estimate from the fully time-dependent model, however, was 0.81 (SE = 0.02; Fig. 3), suggesting

that SIEA was not the only predictor of survival that year. Survival rates for the first year of the study, which correspond to winter 1995, were based on a low number of marked birds, and the goodness of fit for this year revealed a transient effect (i.e., an apparent lower survival probability in the first year of the study). Coincidentally, this year was also characterized by the lowest extent of winter sea ice during the study period. When this year was omitted from the analysis, the quadratic relationship still had better statistical support than the linear relationship.

## Discussion

### Effects of winter sea ice

Survival is a key demographic indicator for long-lived species (Russell 1999; Saether and Bakke 2000), and this study contributes to our understanding of survival in Adélie penguins. Survival probabilities of Adélie penguins from the Edmonson Point colony are influenced by winter sea ice extent (SIE) in the Ross Sea. From 1994 to 2004, survival at this colony was lower during years characterized by both low or high SIE, and was greatest in years characterized by intermediate values of SIE. The winter distribution of Adélie penguins in the Ross Sea ranges from the north of the consolidated pack ice (>80% ice cover) to the south of the unstable ice edge (<15% ice cover; Ainley 2002), approximately coinciding with the narrow marginal ice zone (Ferreyra et al. 2004). Consolidated ice provides resting sites for Adélie penguins, while open water allows access to foraging areas and prey during the limited daylight hours in winter. The limited daylight during winter makes it desirable for penguins to return to winter habitats where bottom topography and oceanic circulation ensure a predictable food supply (Fraser and Trivelpiece 1996; Ribic et al. 2008).

In the Ross Sea, a region of pack ice with a maximum width of 200 km (cf. Gloersen et al. 1992) that partially overlaps the southern boundary of the Antarctic Circumpolar Current (ACC) provides an appropriate winter habitat for Adélie penguins (Wilson et al. 2001). The southern boundary of the ACC has been identified as a region of high biological productivity with associated top predators such as whales (Tynan 1998). Wilson et al. (2001) suggested that extremely high SIE could restrict penguin access to food by displacing them northward and restricting access to productive waters south of the ACC (Tynan 1998). Similarly, an extremely low SIE could negatively affect penguin survival by keeping them south of the good foraging grounds. A displacement from its optimal winter foraging habitat potentially has serious consequences for a species such as the Adélie penguin that has limited ability

**Table 4** Modeling the effects of environmental covariates

Name		$k$	DEV	QAIC	$\Delta$ QAIC relative to set	$w_k$ relative to set	$\Delta$ QAIC relative to all models	$w_k$ relative to all models
Juveniles								
29	SIEA	36	3796.41	2319.73	1.69	0.21	8.27	0.01
30	SIEA2	37	3790.18	2318.04	0.00	0.48	6.59	0.02
31	SOI	36	3796.51	2319.79	1.75	0.21	8.33	0.01
32	SOI2	37	3795.67	2321.29	3.25	0.10	9.84	0.00
Age class 3								
33	SIEA	36	3790.56	2316.26	0.11	0.39	4.81	0.04
34	SIEA2	37	3790.12	2318.00	1.85	0.17	6.55	0.02
35	SOI	36	3790.38	2316.16	0.00	0.41	4.70	0.04
36	SOI2	37	3796.46	2321.76	5.60	0.03	10.30	0.00
Age class 4								
37	SIEA	36	3791.28	2316.69	0.00	0.48	5.24	0.03
38	SIEA2	37	3790.39	2318.16	1.47	0.23	6.71	0.01
39	SOI	36	3793.04	2317.73	1.04	0.29	6.28	0.02
40	SOI2	37	3822.75	2337.32	20.63	0.00	25.87	0.00
Adults								
41	SIEA	31	3818.18	2322.62	5.87	0.05	11.16	0.00
42	SIEA2	32	3804.88	2316.74	0.00	0.95	5.29	0.03
43	SOI	31	3828.99	2329.02	12.27	0.00	17.56	0.00
44	SOI2	32	3827.47	2330.12	13.37	0.00	18.66	0.00
Additive models								
45	SIEA	22	3860.92	2329.92	17.50	0.00	18.47	0.00
46	SIEA2	23	3827.99	2312.42	0.00	1.00	<b>0.97</b>	0.28
47	SOI	22	3863.78	2331.61	19.19	0.00	20.16	0.00
48	SOI2	23	3862.67	2332.96	20.53	0.00	21.51	0.00
Interactive models								
49	SIEA	25	3826.31	2315.43	3.98	0.12	3.98	0.06
50	SIEA2	29	3806.08	2311.45	0.00	0.86	<b>0.00</b>	0.43
51	SOI	25	3842.26	2324.87	13.42	0.00	13.42	0.00
52	SOI2	29	3834.95	2328.54	17.09	0.00	17.09	0.00

$k$ , Number of parameters; *DEV*, deviance; *QAIC*, Akaike's information criterion corrected for overdispersion;  $\Delta$ QAIC, difference in QAIC between each candidate and the model with the lowest QAIC value;  $w_k$ , Akaike's weights; *SIEA*, linear sea ice extent anomaly relationship; *SIEA2*, quadratic relationship; *SOI*, linear Southern Oscillation Index relationship; *SOI2*, quadratic relationship

*Additive models* models in which the covariate had the same effect for all age classes; *interactive models* models with an age per covariate interaction

The  $\Delta$ QAIC of the selected models are shown in bold

to move to more favorable locations when environmental conditions are poor (Weimerskirch 2002).

Changes in winter SIE can potentially affect Adélie penguin overwintering survival by changing migratory routes. Clarke et al. (2003) found that the winter movements of satellite-tracked penguins in East Antarctica followed sea ice motions, which in turn were influenced by oceanic current systems and wind. Clarke et al. (2003) further proposed that oceanic systems provide a means for Adélie penguins to reduce the cost of transport as they

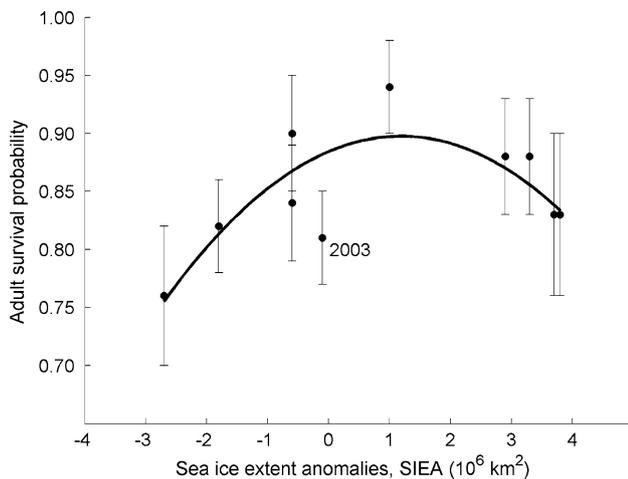
travel into regions of high productivity during winter and return to the breeding colonies in spring. The migratory routes of Adélie penguins in the Ross Sea are poorly known, but winter movements of sea ice could have a similar importance for the penguins of this region (cf. Davis et al. 1996, 2001; Clarke et al. 2003). Finally, reduced winter SIE could negatively affect Adélie penguin survival and recruitment through a reduction in primary production (Smith et al. 2001, 2007) and abundance of krill, a primary prey for the Adélie penguin (Ainley 2002).

**Table 5** Fraction of the temporal variation explained by the environmental covariates

	Covariate and type of function			
	SIEA	SIEA + SIEA2	SOI	SOI + SOI2
Additive models	0.05	0.59	0.01	0.02
Interactive models	0.62	0.95	0.36	0.48

*Additive models*, models in which the covariates had the same effect for all age classes (models 45–48; Table 4); *interactive models*, models with an age-by-covariate interaction (i.e., models in which covariates had a specific effect for the age class considered; models 49–52; Table 4)

*SIAE*, sea ice extent anomalies in the Ross Sea; *SOI*, Southern Oscillation Index



**Fig. 3** Annual estimates of adult survival probability ( $\pm 95\%$  CI) for Adélie penguins at Edmonson Point, Antarctica, plotted against sea ice extent anomalies (SIEA) in the Ross Sea. *Solid circles* are the estimates from the time-dependent model (model 22); the *black line* represents survival estimates from the model with a quadratic relationship with SIEA (model 50). The year 2003 is labeled (see “Discussion”)

Such interactions have been observed for other predators, such as Weddell seals *Leptonychotes weddellii* (Hadley et al. 2007).

Unlike the results reported by Jenouvrier et al. (2006), survival rates of Adélie penguins at Edmonson Point were not correlated with the Southern Oscillation Index (SOI). Positive SOI values are associated with cooler sea surface and air temperatures in the eastern tropical Pacific Ocean and positive SIE in the Ross Sea (i.e., SIE is greater when the  $SOI > 1$ ; Kwok and Comiso 2002). However, in 1995 the SOI was positive ( $SOI = 1.68$ , Fig. 2), and the SIE was the lowest recorded during the study period ( $SIEA = -2.68 \text{ km}^2 \times 10^6$ ). In the winters of 1999 and 2000, the SOI and SIEA were positive but the SIE was higher than predicted by a linear relationship with SOI (Fig. 2). Factors

other than the SOI affect sea ice formation and extent in the Ross Sea (Turner 2004), and the large-scale nature of the SOI does not fully capture local climate variability. The results from this study show that Adélie penguin survival rates are correlated with the SIE but not the SOI, which supports the hypothesis that a combination of local factors determine variations in winter survival in the Adélie penguin (cf. Wilson et al. 2001; Hinke et al. 2007; Ribic et al. 2008).

#### Juvenile and adult survival

A common trait of seabirds is deferred maturity at breeding (Crespin et al. 2006). In the Adélie penguin, pre-breeders typically spend one or more years at sea before becoming sexually mature and returning to the colony to breed (Ainley 2002). This delay in breeding was observed in the Edmondson Point Adélie penguins. The proportion of birds marked as chicks that returned to the natal colony increased with age. On average, the proportion (0.25) returning to Edmondson Point was low in comparison to other studies in the Southern Ross Sea (61% at Ross Island, Ainley et al. 1983) and in East Antarctica (44% at Béchervaise Island, Clarke et al. 2003). As a result, local survival estimates at Edmondson point for the first year of life were lower (0.34) than those estimated for Ross Island (0.52, Reid 1968; 0.29–0.51, Ainley et al. 1983) and Béchervaise Island (0.69–0.77, Clarke et al. 2003), as they include permanent emigration from the area. There is no reason to expect a greater mortality for birds born at Edmondson Point relative to other colonies in the Ross Sea and East Antarctica. Indeed, a low number of marked birds were identified manually outside the automatically monitored area (Olmastroni, personal observation), further suggesting that dispersal occurs within the Adélie penguin metapopulation associated with the Terra Nova Bay polynya (Ainley et al. 1995; Ainley 2002).

Despite low survival in the first year of life, annual adult survival probability at Edmondson Point (0.85, range 0.76–0.94) was similar to that estimated from other Adélie penguin populations in which individuals were marked with passive transponders (0.86, range 0.75–0.91, Clarke et al. 2003; 0.87, range 0.85–0.88, Dugger et al. 2006), and higher than estimates made from studies that used individuals marked with flipper bands (0.76, range 0.64–0.82, Jenouvrier et al. 2006). An annual average survival rate of 0.85 seems to be typical of the species and is consistent with an expected average lifespan of about 11 years (6.6 years after adulthood). The average annual adult survival probability estimated for Adélie penguins in this study is low when compared to estimates for king *Aptenodytes patagonicus* and emperor *A. forsteri* penguins (Barbraud and Weimerskirch 2001; Olsson and van der

Jeugd 2002; Jenouvrier et al. 2005b, c; Le Bohec et al. 2008) and petrels and albatrosses (Weimerskirch 2002).

Because females experience higher reproductive costs, it was suggested that they have a lower life expectancy (Ainley et al. 1983; Dugger et al. 2006). However, this study did not find a sex-related effect on survival, which is in agreement with the findings of Clarke et al. (2003). In penguins in general it is not known whether females and males have similar life expectancies (Williams 1995), but differences in annual survival rates between the sexes seem to arise only under very harsh environmental conditions at breeding (Olsson and van der Jeugd 2002; see also Barbraud and Weimerskirch 2001).

Life-history theory predicts that natural selection tends to decrease the variation of the parameters that more strongly influence individual fitness (Stearns 1992; Morris and Doak 2004; Gaillard and Yoccoz 2004). In the case of long-lived iteroparous species, such as seabirds, adult survival is the parameter that is expected to contribute more to lifetime reproductive success (Saether and Bakke 2000). The Adélie penguin adult survival measured in this study showed little time variability, which agrees with the expectation from life-history theory. Other measured parameters such as juvenile survival (this study) and breeding output (Pezzo et al. 2007) were instead characterized by considerable interannual variability. The pattern of survival variation with age observed for the Edmonson Point Adélie penguins is typical of long-lived species, with elevated mortality in the first year of life (Gaillard et al. 2000). A similar survival curve was described for other penguin species and has been hypothesized as being characteristic of all seabirds (cf. Russell 1999 and references herein).

### Survival and breeding strategy

Lifetime reproductive success in long-lived species depends primarily on adult survival rather than on fecundity (Clutton-Brock 1988; Erikstad et al. 1998). Therefore, these species tend to reduce reproductive effort in years of adverse environmental conditions so as to not jeopardize their future survival (Drent and Dann 1980) and to increase their reproductive effort when favorable environmental conditions prevail (Erikstad et al. 1998). In some long-lived seabirds it is common for parents to desert the eggs and chicks when adult body mass reaches a low threshold (petrels, albatrosses; Monaghan et al. 1989; Chastel et al. 1993; Oro et al. 1996; Jenouvrier et al. 2003; Navarro and González-Solís 2007). In years of bad weather and poor environmental conditions, some species, such as fulmars (Jenouvrier et al. 2005a), skip reproduction. Adélie penguins at Edmonson Point, however, appear to follow a strategy which includes breeding every year, regardless of

environmental conditions. Evidence for this “every-year breeding strategy” is provided by their high breeding propensity (Dugger et al. 2006 also report capture probabilities close to 1) and by their reluctance to abandon the nest even when faced with unfavorable environmental conditions (Olmastroni et al. 2004). This is consistent with the constant and repeatable behavioral patterns of the Adélie penguin, such as high breeding site fidelity, low divorce rate, and traditional wintering habitats (Williams 1995; Fraser and Trivelpiece 1996).

Although much seabird mortality occurs in the winter season, survival can also be partially affected by conditions experienced at breeding (Jacobsen et al. 1995, Davis et al. 2005). For example, increased mortality for breeding individuals has been observed for king penguins after a year of food stress during the breeding season (Olsson and van der Jeugd 2002). The results from this study suggest that the same may have occurred in 2002 for the Adélie penguins at Edmonson Point. Adult survival in winter 2002/2003 was lower than expected from the SIEA relationship and we hypothesize that this is a consequence of an exceptionally stressful breeding season in 2002. The 2002 breeding season (from October 2002 to February 2003) was, in fact, exceptional, as extensive sea ice persisted in front of Edmonson Point during the whole breeding season (Olmastroni et al. 2004, Pezzo et al. 2007). The extensive sea ice delayed the return of females during the incubation period and necessitated longer foraging trips during the chick-rearing period. Consequently, breeding effort was unusually high, and adult mean body mass was lower than that observed in previous seasons (Olmastroni et al. 2004). Olmastroni et al. (2004) hypothesized that reduced food availability or increased foraging effort caused the drop in mean adult body weight during the 2002 breeding season. The results from this study lead to the further hypothesis that the lower survival of Adélie penguins in the subsequent winter (2003) reflected the poor condition of individuals prior to winter migration after the 2002 breeding season. The lower survival of Adélie penguins relative to other seabirds may be in part due to the costs associated with their “every-year breeding strategy,” which is however possibly an evolutionarily stable strategy, as in the case of other long-lived vertebrates (Marrow et al. 1996).

### Conclusions

Large-scale oceanographic conditions affect the Antarctic marine ecosystem (Testa et al. 1991; Ainley et al. 2005; Jenouvrier et al. 2005c), and the effects are known to impact Adélie penguin populations (Wilson et al. 2001; Jenouvrier et al. 2006). Analyses of the fossil record from Victoria

Land have shown correlations between fluctuations in the size of Adélie penguin colonies and changes in sea ice regimes (Baroni and Orombelli 1994; Hall et al. 2006; Emslie et al. 2007). Significant correlations have been found between Adélie penguin demographic parameters and sea ice characteristics throughout the circumpolar distribution of this species (Wilson et al. 2001; Jenouvrier et al. 2006; Forcada et al. 2006; Hinke et al. 2007; Emmerson and Southwell 2008; this study). A common conclusion from seabird population modeling for long-lived species is that the population growth rate is more sensitive to changes in adult survival than to changes in reproductive parameters (Pfister 1998; Saether and Bakke 2000). The same result is also true of the Adélie penguin population at Edmonson Point (Ballerini et al. manuscript). The dependence of the population growth rate on adult survival emphasizes the importance of understanding the environmental factors that affect variability in survival, especially if predictions of population trajectories are desired. Thus, demographic models (see for example Jenouvrier et al. 2009) that include an understanding of the interactions between Adélie penguins and sea ice, especially during winter, are needed. Such models will provide a framework to understand and predict potential future population trajectories that could result from environmental conditions that may occur in the Ross Sea as a result of global climate warming (Trathan et al. 2007).

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