

Contrasting effects of the extent of sea-ice on the breeding performance of an Antarctic top predator, the Snow Petrel *Pagodroma nivea*

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Recent studies have shown that the Antarctic Circumpolar Wave and the related sea-ice cover around the Antarctic continent may have a profound effect on the lower trophic levels of the marine environment. In particular, extensive sea-ice cover enhances the survival of krill. However, the effects of sea-ice cover on top predators remain poorly understood. Using time series from 1973 to 1999, we examine the influence of regional sea-ice extent on a number of indices of breeding performance of an avian predator, the Snow Petrel, in Antarctica. The percentage of breeding pairs was highly variable and there were fewer birds breeding when sea-ice cover was extensive during July. By contrast, overall breeding success and fledgling body condition were improved during years with extensive sea-ice cover during the preceding November and July-September. These results indicate that the same sea-ice conditions may have different effects on the breeding performance of a species. The overall increase in winter sea-ice extent during the last decade appears to have resulted in an overall improvement of the quality of fledglings produced, and thus probably of future recruitment.

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Long-term surveys indicate significant interannual variations in sea-ice extent around Antarctica (White and Peterson 1996) and variability in sea-ice extent is critical to growth of plankton populations, such as krill and salps (Smith and Nelson 1986, Loeb et al. 1997). Because Antarctic seabirds feed directly or indirectly on krill within the pack-ice or beyond the ice edge (Ainley et al. 1984) one might expect anomalies of sea-ice extent to affect breeding performance and distribution of seabirds. However, very few long-term studies have shown fluctuations in the breeding performance of polar seabirds in relation to sea-ice extent, and most of those concern penguins (e.g. Fraser et al. 1992, Trathan et al. 1996) and have examined a limited number of indices of breeding performance.

When estimating the effect of sea-surface temperatures or sea-ice extent on seabird breeding performance, studies have only considered the breeding

success, i.e. the number of chicks raised to fledging per nesting pair (but see Guinet et al. 1998). Other measures of breeding performance, such as the body condition of fledglings or the annual percentage of birds breeding, may be more sensitive to variation in ice cover. Furthermore, since variation in the body condition of fledglings has been shown to have significant consequences in terms of recruitment and survival (e.g. Garnett 1981, Williams et al. 1993), natal dispersal (Ferrer 1992), and other fitness components (e.g. Haywood and Perrins 1992, Lindström 1999), the measurement of breeding performance can be improved by considering variation in body condition of fledglings simultaneously with productivity.

The percentage of pairs breeding in any one season, i.e. the rate of nest occupancy, reflects the proportion of individuals that skip breeding during a particular year. Breeding abstention among long-lived species may

be a response to poor feeding conditions early in the breeding season (Drent and Daan 1980, Aebischer and Wanless 1992, Chastel et al. 1993) or the "norm" as, for example, in some albatross species (Warham 1990). When facing food shortage, individuals may not reach a threshold value of early body condition; below this established breeders will refrain from breeding. For example, in the long-lived Blue Petrel *Halobaena caerulea*, depletion of body reserves early in the breeding season may result in a high proportion of nonbreeders (e.g. Chastel et al. 1995).

In this paper, we first examine the effect of sea-ice extent anomalies prior to and during the breeding season on a series of indices of breeding performance in Snow Petrels *Pagodroma nivea*. Second, we test whether all measures of breeding performance are affected similarly by sea-ice extent anomalies and investigate possible long-term effects on the population.

Methods

Data on the breeding performance of Snow Petrels were obtained from a 35-year study (1964-1999) carried out on Ile des Pétrels (800 m x 400 m), Pointe Géologie Archipelago, Terre Adélie, Antarctica (66°40'S, 140°01'E). Nests were marked and checked every year. During the breeding season three measurements were taken: (1) breeding success was calculated as the number of chicks fledged of number of eggs laid; (2) hatching success as the number of eggs hatched of eggs laid; and (3) fledging success as the number of chicks fledged from eggs hatched. For each year, the percentage of occupied nests was calculated as the number of nests in which laying was observed divided by the total number of nests monitored. Because Snow Petrels are extremely faithful to their nest site (Guillot and Jouventin 1980) we assumed that the percentage of occupied nests reflected the percentage of breeding pairs.

Chicks were weighed and measured 40 days after hatching in 1990 and from 1993 to 1999. Measurements taken were: (1) wing length, maximum flattened chord from carpal joint to tip of longest primary (accuracy ± 1 mm); (2) bill length, from edge of implantation of feathers to bill tip (± 0.1 mm); and (3) body mass (± 5 g). A total of 671 chicks was measured. Body size indices were calculated using the first component (PC1) of a principal component analysis performed on wing and bill length (Rising and Somers 1989). PC1 explained 64% of the total variance in linear measurements and both wing and bill lengths were highly correlated with PC1 (Pearson correlation coefficient $r = 0.80$, $n = 671$, $P < 0.001$ for wing length and $r = 0.81$, $n = 671$, $P < 0.001$ for bill length). Body mass was related to the factor scores (body mass =

$27.18 \text{ PC1} + 435.57$, $r = 0.35$, $n = 671$, $P < 0.001$). As an index of body condition, we used the residuals from this regression of PC1 on body mass (Chastel et al. 1995).

We used sea-ice extent obtained through satellite remote sensing from January 1973 to 1999. Data were provided by the Antarctic CRC, the Australian Antarctic Division Climate Data Sets and by the National Ice Center (NIC), Washington. Data were latitude and longitude of the northern edge of the Antarctic sea-ice digitized at each 10 degrees of longitude. The source is the U.S. Navy/NOAA Joint Ice Facility. Sea-ice extent (SIE) anomalies for each month were calculated as the difference between observed monthly SIE and averaged monthly SIE for the period 1973-1999. Sea-ice extent in one month was correlated with that in the next month only for June and July ($r = 0.67$, Bonferroni corrected $P = 0.012$). Sea-ice extent in May tended to be correlated with SIE in June ($r = 0.61$, Bonferroni corrected $P = 0.067$), and no significant correlation was found between SIE in other months (all Bonferroni corrected $P > 0.2$).

Spatial scale is of primary importance in analysing the relationship between environmental factors and seabird distributions (Hunt and Schneider 1987). Studies in east Antarctica of at sea distribution of Antarctic fulmarine petrels indicate important bird concentrations north (< 200 km) of breeding colonies (Van Franeker et al. 1999). Thus, weekly latitudes of the northern edge of the Antarctic sea-ice for longitude 140°E were averaged for each month from January 1973 to April 1999. A lagged cross correlation was used to investigate possible relationships between sea-ice extent recorded from April preceding the breeding season until the following March (end of the breeding season) and the yearly breeding performance of the Snow Petrels.

Statistical significance of correlation coefficients within our cross-correlation analyses was evaluated by using a randomization procedure. We calculated a 95% confidence interval for the correlation coefficients by means of the bootstrap estimation method (Hall 1992). Breeding performance parameters were randomly rearranged to sea-ice extent values 10 000 times. The resulting set of coefficients provides an approximate sampling distribution of the correlation coefficient (Gleason 1988) and, consequently, 95% confidence intervals of the observed value of the correlation coefficient.

Results

The percentage of breeding pairs of Snow Petrel showed significant year-to-year variation ($\chi^2_{25} = 177.57$, $P < 0.001$), from 19% to 91% of the nests occupied. The percentage of breeding pairs was not significantly

Table 1. Correlation coefficients (n) between breeding parameters and fledgling body condition in Snow Petrels from Pointe Géologie, Terre Adélie. Pearson correlation coefficients were used for hatching success, fledging success, breeding success and percentage of breeding pairs, and Spearman rank correlation coefficients were used for fledgling body condition. * $P < 0.05$, *** $P < 0.001$.

| Variables | Hatching success | Fledging success | Breeding success | Fledgling body condition |
|------------------------------|------------------|------------------|------------------|--------------------------|
| Percentage of breeding pairs | -0.13 (19) | 0.11 (19) | 0.11 (25) | 0.43 (8) |
| Hatching success | | 0.47* (19) | 0.84*** (19) | 0.14 (8) |
| Fledging success | | | 0.77*** (19) | 0.41 (8) |
| Breeding success | | | | 0.50 (8) |

related to other breeding parameters (Table 1). Breeding and hatching success varied significantly between years ($\chi^2_{24} = 176.69$, $P < 0.001$ and $\chi^2_{18} = 99.69$, $P < 0.001$, respectively), but fledging success did not ($\chi^2_{18} = 10.13$, $P = 0.95$; Fig. 1). Snow Petrels experienced particularly poor breeding performance in 1977, 1979, 1993 and 1994 when more than 70% of eggs laid failed to fledge a chick (Fig. 1). Breeding success was explained by both hatching success and fledging success (Table 1).

Annual changes in percentage of breeding pairs were negatively correlated with year-to-year variation in SIE anomalies observed in July (Fig. 2). Fewer birds attempted to breed when SIE was greater than normal in July. Breeding success was positively correlated with SIE anomalies in November (Fig. 2) with depressed breeding success associated with sea-ice retreat. No other correlation was found between SIE anomalies and any of the breeding parameters recorded (Fig. 2). Sea-ice extent was highly variable from year to year for the months of July and November, and variability in average sea-ice extent for the months of June-August increased during 1982-1999 (Fig. 3).

Snow Petrel fledgling body condition varied significantly between years (one-way ANOVA: $F_{7,663} = 25.91$, $P < 0.001$). Body condition was lower in 1990 than in all other years (*post hoc* Tukey's tests, all $P < 0.036$), and was lower in 1993 than in 1995 ($P < 0.001$), 1996 ($P = 0.029$), 1997 ($P = 0.025$), 1998 ($P = 0.005$) and 1999 ($P = 0.006$). In 1995, body condition was higher than in 1996 ($P = 0.014$). Snow Petrel fledgling body condition was not significantly related to other breeding parameters (Table 1). Fledgling body condition was correlated with SIE anomalies in July, September and October (Fig. 2). There was an increase in fledgling body condition from 1990 to 1999 (Spearman rank correlation coefficient $r_s = 0.76$, $n = 8$, $P = 0.016$) associated with an increase in SIE in July ($r_s = 0.60$, $n = 10$, $P = 0.035$) and October ($r_s = 0.63$, $n = 10$, $P = 0.028$).

Discussion

The major result of this study is that sea-ice extent anomalies before the onset of the breeding period had significant effects on Snow Petrel breeding performance. This effect was not evident in five other

commonly used indices. Advance in sea-ice in winter (July) negatively affected the percentage of breeding pairs during the following summer. On the other hand, breeding success and fledgling body condition were enhanced when SIE was greater than average during winter (July, September and October) and November, respectively. Whereas a reduced sea-ice extent favours a large breeding population, it reduces breeding success

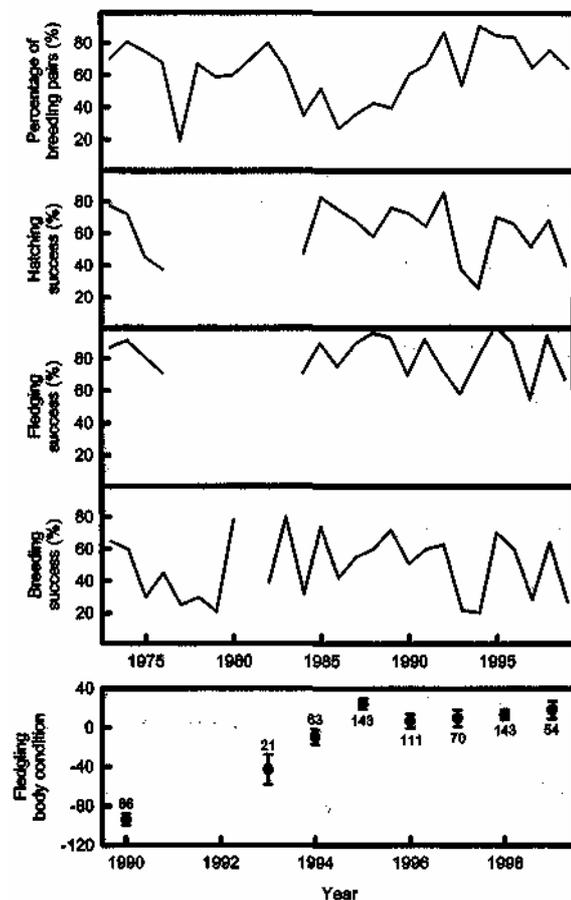


Fig. 1. Annual variations in the percentage of breeding pairs (1973-1999), hatching and fledging success (1973-1976 and 1984-1999), breeding success (1973-1980 and 1982-1999), and fledgling body condition (1990 and 1993-1999) of Snow Petrels on Pointe Géologie, Terre Adélie. Error bars in the lowermost panel indicate standard errors. Statistics indicate significant year-to-year variations except for fledging success (see Results).

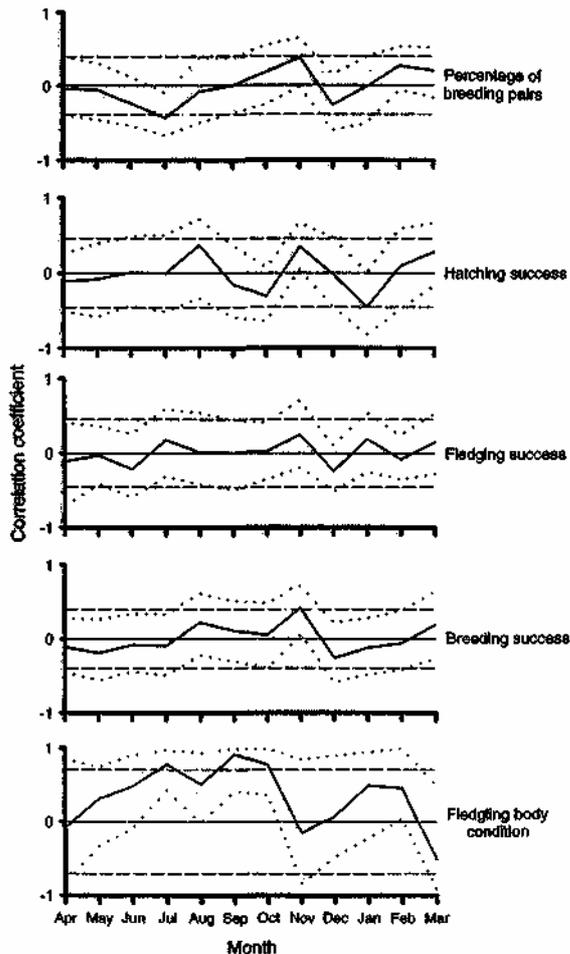


Fig. 2. Variation in correlation coefficients calculated between sea-ice extent anomalies from April (prior to the breeding season) until March (end of the breeding season) and the percentage of breeding pairs (Pearson), hatching success (Pearson), fledging success (Pearson), breeding success (Pearson), and fledging body condition (Spearman). Limits of the 95% confidence interval are indicated by the dotted lines. Statistical significance of the correlation coefficient at $P = 0.05$ is indicated by dashed lines. Results were regarded as significant when the correlation coefficient was significant at the 0.05 level (two-tailed test) and when correlation coefficient values of 0 were not included within the 95% confidence intervals.

and fledging quality, and therefore future recruitment. This apparent paradox highlights the effects of SIE on petrel breeding at two different times of the year. Decisions to breed are affected by food availability in winter, whereas breeding success and fledgling quality are affected by food availability in summer, which in turn is affected by SIE in winter because of a time lag. The response of Snow Petrels to seasonal SIE may reflect SIE's influence on ice-associated biological communities, especially those that provide food for petrels. Snow Petrels forage exclusively over the pack-ice year round (Veit and Hunt 1991), making it the most pagophilic flying seabird. Snow Petrels feed mainly on

krill (*Euphausia superba* and *E. crystallorophias*) whose distribution and abundance seem to be related to sea-ice conditions (Klyaugov 1994, Siegel and Loeb 1995, Pakhomov and McQuaid 1996, Loeb et al. 1997), and fish (*Pleuragramma antarcticum*) both during and outside the breeding season (Ainley et al. 1984, Ridoux and Offredo 1989), although there are indications (Griffiths 1983, Ainley et al. 1984) that cephalopods (*Psychroteuthis glacialis*, *Gonatus antarcticus*) may play a more important role in some localities.

The percentage of breeding pairs and other reproductive parameters (hatching and breeding success) are highly variable between years in Snow Petrels (Chastel et al. 1993, this study). Several factors contribute to this variability, such as weather (Chastel et al. 1993) and predation by South Polar Skuas *Catharacta mac-cormicki* (Barbraud 1999). Food limitation can affect breeding performance in several ways (Martin 1987). The relationship between the percentage of breeding pairs and SIE in winter might reflect depressed food availability during the pre-breeding period when extensive sea-ice cover occurs. Guinet et al. (1998) showed that sea-surface temperatures in winter (July and August) affect the breeding performance of Blue Petrels at the Kerguelen Islands through depressed adult body condition. Two studies suggest that extensive ice cover and long duration of ice conditions during winter may reduce krill mortality by protecting the stock from predation (Siegel and Loeb 1995, Daly et al. 1998). If this is true, then extensive sea-ice in winter might prevent access to some prey species and Snow Petrels would not attain sufficient body condition for breeding.

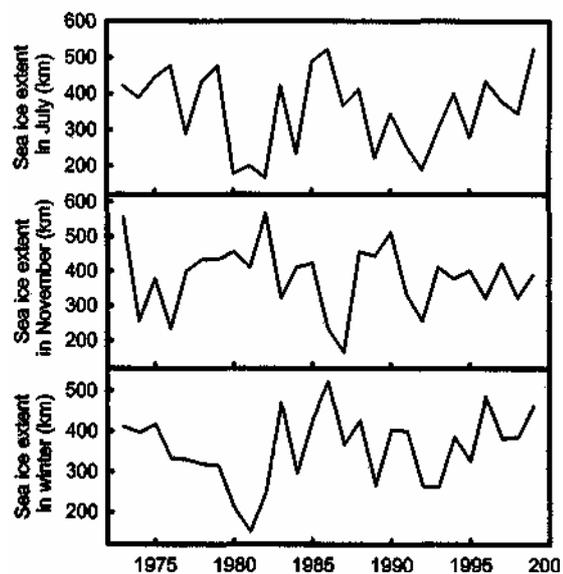


Fig. 3. Annual variations in sea-ice extent at Pointe Géologie (Terre Adélie) for July, November and winter (mean sea-ice extent for June-August) for the period 1973-1999.

Good fledgling body condition may reflect abundant food resources during the chick-rearing period (mid-January to early March). Interestingly, extensive sea-ice cover during the winter months is associated with high krill population densities during summer (Siegel and Loeb 1995, Loeb et al. 1997), i.e. during the Snow Petrel breeding period. At Elephant Island (Antarctic Peninsula), good krill recruitment is positively related to early seasonal spawning (December-January) and both are positively correlated with extensive sea-ice cover the preceding winter. Poor recruitment and late spawning (March) are associated with reduced sea-ice formation (Loeb et al. 1997). Thus, extensive sea-ice cover ensures good survival of the larval krill and high subsequent recruitment to the population (Loeb et al. 1997). Similarly, in the Arctic, several seabirds' prey species depend closely on sea-ice for breeding and are abundant in summers following winters with extensive ice cover (Craig et al. 1982, Bradstreet et al. 1986). Consequently, Snow Petrels breeding after winters with extensive sea-ice cover might raise their chick in good breeding conditions (high food abundance) and fledge chicks in good body condition. The relationship between breeding success and SIE in November preceding the breeding season remains unclear.

Bird species that lay single-egg clutches, such as the Snow Petrel (Brown 1966), have no opportunity to trade off the number of offspring against offspring quality. In such long-lived species, life-history theory predicts that investment in offspring is balanced against the negative effects on future reproductive output or survival (Roff 1992). Such species may increase their investment in offspring under good breeding conditions (Erikstad et al. 1998). This implies that fledging condition may vary with environmental conditions. In poor years average fledging condition should be low, indicating that adults only partially buffer offspring from environmental fluctuations.

Our results suggest that the same factor - sea-ice extent - has opposite effects on the components of the breeding performance of a top predator. The contrasting effects of SIE anomalies on the breeding patterns of the Snow Petrel suggest that it is complicated to predict a top predator's population changes from environmental changes. Such contrasting effects might also be relatively widespread in other pagophilic top predator species. However, optimum sea-ice conditions in winter may exist that minimize the contrasts between fledgling body condition and the percentage of breeding pairs. In Adélie penguins, the existence of optimum ice conditions for population growth has been hypothesized and may provide a conceptual framework for predicting future population change (Fraser and Trivelpiece 1996, Smith et al. 1999). Using the relationships between sea-ice extent, fledgling body condition and the percentage of breeding pairs, we found that the sea-ice extent in July that would minimize the contrast between both

parameters was close to 350 km, a value similar to the observed average sea-ice extent for 1973-1999 (340 km). This suggests that, at present, sea-ice conditions may be close to an optimum for these breeding parameters, which is supported by an observed positive but small (+ 0.9%) population growth rate in Terre Adélie (Micol and Jouventin 2001). Further modeling is needed to predict how Snow Petrel populations will be affected by changes in sea-ice conditions. Such modeling may take into account the relationship between survival and sea-ice (Barbraud et al. 2000) and the possible effect of fledgling body condition on recruitment, which is known for other species (Williams et al. 1993).

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