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## Variations of snow petrel breeding success in relation to sea-ice extent: detecting local response to large-scale processes?

Received: 19 October 2004 / Revised: 14 March 2005 / Accepted: 18 March 2005 / Published online: 23 April 2005  
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**Abstract** Demographic parameters were estimated for snow petrels *Pagodroma nivea* nesting at the study colony of Reeve Hill near Casey station, Antarctica between 1984 and 2003. Average breeding success for the colony varied from 18.2% to 76.5%. Breeding effort, hatching and fledging success were subject to a high interannual variability. We examined the influence of regional sea-ice extent on the breeding performance of snow petrels at Reeve Hill. Fewer birds were breeding when sea-ice had been extensive during April–May. Overall breeding success and fledging success were improved during years with extensive sea-ice cover in winter. Successful breeding effort and breeding success were depressed when there was extensive sea-ice cover during January–February. Sea surface temperatures also correlated to snow petrel breeding performance parameters. Previous work showed that large-scale climatic events (ENSO, Antarctic circumpolar wave) and the related sea-ice cover around the Antarctic might affect the lower trophic levels of the marine environment and consequently food availability for snow petrels. A comparison with the long-term study conducted at Ile des Pétrils (Terre Adélie) suggests that despite similarities in the underlying biological processes that control snow petrel breeding performance, the nature of the correlation of large-scale environmental factors with breeding performance differs substantially between the two colonies, probably because of the confounding effects of other environmental factors acting at a local scale (local weather, nest quality), which also affect bird body condition.

**Keywords** sea-ice · inter-annual variability · snow petrel · breeding success · nest · long-term monitoring

### Introduction

Seabird populations have been suggested as potential bioindicators of the variability of the Southern ocean marine ecosystem (Weimerskirch et al. 2003; Guinet et al. 1994, 1998; Croxall 1992; Hunt et al. 1992). Long-term data sets on variability in population size or reproductive performance of Antarctic seabirds are an invaluable tool to further assess this bioindicator role, especially with regard to sea-ice, a key-component of their ecosystem. For example, population trends were documented for seven species of Antarctic seabirds at Pointe Géologie with this purpose (Micol and Jouventin 2001). But studies that investigate the relationships between demographic trends and various biotic and abiotic variables remain sparse, making interpretation of population responses to regional and large-scale environmental changes difficult, sometimes paradoxical (Croxall et al. 2002).

Most long-term studies, which identified a potential linkage between sea-ice extent (SIE) and breeding success at several locations in Antarctica focused on penguins (Fraser et al. 1992; Trathan et al. 1996; Wilson et al. 2001). Locally, SIE was shown simultaneously to affect the breeding performance of a range of species in the ecosystem (from seals to seabirds) either indirectly (Ainley et al. 1986) or directly (Croxall and North 1988; Whitehead et al. 1990). Physical environmental conditions controlling prey availability were the determining factors influencing breeding performance (Croxall et al. 1988; Ainley and Boekelheide 1990; Jouventin and Weimerskirch 1991). Warm sea surface temperatures modifying zooplanktonic communities affected the breeding performance of blue petrels *Halobaena carulea* in the Kerguelen region (Guinet et al. 1998). Similarly, the demonstrated effect of SIE

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variability on the growth of prey populations such as krill and salps (Smith and Nelson 1986; Loeb et al. 1997) appeared to be central in explaining the linkages between sea-ice, food availability, and the breeding performance of top predators (Barbraud and Weimerskirch 2001; Büßer et al. 2004). More information on long-term population trends is needed to further investigate such linkages for the six petrel species breeding in Antarctica.

As an obligate associate of the sea-ice (Croxall et al. 2002), the snow petrel *Pagodroma nivea* (Forster) is likely to show specific demographic adaptations to a range of weather and sea-ice related environmental conditions (Hudson 1966; Guillotin and Jouventin 1980), in particular food availability. With a circum-polar distribution, this medium sized petrel (250–500 g) breeds in large numbers on ice-free areas along the coast of the Antarctic continent, on nearby islands and inland (Croxall 1995), but is mostly found in close association with open or broken sea-ice, foraging within the marginal ice zone (Griffith 1983; Ainley et al. 1984; Veit and Hunt 1991; van Franeker 2001) where it feeds predominantly on fish, cephalopods and crustaceans such as krill (Ainley et al. 1984; Ridoux and Offredo 1989; van Franeker 2001). By exploiting this particular niche, snow petrels are most likely to be exposed to the effects on sea-ice of a potential climatic shift in the Southern ocean ecosystem (Weimerskirch et al. 2003) and their demography may reflect these changes, which may in turn be detected through long-term studies.

With the long-term data set available for the snow petrel colony at Ile des Pétrels (Terre Adélie), Chastel et al. (1993) studied interannual variations in the breeding performance and adult survival of snow petrels over 27 years (1963–1990). Correlations were found between the reproductive success of the snow petrel study colony and large-scale variations in the marine environment and weather. Sea-ice extent explained 44% of the variation in adult survival of snow petrels at the same colony (Barbraud et al. 2000) and correlated to snow petrel reproductive success with the 1964–1999 time series for the same colony (Barbraud and Weimerskirch 2001). SIE was suggested to modulate food availability during two critical periods: first, in the winter and pre-breeding season, by controlling breeding effort; second, during the breeding season, when breeding success relies on the ability of the parents to both maintain acceptable body condition and feed their chick (Barbraud and Weimerskirch 2001).

Chastel et al. (1993) emphasized the need for long-term monitoring of the same species at different sites because the effects of large-scale (circum Antarctic) environmental variations such as ENSO might affect seabirds differently at separate sites. Because of the limitations associated with interpreting the effect of sea-ice on breeding performance variations based on a single data set (Croxall et al. 2002), the present paper aims to analyse snow petrel breeding performance

variability with the only other long-term snow petrel data set available to date. The 19-year long time series of Reeve Hill colony near Casey station, East Antarctica (located 600 miles from Terre Adélie) is examined in order to support or refine previous ecological interpretations on the mechanisms explaining variations related to large-scale environmental parameters, with particular emphasis on SIE. Results obtained were systematically compared with the demographic parameters obtained for the snow petrel colony at Ile des Pétrels in Terre Adélie, (Chastel et al. 1993; Barbraud and Weimerskirch 2001). Comparing two long-term data sets, on the same species at separate locations can help assessing how breeding performance might reflect varying responses of the species to the same environmental variables at the regional and local scales.

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## Materials and methods

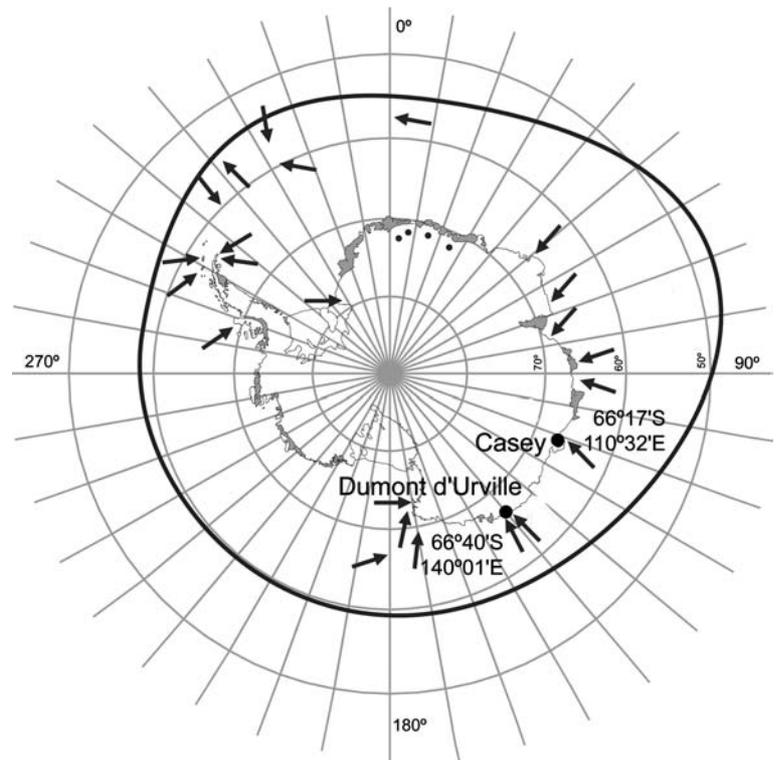
### Snow petrel breeding performance data

Data on the breeding performance of snow petrels were extracted from a database of observations of snow petrel activity of one colony located on Reeve Hill in the vicinity of Casey Station, Antarctica (66°17'S, 110°32'E) for 15 seasons between 1984 and 2003 (Fig. 1). Observations were conducted every season by one or two observers appropriately trained using a set of guidelines (van Franeker 1991). Nests were visually inspected regularly throughout the breeding season. The latest start date of the monitoring was the seventh of December; all other years, checks started in the first 2 weeks of November. Only years with regular nest checks starting early December were taken into account for the census of eggs laid. Dates for egg-laying, hatching, egg failure or chick death were determined for 7 years, when the colony checks were conducted frequently (every 2 or 3 days). Chicks reported missing early March were considered fledged if present at the preceding nest check provided that nest check was conducted on the 23rd of February or later.

Five indices describing breeding performance were defined as follows:

- **Breeding effort:** the number of nests in which an egg was laid divided by the total number of nests monitored in that season (Barbraud and Weimerskirch 2001).
- **Hatching success:** the number of eggs hatched divided by the number of eggs laid.
- **Fledging success:** the number of chicks fledged divided by the number of eggs hatched.
- **Breeding success:** the number of chicks fledged divided by the number of eggs laid.
- **Successful breeding effort:** the number of chicks fledged divided by the total number of nests monitored in the colony.

**Fig. 1** Map showing the location of the two snow petrel long-term study colonies, Reeve Hill at Casey and Ile des Pétrels at Dumont d'Urville, with a map of snow petrel distribution (grey circle) and main breeding locations (coastal: arrows, inland: dots). Adapted from Marchant and Higgins (1990)



Breeding effort and hatching success were calculated for 15 and 14 seasons, respectively, fledging success, breeding success and successful breeding effort for 12

seasons (Table 1). Within year and 1 year lagged correlation coefficients calculated between Reeve Hill and Ile des Pétrels for all breeding performance parameters

**Table 1** Demographic parameters for the snow petrel population at the study colony of Reeve Hill between 1984 and 2003 for a core subset of 42 nests checked every year and for the entire colony

Season	No. of study nests	No. of eggs laid	No. of eggs failed	No. of chicks hatched	No. of chicks failed*	No. of chicks fledged	Breeding effort (%)	Hatching success (%)	Fledging success (%)	Breeding success (%)	Successful Breeding effort (%)
1984–1985	42 52	35 26	11 9	24 17	2	17 22	61.9 64.8	65.4 68.6	91.7 100.0	65.4 62.9	40.5 40.7
1985–86	–	–	–	–	–	–	–	–	–	–	–
1986–1987	42 50	16 12	13 9	3 3	0	3 3	28.6 32.0	25.0 18.8	100.0 100.0	25.0 18.8	7.1 6.0
1987–1988	–	–	–	–	–	–	–	–	–	–	–
1988–1989	–	–	–	–	–	–	–	–	–	–	–
1989–1990	42 95	28 61	12 32	16 29	4	16 27	66.7 64.2	57.1 47.5	100.0 93.1	57.1 44.3	38.1 28.4
1990–1991	42 95	17 46	14 16	13 30	4	12 26	40.5 48.4	76.5 65.2	92.3 86.7	70.6 56.5	28.6 27.4
1991–1992	42 52	5 7	5 6	–	–	–	11.9 13.7	–	–	–	–
1992–1993	42 50	11 13	2 2	9 11	–	–	28.2 26.0	81.8 84.6	–	–	–
1993–1994	42 54	30 34	14 16	16 18	0	16 18	71.4 63.0	53.3 52.9	100.0 100.0	53.3 52.9	38.1 33.3
1994–1995	42 51	11 14	5 8	6 6	1	5 5	26.2 27.5	54.5 42.9	83.3 83.3	45.5 35.7	11.9 9.8
1995–1996	42 51	10 11	4 5	6 6	4	2 2	23.8 21.6	60.0 54.5	33.3 33.3	20.0 18.2	4.8 3.9
1996–1997	42 53	32 42	22 30	10 12	0	10 12	76.2 79.2	31.3 28.6	100.0 100.0	31.3 28.6	23.8 22.6
1997–1998	42 59	24 34	3 3	21 31	5	16 26	57.1 57.6	87.5 91.2	76.2 83.9	66.7 76.5	38.1 44.1
1998–1999	42 79	33 55	13 24	20 31	3	17 28	78.6 69.6	60.6 56.4	85.0 90.3	51.5 50.9	40.5 35.4
1999–2000	42 78	3 4	–	–	–	–	7.1 5.1	–	–	–	–
2000–2001	42 58	9 9	8 8	0 1	–	–	21.4 15.5	11.1 11.0	–	–	–
2001–2002	42 79	29 54	18 42	11 12	2	10 10	69.0 68.4	37.9 22.2	90.9 83.3	18.5 34.5	23.8 12.7
2002–2003	42 75	29 47	13 18	16 29	8	11 21	69.0 62.7	55.2 61.7	72.4 68.8	44.7 37.9	26.2 28.0
Average	65.3	19.3 30.9	14.3	10.3 15.8	2.8	8.4 17.0	46.1 45.2	54.1 50.7	85.8 84.5	46.6 42.5	26.8 24.6
STD	18.3	7.5 21.0	12.7	7.1 13.0	2.4	6.9 11.1	24.9 24.3	21.6 23.9	19.6 18.1	16.9 18.9	13.0 13.6

Numbers in italic, all nests monitored each year are included

– Missing values

\*Recorded for the entire colony

but were limited to data available at both locations ( $n = 10$  or  $n = 9$ ).

#### Sea-ice data

Passive microwave sea-ice data from January 1984 to March 2003 were obtained from the National Snow and Ice Data Centre in Boulder, Colorado. SIE is the latitude of the northernmost edge of the pack ice. The ice edge was defined as the point at which the ice concentration dropped below 15% (commonly used cut-off point to distinguish the pack ice from the newly formed ice with passive microwave data). Daily latitudes of the ice edge were averaged monthly across the longitude band 105°E–115°E for consistency with Barbraud and Weimerskirch (2001). Given the lack of spatial data on snow petrel foraging trips, we postulate that averaging SIE over 10° zone would likely include foraging grounds for snow petrels nesting around Casey station [from foraging trip durations recorded for Ardery Island in: Barbraud (1999) and van Franeker et al. (2001a, b) and Steele (1994)]. Monthly SIE anomalies (SIEA) were calculated as the difference between monthly SIE and averaged monthly SIE for the period 1984–2003. In addition, 3-monthly SIE averages (March–May, June–August and September–November) were calculated to investigate correlations on a longer time scale during the winter months. Averages for the duration of the incubation phase (1st Dec–15th of January) and nestling phase (16th January–2nd March) were obtained to calculate correlations on a more biologically relevant time scale during the breeding season.

The relationship between monthly SIE and reproductive performance of the snow petrels at the colony was investigated for each season by conducting a lagged-cross correlation study following the methods described in Barbraud and Weimerskirch (2001). Pearson correlation coefficients were calculated between SIEA and each of the reproductive performance parameters from April preceding the breeding season until the end of the breeding season in March. Correlations were plotted separately for each breeding parameter with a 95% confidence interval (CI) versus the monthly SIEA. In an attempt to explain differences in the processes controlling snow petrel breeding performance between the two locations, the structure of the sea-ice was investigated for a 10° longitude window centred at each colony site (105°E–115°E for Casey and 135°E–145°E for Dumont d'Urville). As snow petrels are generally associated with loose pack ice [10–30% ice cover, Weddell Sea, Cline et al. (1969); 0–25%, Prydz Bay, Montague (1988)], AVHRR sea-ice images (25-km resolution) were used to calculate areas of open water (defined as less than 15% ice concentration) between the coast and the ice edge for the winter months (April–September). Correlations between snow petrel breeding effort and proportion of open water were investigated for Casey with the time-lagged method described above.

#### Sea surface temperatures

Interannual variations in SIE are thought to be coupled with interannual variations in sea surface temperatures (SST) and wind force in a system referred to as Antarctic circumpolar wave (or ACW, see White and Peterson 1996 for detailed definition). To search for the potential effects of any ACW-like cyclic climate phenomena, relationships between reproductive performance parameters and SST were investigated using similar methods to investigate the relationships between sea surface temperature anomalies (SSTA) and snow petrel breeding performance. Monthly SSTs were obtained from the Lamont Doherty Earth Observatory at Columbia (Reynolds Smith OIV2 SST data set, Reynolds and Smith 1995) on a 1° by 1° grid. SST data were averaged along the pack ice edge from 105° to 115°E. For each pixel, in the ice data, which was deemed to be part of the pack ice edge in the longitude band 105°–115°E, the nearest SST grid point, which was north of the pack ice edge was determined.

#### Comparison of the two long-term data sets

Methodological choices made, in this paper, were pre-determined by the need for comparison to the studies conducted with the data set from Ile des Pétrels and justifies for example the use of SIEA and SSTA over SIE and SST. Additional data analysis methods are also explored. In the study conducted at Ile des Pétrels (Chastel et al. 1993) demographic parameters for the study colony were calculated over a slightly increasing set of nests. The colony on Reeve Hill comprises up to 95 nests individually marked with yellow paint numbers on the rocks near the nest entrance. The number of nests for which observations were recorded varies from year to year and from check day to check day due to logistics, weather conditions and the ability of the observer to find the nest if buried under snow (between 50 and 109, Table 1). Consequently, the colony was not monitored exhaustively every season. In order to be consistent with the long-term study conducted at Ile des Pétrels, we also calculated reproductive parameters over all the nests monitored in the study colony. However, we also conducted the long-term study on a permanent group of nests in order to make appropriate inter-annual comparisons. Because nests are marked individually, a core subset of 42 nests checked systematically for 15 seasons between 1984 and 2003 was extracted from the data set. To investigate for the potential bias introduced in inter-annual variations caused by the use of a varying number of nests, we compared the reproductive parameters obtained for the whole study colony and the core subset of 42 nests (See Appendix 1 for detailed comparison method). Subsequent correlational analyses with SIE variations were also conducted with both the core and the entire data set. Breeding parameters calculated for the entire colony were highly correlated to those

calculated for the subset of 42 nests ( $P < 0.01$ ). Therefore, the use of a varying number of nests did not affect the level of significance of correlations coefficients calculated with SIEA, confirming that the monitoring reflected the year rather than the sample. Despite a smaller sample size, it was preferable to conduct the comparison with Ile des Pétrels by calculating correlation values with the core subset of 42 nests, assuming that both data sets were affected by a similar amount of observer variability. Breeding performance parameters, SIEA and proportions of open water were compared between Casey and Dumont d'Urville by calculating within year correlation coefficients. In light of the possible regional effects of an ACW type of phenomena, lagged correlation coefficients were also calculated between year  $Y$  at Ile des Pétrels and year  $Y-1$  at Casey as the ACW drives climatic anomalies eastwards.

### Statistical analysis of the data

Statistical significance of the correlation coefficients within the cross-correlation analyses was evaluated using a randomization procedure, which enables to check that correlations, even with small samples, are not the result of chance alone. Standard deviations provided for percentages were calculated on transformed data (for reasons of normality). A 95% CI for the correlation coefficients was calculated with the bootstrap estimation method (Hall 1992; Haddon 2001). Breeding performance parameters were randomly re-arranged with SIE values 1,000 times. The resulting SIEA—breeding coefficients provide an approximate sampling distribution of the correlation coefficient (Gleason 1988) and 95% CI. This procedure was used to estimate the robustness of the coefficient and was necessary because correlation coefficients (SIEA versus breeding parameters) were calculated over 12–19 seasons. The same procedure was used for the analysis of SSTA data, both being consistent with methods from Barbraud and Weimerskirch (2001). Significance of the results was defined at the 0.05 level. Standard deviations (SD) are also presented as another measure of variance for breeding parameters.

## Results

### Breeding performance

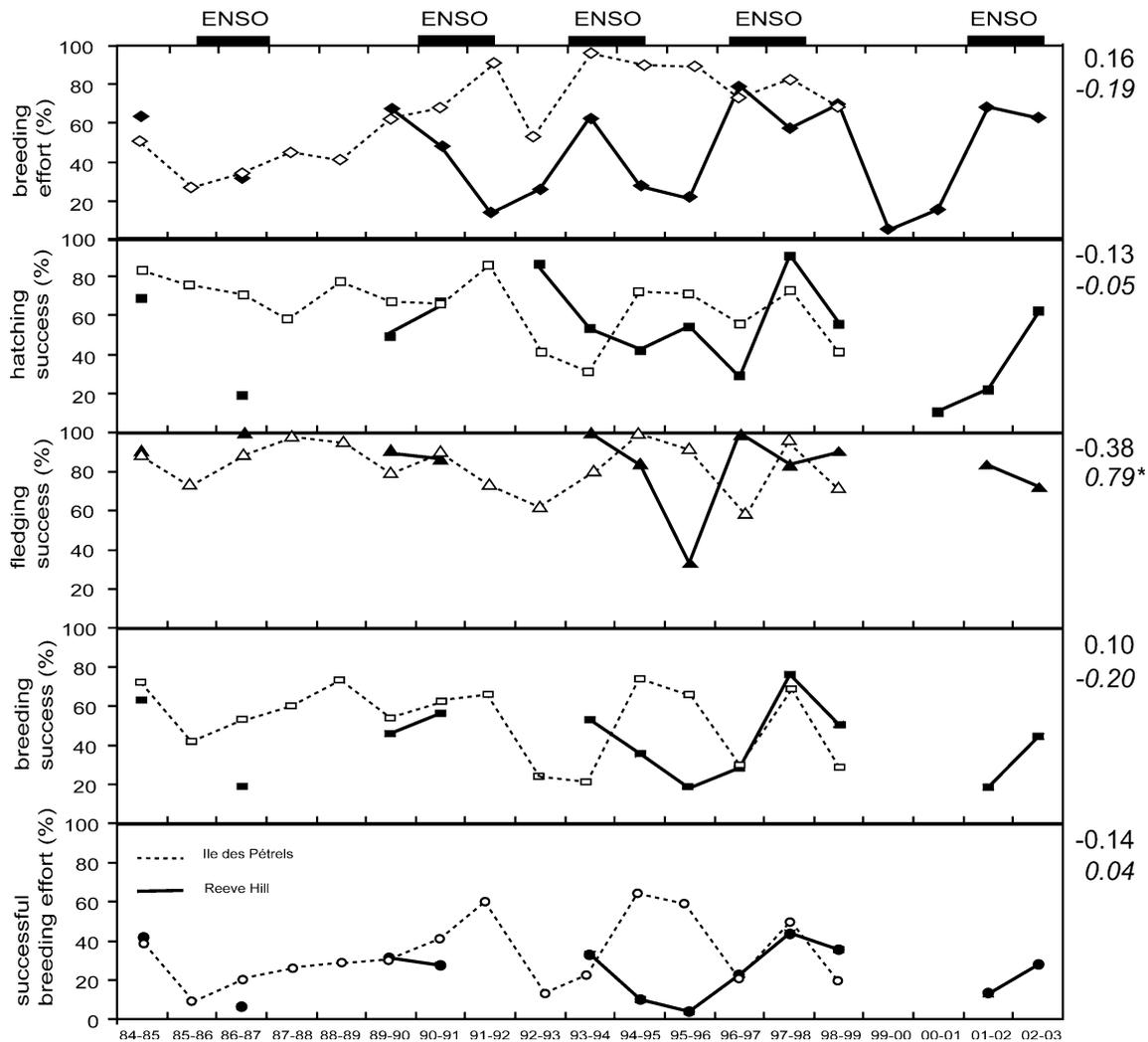
On average, less than half the sites known to be potentially occupied by breeding pairs were used for a breeding attempt: mean breeding effort, was  $45.2 \pm 24.3\%$  (Table 1). The average breeding success for the colony was  $42.5 \pm 18.9\%$ . Successful breeding effort remained low ( $24.6 \pm 13.6\%$ ). The average hatching success ( $50.7 \pm 23.9\%$ ) was high for a single egg clutch species. Average fledging success was high ( $84.5 \pm 18.1\%$ ). High standard deviations for all breeding parameters show high interannual variability. Based

on the number of eggs laid in the subset of 42 nests, breeding effort varied significantly from year to year ( $X^2_{13} = 126.26$ ,  $P < 0.001$ , Fig. 2), ranging from 7.1% to 78.6%. Other reproductive parameters also varied significantly between years: Chi square values were calculated for breeding success ( $X^2_{11} = 62.53$ ,  $P < 0.001$ ), hatching success ( $X^2_{11} = 152.76$ ,  $P < 0.001$ ) and fledging success ( $X^2_{11} = 149.95$ ,  $P < 0.001$ ). Nevertheless, fledging success remained high and constant among years, ranging between 83.3% and 100% for all seasons, but one (1995/1996), when it dropped to 33.3% (Fig. 2). Low fledging success, combined with a low breeding effort, severely impacted on successful breeding effort that year (3.9%). By contrast, 1996/1997 and 2001/2002 were years of high breeding effort but returned a low breeding success. 1997/1998 was characterized by a particularly high hatching success (Fig. 2) and the resulting successful breeding effort was the highest of the time series (44.1%). On the other hand, very low values for successful breeding effort in 1986/1987 and 1995/1996 (6.0% and 3.9%, respectively) were either explained by a very low hatching success (18.8%) or low breeding effort (21.6%).

Breeding failure resulted mostly from failure during incubation (Table 2): the proportion of eggs that failed is significantly higher than the proportion of chicks that failed over the study period (Paired  $t$  test,  $P = 0.007$ ). Egg desertion was identified as the main cause of breeding failure during the incubation, confirming that the incubation period is critical to the overall breeding success. Fledging failures occurred more often early during the chick-rearing phase (first 2 weeks post-hatching, from mid to late January). 65% of chick failures were recorded before the 20th–24th of January (Olivier, unpublished data). Overall, a low breeding effort and a low hatching success were the two common contributors to a low breeding performance (Fig. 2). Correlation coefficients calculated between the breeding performance indices confirmed these observations (Table 2). Breeding success was not explained by fledging success, which showed very little inter-annual variability. All reproductive parameters calculated above were independent of breeding effort, i.e. the number of fledglings produced in the season was not correlated with the percentage of breeding pairs or the numbers of eggs laid and may vary according to environmental factors (weather/sea-ice) during the breeding season or other factors (predation). However, breeding effort correlated negatively with breeding success of the previous year ( $r = -0.860$ ,  $P = 0.35$  and  $P = 0.006$  level if year 1997–1998 is removed, Table 2).

### Correlation between sea-ice and reproductive parameters

Breeding effort was negatively correlated with SIEA observed in May (weak correlation for April, just under level of significance). Fewer birds attempted to breed



**Fig. 2** Annual variations in snow petrel breeding effort, hatching success, fledging success, breeding success and successful breeding effort for the period 1984–2003 at the Reeve Hill colony (Casey) and at Ile des Pétrels (Dumont d’Urville). *Dotted lines* are Dumont D’Urville, *continuous lines*, Reeve Hill. Within year correlations of breeding performance parameters between locations are presented on the right, along with one-year lagged for Dumont (*in italic*; \*significance at 0.05 level). ENSO events are marked as periods of warm anomalies from the multivariate ENSO index (Calculated after Wolter and Timlins 1998)

when sea-ice was greater than normal early in the winter preceding the breeding season (Fig. 3). Successful breeding effort and breeding success were positively correlated with SIEA in July and August. SIE was highly variable from year to year for the months of May and July but less variable in January (Fig. 4). In January, breeding success correlated negatively (very strongly,  $r = -0.652$ ) with SIEA. The two components of breeding success, hatching success and fledging success followed different trends. There was no significant correlation between SIEA and hatching success although hatching success followed the same trends as breeding success, showing a weak negative correlation with SIEA in January. Fledging success was strongly correlated

negatively with SIEA in January. Fewer birds fledged when SIE was greater than normal in January, suggesting that fledging success is more sensitive to variations in SIEA in the first phase of chick growth. Correlation coefficients calculated at the coarser temporal scale (3-monthly) for post-breeding (March–May), winter (June–August) and pre-breeding (September–November) periods were not above significance level. Correlation with SIEA calculated for the fledging period was  $r = -0.507$  ( $P < 0.05$ ) suggested a negative effect of extensive sea-ice during this time (Fig. 3). This negative effect was detected during the incubation phase, although not as strong ( $r = -0.405$ ,  $P < 0.1$ ). This was not revealed by the monthly average SIEA correlation coefficients.

#### Effects of SST

No significant correlations were found among SSTA and breeding effort. Hatching success correlated positively with SSTA in August of the previous year ( $r = 0.665$ ,  $P = 0.090$ ). Fledging success correlated negatively with

**Table 2** Pearson correlation coefficients between reproductive parameters

Variable	Hatching success	Fledging success	Breeding success	Successful breeding effort
Number of seasons used in brackets				
With season 1997/1998 removed				
* $P < 0.01$ ; for all other values $P > 0.05$				
Breeding effort	0.307 (13)	0.534 (12)	0.349 (12)	0.498 (12)
Breeding effort of the following year			-0.353 (9)	-0.265(9)
Hatching success		-0.223 (12)	0.870 (12)*	0.756 (12)*
Fledging success			0.280 (12)	0.342 (12)
Breeding success				0.926 (12)*

SSTA in January ( $r = -0.596$ ,  $P = 0.041$ ). The removal of 1 or 2 years with very low fledging success did not decrease this correlation. Breeding success increased when SSTA were positive and high in July during the winter preceding the breeding season ( $r = 0.670$ ,  $P = 0.024$ ). Successful breeding effort followed the same trends as breeding success ( $r = 0.449$ ,  $P = 0.143$  for July SSTA,  $r = -0.602$ ,  $P = 0.038$  for November SSTA). Significant correlations between reproductive parameters and either SIEA or SSTA were generally synchronized throughout the year (July and April) but not in November: SIEA in November was not correlated with any of the breeding parameters at Reeve Hill, whereas, negative SSTA related to a decreased breeding success.

#### Comparison of breeding performance variability between Ile des Pétrels and Reeve Hill

Mean breeding performance parameters were similar between the study colony at Ile des Pétrels (1963–1990, Chastel et al. 1993) and Reeve Hill (1984–2003, Table 1, Fig. 2). Fledging success was generally high (83.3% at Ile des Pétrels, Chastel et al. 1993; and  $84.5 \pm 18.1\%$  at Reeve Hill), and average hatching success higher at Ile des Pétrels (63.3%) than Reeve Hill (50.7%) where it was subject to stronger fluctuations. Accordingly, average breeding success was higher at Ile des Pétrels ( $51.3 \pm 16.3\%$ ) than at Reeve Hill ( $42.5 \pm 18.9\%$ ). At both locations, all reproductive parameters were highly variable among years (Fig. 2). Breeding effort was higher and more sustained ( $t$  test,  $P < 0.05$ ) at Ile des Pétrels ( $63.9 \pm 21.3\%$ ) than at Reeve Hill ( $45.2 \pm 24.3\%$ ). Successful breeding effort at Ile des Pétrels ( $33.4 \pm 17.1\%$ ) and Reeve Hill ( $24.6 \pm 13.6\%$ ) did not differ significantly between colonies. No significant correlation was detected in breeding performance parameters between the two colonies, except for fledging success between years (Year  $Y-1$  at Casey versus Year  $Y$  at Dumont d'Urville, Fig. 2) although this may be mostly due to fledging success being constantly high at both locations, with a bad year in 1995/1996 at Reeve Hill distinctively followed by a bad year in 1996/1997 at Ile des Pétrels.

Correlation between breeding performance parameters and SIEA occurred at different months for Ile des Pétrels and Reeve Hill (Fig. 2). In the summer months (October–February), monthly SIE variations did not show any positive within year correlation between

locations. However, lagged correlation coefficients indicated that years of extensive sea-ice at Casey were generally followed by years of extensive sea-ice at Dumont d'Urville in winter. On average, sea-ice extended further at Casey, especially in summer with very low SIEs occurring more frequently at Dumont d'Urville in the summer months (Fig. 4a), potentially influencing foraging distances. Differences between the two locations in the extent of open water present between the coast and the northern edge of the pack ice during the winter months were investigated. Within and between year comparison of the proportion of open water during the winter months (Fig. 4b) did not reveal significant correlations, except during ice formation, (April: lagged correlation, May: within year correlation), suggesting strong differences in winter sea-ice structure between locations. Breeding effort correlated positively with the extent of open water present in July only in the Casey area.

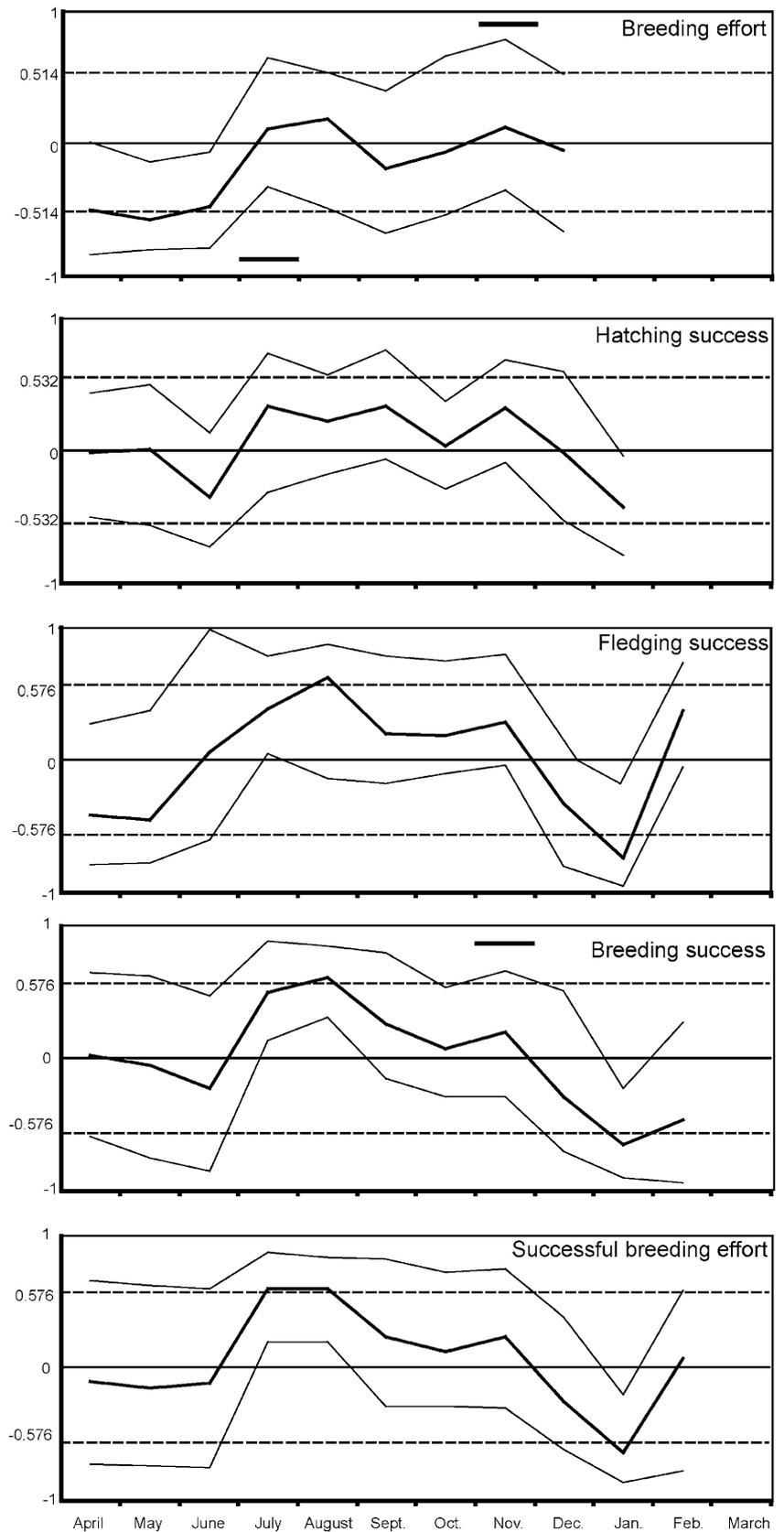
At both colonies, there was no correlation between breeding effort and breeding success, illustrating low breeding frequency of the snow petrel (Chastel et al. 1993). Despite the presence of one outlier, the negative correlation of breeding effort with breeding success of the preceding year shows that snow petrels breed on average every second year and tend to avoid breeding when food availability is limited or when local weather conditions (snow, ice) limit nest attendance and egg laying (Table 2). The single outlier in our data (1997/1998) occurred after the 1998 winter, which had the heaviest July ice cover (Fig. 4), suggesting an atypical response to these particular ice conditions.

## Discussion

### Winter and summer sea-ice

Overall, similarities in the trends and correlations identified for Reeve Hill and Ile des Pétrels support previously generated hypotheses on the environmental factors affecting snow petrel breeding performance. Barbraud and Weimerskirch (2001) interpreted the contrasting effects of SIE on the breeding performance of snow petrel in terms of food availability for this top predator. Although the relationship between sea-ice and prey distribution and abundance was best demonstrated for krill (Loeb et al. 1997), SIE variations may affect the whole under-ice community (Whitehead et al. 1990).

**Fig. 3** Variations in correlation coefficients calculated between sea-ice extent anomalies from April (prior to the breeding season) to the following March (end of the breeding season) and breeding effort, hatching success, fledging success, breeding success and successful breeding effort. Correlations coefficients calculated for each month are presented in *bold*. Limits of the 95% CI are the thinner lines. Results were considered as significant at the 0.05 level when the value 0 was not included in the 95% CI. *Dashed lines* indicate statistical significance of the correlation at the 0.05 level. Months for which significant correlations were found at Dumont d'Urville are identified with a *black line* positioned according to the sign of the correlation

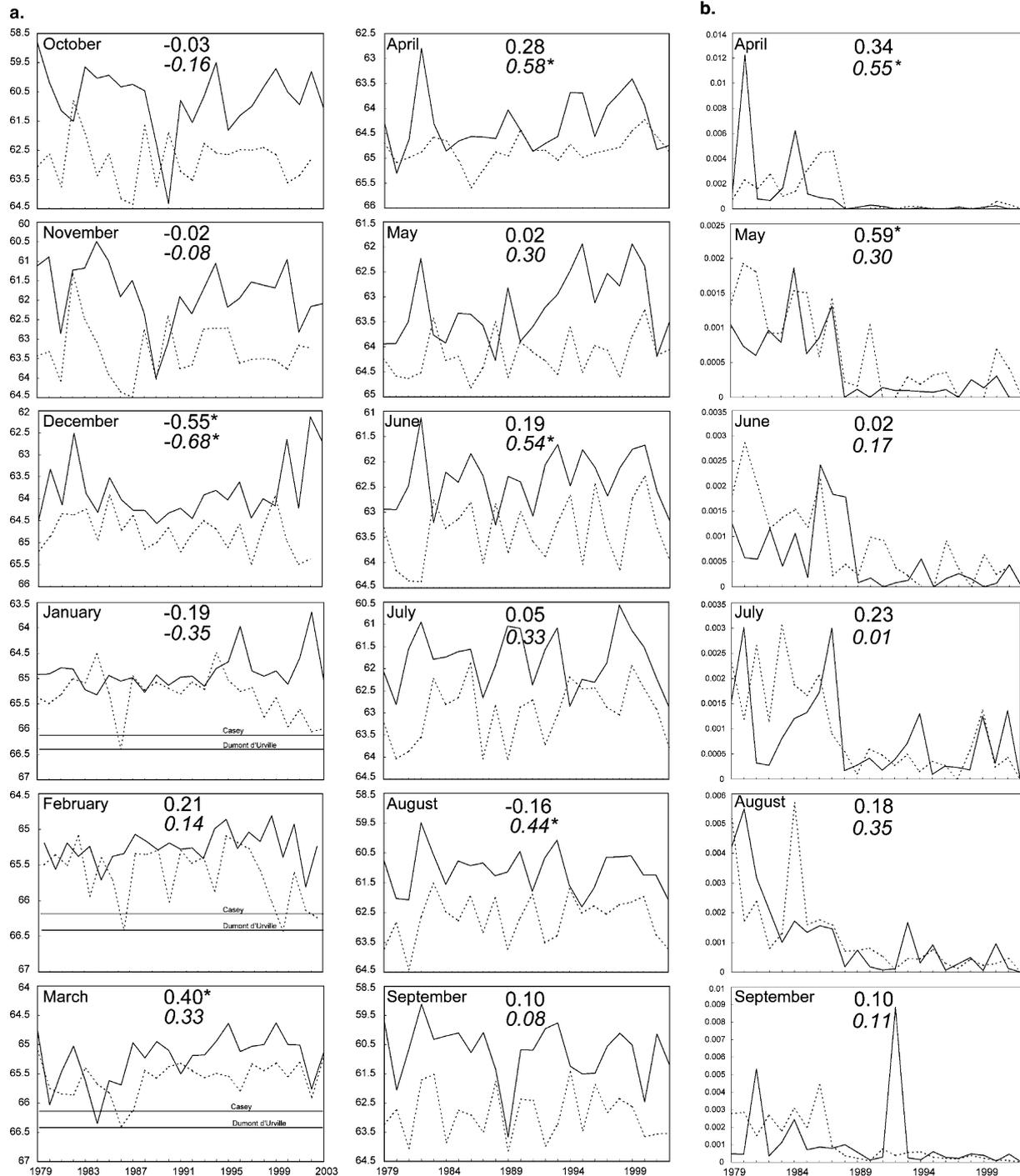


Thus, despite the fact that the snow petrel is not primarily a krill eater, its diet depends on secondary production under the ice cover and may be influenced by

SIE, although there may be food web delays in prey abundance. Due to the general lack of proven knowledge on ecological interactions between sea-ice and seabird preys, detailed comparative work is necessary to highlight other explanatory factors that have to be accounted for when explaining breeding success variability.

As demonstrated for another seabird prey species, the Arctic Cod, (Craig et al. 1982), winter sea-ice may protect the under ice community from predation. Increased ice cover may thus reduce food availability for snow

**Fig. 4** Annual variations of monthly sea-ice extent (SIE) averages (a) and proportions of open water (b) between 1979 and 2003 at Casey (continuous lines) and Dumont d'Urville (dashed lines). Y axis: latitude south in degrees. Pearson correlation coefficients between locations ( $n=23$ ) are presented for SIEA within year and 1-year lagged (*italicised number*) comparisons (\*significant at the 0.05 level)



petrels during the pre-breeding period (July–October), which might prevent reaching acceptable body condition prior to breeding. In this way, Chastel et al. (1993) and Barbraud and Weimerskirch (2001) interpreted their finding of a negative correlation of breeding effort with July SIE anomalies found at Ile des Pétrels. At Reeve Hill, breeding effort was negatively correlated with SIEA earlier in the winter, when winter sea-ice reforms in April–May: fast sea-ice re-growth may also reduce food availability when the birds need to regain body condition after the breeding season and during moult. This assumption is supported by Barbraud et al. (2000) who suggest this period as being critical also for the survival of adult snow petrels.

As opposed to Ile des Pétrels, where winter SIE was suggested as a major determining factor of breeding effort (Barbraud et al. 2000), breeding effort at the Reeve Hill colony did not appear to be determined by sea-ice conditions in July–September, when SIE reaches its maximum. Thus, food availability during the winter months may not be a function of SIE around Casey and snow petrels might be able to feed more easily throughout winter, potentially due to a different structure of the winter pack ice in the Casey area. Croxall et al. (2002) suggest that polynyas are favoured by foraging snow petrels. However, snow petrels may be dependent on other types of sea-ice habitats rather than solely on large areas of open water (despite the potential presence of marginal ice zones within these polynyas) because of their feeding behaviour, which consists of scavenging at the edge, in open water or loose ice leads within the pack ice itself (Ainley et al. 1993; Chastel et al. 1993; van Franeker 2001). Therefore, the pixel size over which areas of open water were calculated (625 km<sup>2</sup>) may be too large to detect such finer scale effect of sea-ice/open water characteristics.

While extensive winter sea-ice may reduce food availability for adult birds during the pre-breeding season, it increases survival of krill and larval recruitment throughout winter (Siegel and Loeb 1995; Loeb et al. 1997), subsequently enhancing food availability for the birds during the following summer (Barbraud and Weimerskirch 2001). Hatching, fledging and consequently breeding success are likely to be directly affected by food availability in summer (feeding during incubation and feeding of the chicks) through this indirect mechanism. This time-lagged effect of winter sea-ice cover on food availability identified at Ile des Pétrels was also reflected at Reeve Hill by an increased breeding success for years with extensive sea-ice in winter.

Sea-ice extent during the summer months may also play a role in controlling snow petrel reproductive parameters at the Reeve Hill colony. Hatching success is not subject to variations in SIEA, but fledging success is heavily affected by SIEA early during the chick-rearing period (January). Interestingly, the effect of variations in summer SIEA (December–March) on breeding performance parameters was hardly detected at Ile des Pétrels during the summer months: only a weak negative

correlation of SIEA with hatching success was detected in January (Barbraud and Weimerskirch 2001). The ice edge was on average 35% further from the colony at Reeve Hill during the summer months (Fig. 4), suggesting that extensive sea-ice cover during the breeding season may reduce areas of open sea-ice suitable for foraging and lower food availability, therefore, increasing energetic requirements during incubation shifts and chick feeding, due to longer foraging trips.

### Body condition

The discrepancies between the two studies suggest that parent body condition may outweigh the effects of environmental variations (in particular SIE variations). In our non-intrusive study, the lack of measure of parent/chick body condition hampered to separate the effects of environmental conditions and individual bird condition on breeding performance. However, previous studies showed that, in the Antarctic, parental body condition of petrels may buffer some of the negative effects of variations in food availability and environmental conditions for both stages of the breeding cycle, incubation and chick rearing (Saether et al. 1997; Barbraud and Chastel 1999; Tveraa and Christensen 2002). This may partly explain why, at Ile des Pétrels, fledging success did not vary significantly between years although overall breeding success was correlated with fledging success (Barbraud and Weimerskirch 2001). If long-lived species tend to increase their investment in offspring in good breeding conditions (Erikstad et al. 1998), fledging success should vary with environmental conditions. Fledgling mortality increased in summers with extensive sea-ice cover at Reeve Hill but not at Ile des Pétrels (Fig. 3). However, overall breeding success at Reeve Hill was not significantly correlated to fledging success but only to hatching success (Table 2). Early body condition of adult snow petrels (mostly females) was also shown to clearly influence hatching success (Barbraud and Chastel 1999). This may imply that breeding failure is more likely to occur during the incubation period (through egg abandonment) than during the fledging period. At both Reeve Hill and Ile des Pétrels, the most critical phases of the breeding cycle appear to be early incubation and chick brooding period (Chastel et al. 1993; Olivier, unpublished data).

### Large-scale versus local environmental factors

In the study conducted at Ile des Pétrels, patterns of variations in snow petrel breeding success in relation to SIEA were relatively clear due to the use of a large data set (27 years for Chastel et al. 1993, 35 years for Barbraud and Weimerskirch 2001). The correlation coefficients calculated for the Reeve Hill colony were generally weaker owing to the shorter length of time over which the study was conducted (only 16 years and

12 seasons with a complete data set). However, similar correlations with SIEA and SSTA were found with both datasets, and can safely be attributed to variations explained by the specific ecological processes examined rather than observer variability. The comparison of long-term data sets at two separate locations helped identifying the snow petrel demographic traits that are inherent to the species rather than location-specific. Strong similarities were found between Reeve Hill and Ile des Pétrels especially in the high variability of reproductive performance parameters. The range of fluctuation for breeding success at Reeve Hill was 400%, which is comparable with that of Ile des Pétrels (500%, Chastel et al. 1993) and regular catastrophic events affected both colonies. At both locations, part of the variability is explained by the variations in large-scale environmental parameters such as SIE and SST.

In the period when data overlap between Casey and Dumont d'Urville (1984–1999), reproductive performance parameters at Reeve Hill did not vary in parallel with that of Ile des Pétrels. Years of particularly low breeding success at Reeve Hill were not paralleled or followed by years of low breeding success at Ile des Pétrels, even though the two monitoring colonies are only 1,300-km apart. Large-scale climatic events such as ENSO and the ACW-type phenomena may modify oceanographic conditions and thus food availability all around the Antarctic continent (Chastel et al. 1993). Usually, the ACW is associated with SST lower than normal, strong winds and an increased SIE and is subject to a positive feedback from ENSO events (White et al. 2002). Generally, increased SST negatively affects primary production (Sullivan et al. 1993). Therefore, the mechanism through which breeding success increases with SSTA is probably mostly ice-related. However, as for Ile des Pétrels (Barbraud and Weimerskirch 2001), there was no clear biological explanation of the relation between breeding success and environmental (SST and SIEA) variability in November.

Due to their relative proximity, both Dumont D'Urville and Casey may be affected by these large-scale climatic cycles in the same way, with a delay shorter than a year. One-year lagged correlations were only observed in sea-ice for three of the winter months. Several ENSO events occurred between 1984 and 1999 (1982, 1987, 1991, 1994 and 1997, Fig. 2). At Ile des Pétrels, seasons with particularly low breeding success and survival for the snow petrels occurred 1 year after strong ENSO events (Chastel et al. 1993). The Reeve Hill dataset is not continuous and does not reveal any relation between seasons of very low breeding success and the delayed effect of an ENSO event. On the other hand, years with remarkably high breeding effort (1984/1985, 1989/1990, 1996/1997, 1998/1999 and 2001/2002) were associated with years characterized by a negative multivariate ENSO index (mostly cold SST, La Niña). Demonstrated differences in the productivity of lower trophic levels such as squid (Jack son and Domeier 2003) between El Niño and La Niña may largely explain why

increased food availability may relate to increased breeding effort in colder (La Niña) conditions.

Other local conditions such as nest quality and microhabitat structure may also affect the early stages of the breeding cycle. Local snow accumulation can change accessibility of nest sites. Hatching success was definitely subject to local weather conditions, especially snowfall. Several studies highlighted the role of breeding sites and nest quality as controlling factors (Duffy 1983; Coulson 1968; Chastel et al. 1993). Nest quality may play an important role in the control of energetic requirements during incubation or chick growth (Weathers et al. 2000). Melting snow in the nests was identified as the major cause of breeding failure at Ile des Pétrels (Chastel et al. 1993). Nest characteristics also influences fledging success through differential predation (Barbraud 1999). If we assume that the high fidelity of snow petrels to their colony and to their nest site is a trait of the species (Guillotin and Jouventin 1980; Jouventin and Bried 2001), the use of the breeding history of individual nests rather than individual birds to conduct a long-term population study is justified and may partly compensate the lack of information on individuals. Therefore, the breeding history of nests may provide valuable information in terms of nest quality. A later publication will be dedicated to the effects of microhabitat conditions and local weather on the inter-annual variability in the breeding success of individual nests at Reeve Hill.

The main outcome of this study is that snow petrel breeding performance variability at Reeve Hill is partly controlled by environmental factors such as SIE variations, consistent with earlier studies at Ile des Pétrels. However, differences in the way breeding performance parameters vary between the two locations, despite partially correlated sea-ice conditions, revealed that the effects of large-scale environmental variations on snow petrel breeding performance may be confounded by the effects of regional or local sea-ice conditions either at the feeding grounds, in the vicinity of the colony (food availability), or at the nest (nest quality). In a review on environmental change and Antarctic seabird populations, Croxall et al. (2002) insist on analysing long-term demographic variations in conjunction with accurate data on the distribution, extent and nature of their habitat during breeding and non-breeding seasons. Due to the confounding effects of a series of environmental parameters at various spatial and temporal scales, the prediction of snow petrel population changes from environmental changes remains complicated even at a well-monitored location. Further investigations are needed to elucidate how local and micro-environmental conditions (at the colony or at the nest) may modulate the effects of large-scale environmental variations. There is a strong need to study the factors that control population dynamics at the local/regional-scales and how they differ between locations before making any general assessment of the effects of global warming and sea-ice on long-term populations trends around the Antarctic continent. Our study confirms that the way seabird

populations are impacted by large-scale environmental processes differs between regions. A set of monitoring locations located around the Antarctic continent is necessary to conduct useful comparative studies on the local effects of global climate events on seabird population trends.

**Acknowledgements** The authors are grateful to L. Belbin, G. Jackson and B. Raymond for their comments on an early draft. B. Raymond also provided very valuable help for sea-ice data processing and Dr S. Wotherspoon helped with some of the statistical analysis of the data. We thank three anonymous reviewers, who kindly suggested improvements to the original manuscript. We are grateful to A. Beinssen, P. Bell, A. Breed, G. Browning, E. Bulling, S. Creet, C. Deacon, T. Donohue, R. Givney, A. Hackett, O. Hentschel, M. Hovenden, A. Jackson, A. Lee, T. Maddern, B. Matheson, T. Montague, P. Nicholls, M. Pertout, S. Pearce, A. Post, J. Reynolds, J. Stark, R. Seppelt, D. Simon, A. Watson, R. Watzl, G. Browning and many unnamed Casey personnel for their participation in the Reeve Hill long-term monitoring program. This project is now part of an ongoing program on long-term monitoring of bird populations supported by the Antarctic Science Advisory Committee (ASAC project 1219).

## Appendix 1

Methods used for the comparison of breeding parameters obtained for a constant subset of nests and a varying number of nests at Reeve Hill between 1984 and 2002.

Logistic regression was used for four of the five reproductive performance parameters studied. Data were separated into two groups: group A, the subset of 42 nests and group B, all the remaining nests (this number varied from year to year). A logistic regression model of the form  $\text{logit}(\pi_{ij}) = M + \text{Year}_i + \text{Group}_j$  was fitted. With this model,  $M$  was a constant, Year was treated as a factor (not as a covariate), and the significance of the term group (A or B) was tested. Analyses were conducted for breeding effort, hatching success, fledging success and breeding success. The four analyses compared the fit of the model that allowed the proportion of success to vary between years and between groups to the fit of the model that only allowed the proportion of success to vary between years. Group A and B did not differ significantly in breeding effort, hatching success, or breeding success ( $P > 0.1$  for each model). For fledging success, the dataset on which the fit of the models was tested was greatly reduced due to the presence of null values (0 fledging against 0 egg hatched in group B). The difference between groups was significant ( $P = 0.020$ ), but is not clear which years were associated with group differences and the reduced number of data points (only nine) limits conclusions. Overall, we are confident that breeding performance parameters obtained for a subset of nests consistently checked were not significantly different from those obtained for the entire study colony (with a varying number of nests). Thus, in order to remain consistent with the study at Ile des Pétrels, all subsequent analyses and

results presented, in this paper, were conducted with breeding performance parameters calculated for the entire study colony.

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