

# Ultimate and proximate factors affecting the breeding performance of a marine top-predator

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Pinaud, D. and Weimerskirch, H. 2002. Ultimate and proximate factors affecting the breeding performance of a marine top-predator. – *Oikos* 99: 141–150.

Variability in ecosystems affects the life history of organisms. In marine ecosystems where interannual variability is high, relationships between fluctuations in oceanographic parameters and top-predator breeding performance are increasingly documented but it is less clear why such relationships exist. In this study, we examined the connections between marine environment fluctuations and breeding performance of a long-lived top-predator, the black-browed albatross *Diomedea melanophris* at Kerguelen, through study of resource acquisition and allocation processes. Our results show that this population used the same foraging zones and spent similar time foraging year after year, but adult body condition varied between years. Foraging trips are regulated mainly by changes in body condition. During years of low resource availability, birds return to their nest with lower body condition and adults in low body condition were more frequent and therefore were more likely to stop breeding. Poor breeding success was related to the presence of colder waters in the foraging zones of breeding albatrosses as measured by the positive correlation between sea surface temperatures and breeding success measured over 18 years. Lower breeding success was mainly due to failure by inexperienced birds. The results of this study demonstrate how oceanographic conditions affect breeding performance through allocation processes. We compared these results to those at South Georgia where the breeding success is lower and more variable. This population relies mainly on krill, a resource that shows a very variable year-to-year availability compared to fish prey consumed by Kerguelen birds. This study shows that, in the same species, differences in resource variability and availability affect the demographic strategies probably through differences in allocation strategies.

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Variability in ecosystems is probably a major constraint in the evolution of life history traits of organisms (Stearns 1992, Begon et al. 1996). In marine ecosystems, interannual variability is a well-recognised phenomenon with very variable and sometime unpredictable fluctuations in oceanographic parameters, or cyclic patterns such the El-Niño-Southern Oscillation (Schreiber and Schreiber 1984) and the North Atlantic Oscillation (O'Brien et al. 2000). This variability is expected to affect all levels of the trophic web and especially marine top-predators populations (Croxall 1992). Several studies (Guinet et al. 1998, Thompson and Ollason 2001, Weimerskirch et al. 2001) showed that the productivity and recruitment of seabirds were

negatively affected by sea surface temperatures (SST), a parameter mainly used to describe oceanographic conditions affecting marine ecosystem (Nicol et al. 2000). Other studies have shown the same negative effect of warm SST events, such as El Niño, on seabird reproductive performances (Boersma 1978, Schreiber and Schreiber 1984). The connection between the marine environment and breeding performances is likely to be achieved through resource acquisition and allocation processes (Boggs 1992, Stearns 1992). However, although relationships between oceanographic parameters and breeding performances are increasingly documented, the reasons why such relationships exist is not well understood.

Accepted 4 April 2002

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ISSN 0030-1299

Variations in the physical marine environment are likely to affect the availability and accessibility of resources for foraging seabirds that should allocate resources toward maintenance and reproduction according to life history theory (Stearns 1992), and therefore affect ultimately breeding performances of top-predators like seabirds (Weimerskirch 2001). Oceanic seabirds such as Procellariiforms are typically central place foragers with long distances between resource and breeding grounds. They forage for marine resources which are supposed to be patchy and unpredictable (Ashmole 1971) but the prey distribution can be associated with environmental features, such as frontal zones, shelves and shelf slopes (Hunt 1991). The temporal and spatial separation between feeding areas and breeding grounds represents an important energetic constraint during reproduction. Oceanic seabirds have to catch prey far from the nest, store this energy and then later draw upon it, for themselves during fasting in incubation, or for feeding the chick. Thus, resource availability within the foraging range of a species should be crucial for its success of reproduction. However, spatial scale is of crucial importance to understand the interactions between the marine environment and wide-ranging top-predators (Hunt and Schneider 1987). Recently, satellite-tracking of large seabirds (Jouventin and Weimerskirch 1990) has enabled the definition of this scale of interaction at the individual level.

Oceanic seabirds, such as Procellariiforms, are long-lived organisms that should be less prone to trade their own survival for that of their offspring because any reduction in adult survival would greatly reduce lifetime reproductive success (Goodman 1974, Charlesworth 1980). It has been proposed that these allocation decisions are dependent on the individual physiological state, and especially the body condition related to the amount of energy stored (McNamara and Houston 1996). Weimerskirch (1999) showed the important role of body condition in allocation decisions for foraging and breeding albatrosses and petrels. These species behave as prudent parents (Drent and Dann 1980) in never allowing their body condition to deteriorate to a level that may jeopardise their lifetime reproductive success. In such species a lower mass threshold exists, where the birds abandon the reproduction (Chaurand and Weimerskirch 1994, Weimerskirch 1999). The regulation of foraging trips and foraging efficiency is thus important to maintain a sufficient amount of body reserve for the success of reproduction.

The majority of breeding failure in albatrosses and petrels occurs during the incubation period, mainly by desertion (Warham 1990). During this time, mates alternate foraging at sea and incubating at the colony, typically in shifts lasting from two days to several weeks while the partner fasts on the nest. The decision to stop incubation and to begin foraging is subordinate

to the relief by the partner, since the temporary desertion of the egg would increase the risk of nest predation. However, the foraging trip duration is very variable because of long distance to feeding areas and unpredictability of resources. The foraging partner has to return before incubating partner runs out of body reserve and then deserts. Thus, the regulation of the foraging trip length and its interaction with the body condition variations during incubation are very important to explain the breeding success (Chaurand and Weimerskirch 1994).

The aim of this study was to investigate the links between variations in marine environment, foraging efficiency, body condition and breeding success of a marine top-predator, the black-browed albatross *Diomedea melanophris*, for which we have a long-term demographic data set. To do this, we first examined the foraging behaviour and foraging areas of the population by satellite telemetry. Then we examined whether individuals regulated their foraging effort according to their body condition, and to what extent the body condition affected breeding success. Finally we examined the relationship between an environmental parameter (sea surface temperature) in the foraging zones of the population to its breeding success.

## Methods

### Field procedures

The study was carried out in the colony of Cañon des Sourcils Noirs (1200 pairs), Kerguelen Islands (49°40' S; 40°15' E). In the study colony (250 pairs in 1999), all breeding birds are banded and their breeding performances have been monitored every year since the season 1979–80 (Weimerskirch and Jouventin 1987). Hereafter, the breeding seasons are designated by their spring year, i.e. 1979 for 1979–1980. The breeding success is the percentage of eggs giving chicks alive prior to fledging at the same date for each year. Between 17 November and 8 December 1999, eight incubating birds were fitted with 32 g satellite transmitters (PTTs; platform terminal transmitters, PTT100, Microwave Telemetry, Columbia, MD, USA,) and wet/dry activity data loggers (mass 12 g, Francis Scientific Instruments, Caxton, UK) which record immersion period in salt water at a sampling rate of 5 s. The PTTs were fitted on back feathers with adhesive tape (Weimerskirch et al. 1994) and left on the birds for the foraging trip. The wet-dry loggers were attached to the tarsus on plastic bands using adhesive tape. The overall weight of the instrumentation carried by each bird was 44 g, i.e. 1.2% of the average body mass of the black-browed albatross during the incubation period. Satellite locations were filtered following Weimerskirch et al. (1992). The locations of the landings on water from the

wet-dry loggers were estimated by a home-made program, considering that birds moved at an average speed calculated from the distance covered between two satellite fixes divided by the time spent in flight.

To measure foraging performance and mass changes on land, 40 nests were observed continuously by two observers during daylight hours from 0730 h to 1800 h (UTM + 5 h). To make identification easier at a distance, one adult from each pair was marked on the breast with a yellow patch of picric acid. The times of arrival and departure of the adults were noted continuously. From these 40 pairs, 30 were used to measure the mass gain at sea and the mass loss during incubation shift. Birds were weighed using a portable false nest integrating a balance accurate to 0.5% (Francis Scientific Instruments, Caxton, UK). For each weighing, the adult was delicately displaced from its nest after removing carefully the egg, and the false nest with a dummy egg was installed on the nest. The bird returned on the false nest to incubate the dummy egg and was weighed. The maximum total duration of the weighing was 2 minutes. Birds were weighed on the arrival day, then every 2 days until departure for the sea.

To compare average body mass between years during mid-incubation, a random sample of birds was weighted using a Salter spring balance accurate to 0.5% in 1984 and 1991. Data for 1999 were randomly chosen, one weighing per individual, to avoid pseudo-replication. We compared foraging trip durations between these three years by using the same method. During 7 days in 1984, 11 days in 1991 and 19 days in 1999, a sample of nests (77 in 1984, 39 in 1991 and 33 in 1999) was checked every two days to determine the number of changes occurring during this interval of time. Thus, we obtained a proportion of nests where a change occurred per day.

## Data analysis

Main areas used at sea by albatrosses during the breeding season were determined by kernel density estimators (Silverman 1986). This non-parametric approach allows assessment of foraging areas (Wood et al. 2000) where the density of satellite locations reaches a maximum. Typical foraging trips of black-browed albatross can be split into three distinctive parts according to differences in the density of fixes (Weimerskirch et al. 1997a): 1) a movement part when birds commute rapidly from the colony to a specific area, 2) a foraging movement when birds move in a specific area where they probably search for food, 3) a return trip to the colony. Kernel analysis was performed on each foraging trip to isolate foraging areas where fixes density is maximum ("core") from commuting parts. The kernel bandwidth parameter  $h$  was chosen using least squares cross validation (Powell 2000). We used "Animal Movement" extension

(Hooge and Eichenlaub 1997) to GIS ArcView (ESRI Inc., Redlands, CA, USA). For each foraging trip, the relationship between probability of use (percentages of fixes) and percentage of area with the probability of use was plotted. The intersection with the tangent with a slope of  $-1$  constituted the boundaries of the core (Powell 2000). Core fixes were extracted for each foraging trip and compared to the areas where albatrosses landed frequently determined by wet-dry loggers. Landings can be associated with foraging behaviours (Weimerskirch et al. 1997b). A second kernel analysis was performed on core fixes by year to define main foraging area used by season. We used "Albers Equal Area Conic" projection to respect surfaces. This analysis was performed on the foraging trips of 1999 during incubation and on data from Weimerskirch et al. (1997a) concerning two seasons (1993 and 1994) during chick rearing period. A total of 1555 fixes (809 core fixes) from 53 foraging trips concerning 26 individuals was analysed.

The environmental conditions prevailing in the foraging areas were estimated from sea-surface temperature (SST) measured through satellite remote sensing. These data adjusted for biases were obtained from the web site of the Integrated Global Ocean Service System (<http://ingrid.ldgo.columbia.edu/SOURCES/IGOSS/>, Reynolds and Smith 1994). The spatial scale chosen to extract SST anomalies (SSTa) corresponded to the main foraging area for the three years determined by kernel analysis, including 95% of the core fixes (Fig. 1). SSTa were extracted monthly from November 1981 to April 2000 with a  $1^\circ$  scale. For each breeding cycle (1981 to 1999), Spearman correlation coefficients were calculated between annual breeding success and monthly SSTa from May (six months before laying) to April (end of the breeding season). We used a randomisation procedure to evaluate the statistical significance of correlation coefficients. We estimated a 95% confidence interval on the correlation coefficient using a bootstrap estimation method (Hall 1992). Breeding success data were randomly rearranged to SSTa values 1000 times. The resulting set of coefficients provides an approximate sampling distribution of the correlation coefficient (Gleason 1988) and consequently, 95% approximate confidence intervals of the observed value of the correlation coefficient. Results were found to be significant when the correlation coefficient was significant at  $p = 0.004$  with Bonferroni adjustment (two-tailed test), and when a correlation coefficient value of 0 was not included within the 95% confidence interval.

We estimated the body mass at arrival and at departure using the equation  $W_t = W_0 e^{-kt}$  (Croxall 1982), where  $W_t$  is the body mass at time  $t$ ,  $W_0$  is the body mass at arrival, and  $k$  is the proportion of mass loss per day. With data when the time between the arrival and the first weighing were less than 6 h (then we assumed  $W_t = W_0$ ),  $k$  was 0.0136 ( $n = 28$ ,  $R^2 = 0.86$ ,  $p = 0.001$ ),

very close to the value of 0.014 found by Prince et al. (1981) and Croxall (1982). Using molecular sexing (Fridolfsson and Ellegren 1999, Schaffer and Weimerskirch unpubl.), no significant differences were found between sexes in body size and body mass.

To explain variations in two variables, the body mass gain after a foraging trip (*GAIN*), and the time spent at sea (*DURTRIP*), we performed two stepwise backward multiple linear regressions in "listwise" mode. The independent variables were the duration of the incubation shift before the foraging trip (*DURINC*), the body mass loss during this incubation shift (*LOSS*), the body mass at departure (*MASDEP*), and, according to the dependent variable, *DURTRIP* or *GAIN*. Thus, the two models were  $GAIN = DURINC + LOSS + MASDEP + DURTRIP$  and  $DURTRIP = DURINC + LOSS +$

$MASDEP + GAIN$ . The independent variables with  $\alpha \leq 0.05$  were kept by the model. To avoid pseudo-replication, one bout per individual (an incubation shift and a foraging trip) was randomly selected.

No data were available on the value of a desertion mass threshold for black-browed albatross. So, we estimated this value according to the allometric relationship from Weimerskirch (1999), with the average body mass at the beginning of an incubation shift during mid-incubation in 1999. The equation is:  $M/M_t = -0.2467 [\log_{10}(M)]^2 + 1.7104 \log_{10}(M) - 1.3816$  ( $n = 7$  species,  $r = 0.96$ ,  $p = 0.004$ ) with  $M$ : mass and  $M_t$ : mass threshold.

Statistical tests were carried out using SYSTAT 9.0 software (SPSS Inc., Chicago, IL, USA). All values are expressed as means  $\pm 1$  SD. Tests are two-tailed and  $p$ -values  $< 0.05$  were considered statistically significant.

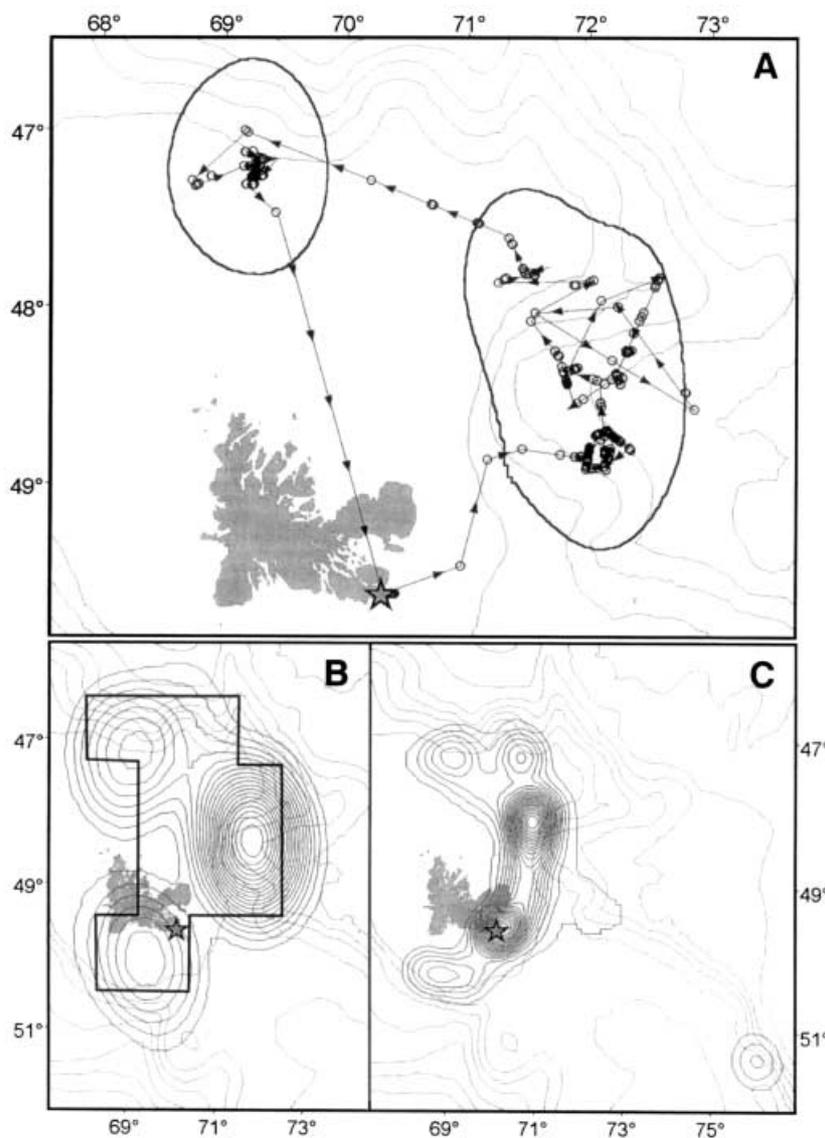


Fig. 1. (A) Example of a foraging trip during incubation in 1999. The open circles indicate the landings of the bird. The two foraging zones for this trip are indicated by solid, black lines and were determined by a kernel analysis on the Argos locations. (B) Areas used by black-browed albatrosses during 1999 incubation and (C) 1993, 1994 chick-rearing periods. Density contours resulting from kernel estimation (see Methods: data analysis). Contour levels are indicated by concentric circles with decreasing step of 5% location densities. Positions of isobaths (step of 500 m) are shown. The colony is indicated by a grey star. The area used to extract SSTa at 1° scale according to the 3-year distribution is shown by solid, black line (B).

## Results

### Foraging behaviour and foraging areas

During incubation, black-browed albatrosses show a typical foraging behaviour with commuting and foraging sections (Weimerskirch et al. 1997a). The foraging areas given by the kernel method were located in the same zones where albatrosses landed frequently (pattern associated with foraging behaviour, Fig. 1A). The areas prospected by albatrosses from the Cañon des Sourcils Noirs colony in 1999 were located mainly on the inner shelf break in the north-east (Fig. 1B). Areas used were very similar in 1993 and 1994 (Fig. 1C), with overlap from 68% to 95%.

For the three years grouped, the main foraging zone was located on the inner shelf break in the north-east. SSTa were extracted from this distribution with 95% of core fixes (Fig. 1B).

### Mass regulation

Birds lost mass on the nest and generally gained mass at sea. The average duration of foraging trips during incubation was  $4.3 \pm 1.4$  days. The mass gain was explained by the mass loss during the fast in the previous incubation shift (last step:  $GAIN = 1.66 LOSS + 0.08$ ,  $n = 22$ ,  $R^2 = 0.23$ ,  $F_{1,20} = 5.99$ ,  $p = 0.024$ ; Fig. 2A). The relationship between time spent at sea and the mass gain was significant ( $DURTRIP = 1.78 GAIN + 2.97$ ,  $n = 23$ ,  $R^2 = 0.17$ ,  $F_{1,21} = 4.43$ ,  $p = 0.047$ ; Fig. 2B). This suggests that in 1999 albatrosses tried to restore the mass lost during the previous incubation shift, and the greater the mass gain, the longer the time spent at sea. We calculated a body mass recovery index (in%) where the mass gain at sea was divided by the mass lost during the previous incubation shift. This value was on average  $191 \pm 268\%$  ( $-616-707$ ,  $n = 22$ ) and was not significantly related to the time spent foraging (linear regression:  $n = 22$ ,  $R^2 = 0.08$ ,  $F_{1,21} = 1.78$ ,  $p = 0.196$ , power = 0.249). This suggests that time spent at sea in 1999 was not a critical parameter affecting the reconstitution of the body mass and that black-browed albatrosses stayed at sea until they restore body reserves.

The average body mass during 1999 mid-incubation was  $4.360 \pm 0.460$  kg ( $n = 59$ ). From the allometric relationship between body mass and desertion mass threshold with six species (Weimerskirch 1999), the desertion mass threshold calculated for the black-browed albatross was 2.72 kg for the 1999 mid-incubation period. The average maximum fast duration before reaching mass threshold for desertion, modelled from the mass loss rate, was 30 days (Fig. 3). For the lighter individuals, this duration was lower

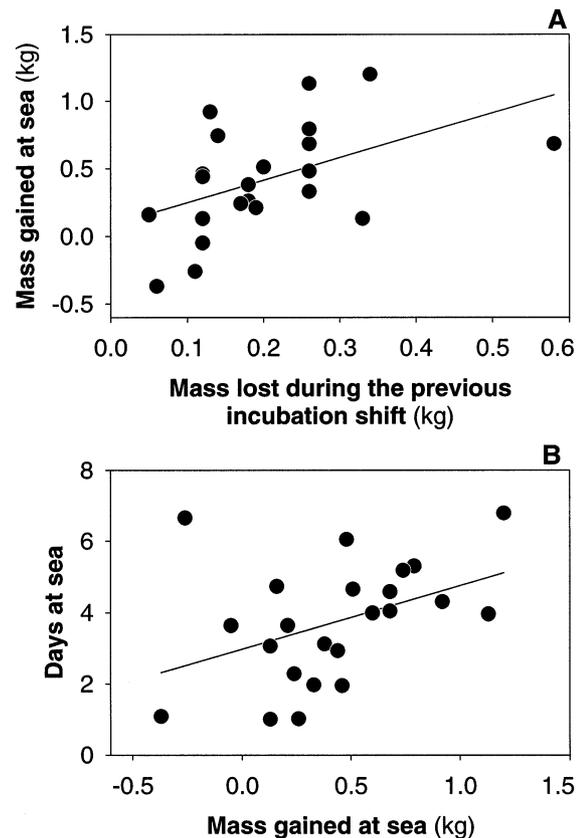


Fig. 2. Regulation of body mass during incubation in black-browed albatross. (A) Mass gained at sea in relation to the mass lost during the previous incubation shift. Result of stepwise regression:  $GAIN = 1.66 LOSS + 0.08$ ,  $n = 22$ ,  $R^2 = 0.23$ ,  $F_{1,20} = 5.99$ ,  $p = 0.024$ . (B) Duration of foraging trip in relation to the mass gained during this trip. Result of stepwise regression:  $DURTRIP = 1.78 GAIN + 2.97$ ,  $n = 23$ ,  $R^2 = 0.17$ ,  $F_{1,21} = 4.43$ ,  $p = 0.047$ .

(ca 16 days) and was close to the maximum observed fasting duration (12 days; Fig. 3).

### Body mass and trip duration variations

Incubating birds were lighter in 1984 than in 1991 and 1999 (ANOVA,  $n = 157$ ,  $F_{2,154} = 9.68$ ,  $p < 0.001$ , post-hoc tests 1984 vs 1991 then 1999 with Bonferroni adjustment, both  $p < 0.001$ ; Fig. 4). No significant difference was found between the body masses of 1991 and 1999. The number of change per day was very similar between the three years. The ratio of changes occurred was 103 for 231 nest  $\times$  day in 1984 (0.223 change per day), 97/195 in 1991 (0.249 per day) and 145/305 (0.238 per day) in 1999. These proportions were not significantly different according to the year ( $\chi^2_2 = 0.61$ ,  $p = 0.89$ ). This indicates that the foraging efficiency rather than the trip duration contributes to these interannual mass variations.

## Reproductive success and SST

The average overall reproductive success from 1979 to 1999 was  $65.73\% \pm 9.08$ , ranging between 44 and 88%, and showed significant year-to-year variations (Fig. 5). In 1980, 1984 and 1989, the percentages of young fledging were low, below 50%. In 1984, the breeding success was 30% lower than in 1991 and 1999 ( $\chi^2_1 = 19.9$ ,  $p < 0.001$  and  $\chi^2_1 = 13.4$ ,  $p < 0.001$ , respectively). Distributions of body mass in incubation show that a large part of birds in 1984 was closer to the desertion threshold mass than those in 1999 (Fig. 4).

On average from 1985 to 1999, breeding failure was  $19.97 \pm 6.94\%$  (7.02–35.40,  $n = 15$ ) in incubation and  $10.63 \pm 6.43\%$  (2.72–25.15,  $n = 15$ ) during chick rearing. We provided a decomposition of variance. Contribution to the total variation (Saporta 1990) was 58.5% for incubation failure, 50.0% for rearing (including brooding period) and joint contribution was 8.5%.

The overall breeding success showed significant positive correlation with the SSTa on the foraging areas determined by satellite tracking. This relationship was observed with coefficient from 0.63 to 0.68, for the months of September to November, corresponding to pre-breeding and incubation stage (Fig. 6).

## Influence of breeding experience

The overall breeding success (BS) was different between individuals according to their reproductive experience, with the two groups “inexperienced birds” (first time of

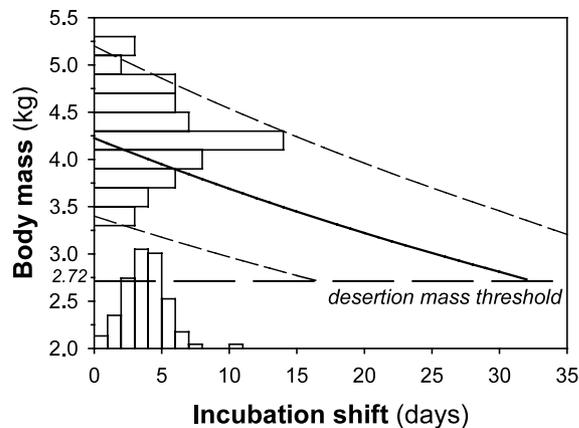


Fig. 3. Distribution of incubation shift durations ( $n = 66$ ) and body masses at the beginning of a shift ( $n = 59$ ), and weight loss function of time incubating for black-browed albatrosses in 1999. The solid line indicates the weight loss for a mass of 4.3 kg (average value at the beginning of the fast), the two short, dashed lines indicate the weight loss for the maximum and the minimum values observed. The desertion mass threshold for this species (calculated from Weimerskirch 1999) is shown by the long, dashed line. The lower the mass at the beginning of the fast, the shorter the maximum fasting duration.

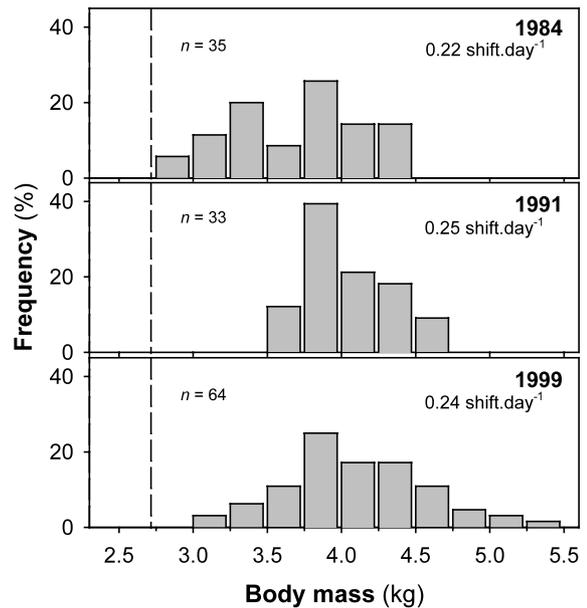


Fig. 4. Distributions of body mass and number of shift per day during incubation in 1984, 1991 and 1999 breeding seasons. Incubating birds were lighter in 1984 than in 1991 and 1999 (ANOVA,  $n = 157$ ,  $F_{2,154} = 9.68$ ,  $p < 0.001$ , post-hoc tests 1984 vs 1991 then 1999 with Bonferroni adjustment, both  $p < 0.001$ ). No difference was found between the body masses in 1991 and 1999. The number of shift per day was very similar between the three years. These proportions were not significantly different according to the year ( $\chi^2_2 = 0.61$ ,  $p = 0.89$ ). The desertion mass threshold is indicated by the dashed line. The mass of a large part of birds in 1984 was close to this threshold.

breeding) vs “experienced birds” (at least one breeding attempt). We performed a GLM with model  $BS = SSTa + EXP + SSTa \times EXP$  with data for 1988 to 1999. Both SSTa on the foraging zones ( $F_{1,20} = 22.3$ ,  $p < 0.001$ ) and experience ( $F_{1,20} = 30.9$ ,  $p < 0.001$ ) influenced the breeding success, with an interaction between the two variables nearly significant ( $F_{1,20} = 3.3$ ,  $p = 0.083$ ; Fig. 7). In years with cold SST conditions on the

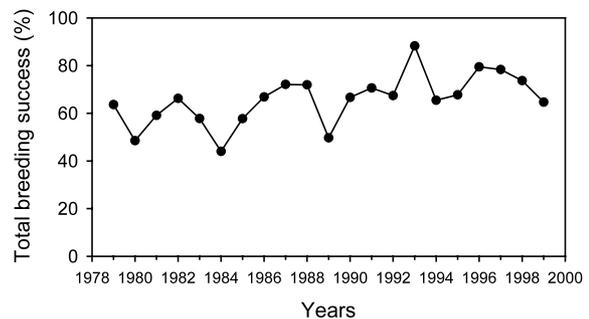


Fig. 5. Annual variations in overall breeding success of black-browed albatrosses from Cañon des Sourcils Noir colony, Kerguelen Island, from 1979 to 1999. Sample size varied from 44 (1979) to 255 nests (1999). Year-to-year variations were significant ( $\chi^2_{19} = 51.95$ ,  $p < 0.001$ ).

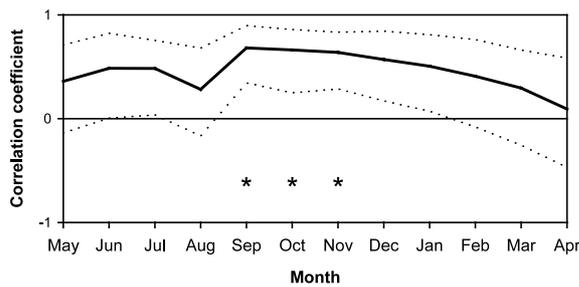


Fig. 6. Variation in the Spearman correlation coefficient calculated between SSTA measured in the foraging areas from May (previous the breeding season) until April (at the end of the breeding season) and overall breeding success of black-browed albatrosses in Kerguelen. Limits of the 95% confidence interval are indicated by the short, dashed lines. Statistical significance of the Spearman correlation is considered at  $p = 0.004$  with Bonferroni adjustment and is indicated by a star. The numbers of years were  $n = 18$  from April to October and  $n = 19$  from November to May, because satellite observations for SST data began in November 1981.

foraging areas, inexperienced birds seemed to have lower breeding success than expected.

## Discussion

The population of black-browed albatrosses at Kerguelen appeared to forage in a restricted area, the north, east and south edges of the Kerguelen shelf, close to the colony (200–300 km) during incubation. The main area used was located in the north-east of the shelf. Black-browed albatrosses exploit year after year this area as indicated by other studies on the same colony at different stages (chick rearing, Weimerskirch et al. 1997a)

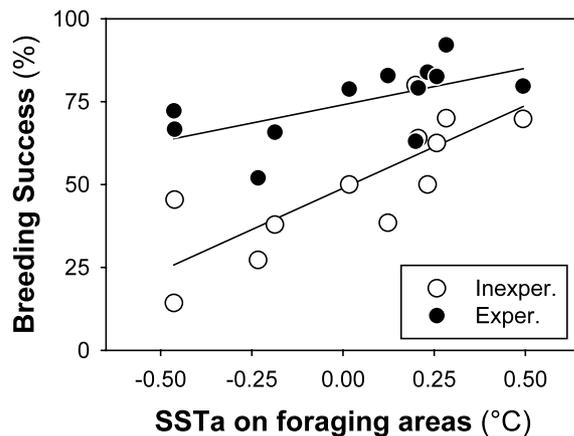


Fig. 7. Overall breeding success (in%, %BS) in relation to the SSTA in October on the foraging areas for experienced and inexperienced birds, for 1988 to 1999. GLM,  $\%BS = SSTA + EXP + SSTA \times EXP$ ,  $F_{1,20} = 22.3$ ,  $p < 0.001$ ;  $F_{1,20} = 30.9$ ,  $p < 0.001$ ;  $F_{1,20} = 3.3$ ,  $p = 0.083$ , for each term respectively.

using different techniques (dyed birds, Weimerskirch et al. 1988a). This zone shows an enhanced primary productivity that can be related to water movements occurring in this area due to a “mass island effect” (Blain et al. 2001). The location of the main foraging area of albatrosses is related to this high productivity zone nearby the colony. Thus, resources for black-browed albatross are spatially predictable at this large scale but its availability is probably different from one year to the next (Cherel et al. 2000).

Variations in SST can be related to the water mass dynamic and the position of frontal zones (Park et al. 1998) and this affects distribution and abundance of zooplankton, fish and squid (Hunt et al. 1981) and the distribution of their predators (Deacon 1982). The SST occurring in the foraging areas of black-browed albatrosses varied extensively from one year to the next, indicating that oceanographic conditions, and therefore probably prey availability for albatrosses varied accordingly. Several studies have shown that the reproductive performance of seabirds is affected negatively by warm water events that modify prey availability in foraging areas (Schreiber and Schreiber 1984, Guinet et al. 1998). Kitaysky and Golubova (2000) showed on different seabird species that the trends of these effects on reproductive performance depend upon diet characteristics (fish vs zooplankton). Black-browed albatrosses show a different pattern with positive effect of warm events on productivity, the breeding success increasing with SSTA on foraging areas. The reasons why black-browed albatross are affected positively by warm water events are not clear, but it seems that the response of a species to environmental fluctuations depends of its trophic position in the food web and the scale of interaction between the population and its environment. The relationship is very significant, suggesting that it is not an artefact.

The main result and most novel aspect of this study is to be able to determine the process by which breeding success is affected by environmental variability. Breeding success of most seabirds is mainly due to spontaneous desertion of the nest by breeders (Warham 1990). The consequences of a temporal desertion of the nest are irreversible during incubation when the egg is predated if abandoned, even temporarily, whereas the chick can be left alone and sustain periods of fast. Therefore, breeding success is mainly affected by failure during incubation.

Although the same foraging areas were used and trip durations did not vary significantly between years, the foraging efficiency appeared to affect mainly the body mass of foraging birds. During incubation, the mass lost on the nest depends of the shift duration and thus on the foraging success of the partner. The body mass recovery in 1999 was not related to time spent foraging, and this suggests that, during good years, albatrosses

tried first to restore body condition and did not adjust time at sea to the body condition of the partner. This compromise between the bird's own foraging success and its mate's fasting ability was suggested during incubation in other seabirds (Chaurand and Weimerskirch 1994, Tveraa et al. 1997) where time spent at sea was negatively correlated to mass gain. These two petrels are smaller species compared to albatrosses, and their safety margins are smaller too (Weimerskirch 1999). During incubating shift, they lost between 15 and 20% of their body mass, i.e. their mass comes close to the mass at desertion (Chaurand and Weimerskirch 1994, Lorentsen and Røv 1995). The regulation of the foraging trips in relation to the body mass of the mate may be an important factor reducing the desertion rate in these species (Chaurand and Weimerskirch 1994, Tveraa et al. 1997). In black-browed albatross, foraging trips in 1999 as well as during other years are short on average (4 days) whereas the predicted average maximum duration of fasting shift is 30 days. This means that black-browed albatrosses have a large safety margin before desertion and probably explains why the breeding success is on average high for this population (65% vs 29% in South Georgia, Croxall et al. 1997). When foraging success is lower, mass gain is lower, risk of desertion by the partner on its nest is higher and consequently breeding success is lower. This is clearly shown by the lower mass of incubating birds in one of the years with low breeding success. Thus, the correlation found between oceanographic conditions (through SST) and breeding performance of black-browed albatross appears to be mediated by allocation processes, through foraging efficiency of the adults and their ability to store enough energy during a foraging trip for incubation. The greater fasting ability is found in large species such as wandering albatross where adults in incubation could fast for up to 40 days (Weimerskirch 1995).

Our results suggest that the lower breeding success of black-browed albatross during some years with colder waters in foraging areas could be amplified by the lower foraging efficiency of inexperienced birds during these years. Inexperienced birds are expected to be lighter, and therefore closer to the body mass threshold. This result is important since it suggests that the foraging efficiency of experienced adults is less affected by poorer oceanographic conditions. Breeding performances are known to be age-related and age-specific increases in breeding success have been attributed to a lack of breeding and/or foraging experience in young seabird adults (Hamer et al. 2001). In two other species of Procellariiforms, inexperienced birds spent more time at sea but with the same foraging efficiency than experienced birds (Weimerskirch 1990, 1995), suggesting that inexperienced birds could be less effective in body mass regulation and could take longer time to find productive areas.

## Comparison with South Georgia population

Populations of the same species relying in different resources are likely to show different allocation strategies, and therefore demographic strategies (Weimerskirch 2001). Two populations of black-browed albatross are well studied and differ in several demographic parameters. At Kerguelen, the breeding success is on average high (65%, 44–88%) and shows little variations (CV: 13%), whereas at South Georgia (Prince et al. 1994, Croxall et al. 1997), breeding success is lower (29%, 0–64%) and more variable (CV: 76%). Differences between the two populations could be explained by differences in feeding ecology and body mass regulation. The foraging areas are on average farther at South Georgia than at Kerguelen (100–600 km vs 250 km, respectively, Prince et al. 1999), and consequently average foraging trips and time fasting on the nest during an incubation shift during incubation are three time longer at South Georgia (9–12 days, Tickell and Pinder 1975). At South Georgia, adult body mass is lower during this period than at Kerguelen, (3.70 kg vs 4.15 kg, respectively), for the same size (Tickell and Pinder 1975, Weimerskirch et al. 1988b) and the same body mass at the beginning of reproduction (Huin et al. 2000). Thus, the South Georgia individuals are probably closer to the mass threshold and therefore more likely to desert. This smaller safety margin could explain the low average breeding success for this population compared to Kerguelen.

The South Georgia population relies mainly on krill *Euphausia superba* (Prince 1980, Croxall et al. 1999). Availability of krill is very variable, with extreme variations in abundance and/or location (Croxall et al. 1999). Black-browed albatrosses at Kerguelen have a more diversified diet and feed at an upper trophic level compared to those at South Georgia (Cherel et al. 2000). These differences in feeding ecology probably explain the greater variance of breeding success at South Georgia. The two populations differ also in life history traits, with higher adult survival and lower fecundity at South Georgia population (Weimerskirch 2001). These differences show how the variability and availability resources may affect allocation processes and demography in seabirds and also show the interest of comparing populations of the same species relying on different environments to understand the influence of the environment on the evolution of life history.

*Acknowledgements* – This study was supported by the Institut Français pour la Recherche et la Technologie Polaire (IFRTP, programm no. 109). We thank all the people involved in the monitoring programs of black-browed albatross at Kerguelen over the past 20 years; S. Chamaille-Jammes, S. Schaffer and F. Bonnadona for help with the field study and genetic data; X. Hindermeyer for the 1991 field study; D. Besson for managing the demographic database; S. Saïd-Delcros and L. Dubroca for help with GIS and Paul Thompson and an anonymous referee for constructive criticism of the manuscript.

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