

# Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross

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The provisioning parameters, breeding success, adult mass, and survival of yellow-nosed albatrosses were studied over 7 successive years at Amsterdam Island, southern Indian Ocean. We examined the ability of this long-lived seabird to adjust its breeding effort under different environmental conditions and the fitness consequences in terms of survival and quality of offspring produced. Provisioning rate and adult mass varied extensively between years, and the lowest and highest values were associated with sea surface temperature anomalies. When waters around the island were colder, adults were in good condition and brought large meals at short intervals, whereas warmer waters resulted in lower provisioning rates, lower adult mass, and lighter chicks at fledging. Adult survival and fledging success were not affected by sea surface temperature anomalies. Yellow-nosed albatrosses appear to be unable to adjust their breeding effort every season, and their differential breeding investment probably primarily reflects different levels of food availability. Yellow-nosed albatrosses are able to regulate their provisioning behavior according to the nutritional status of their chick only when conditions are favorable. Birds appear to invest primarily in their own future maintenance rather than in provisioning. They have a wide safety margin in body mass that limits mortality risks during good years as well as during poor years. However, during unfavorable seasons adults continue to provision chicks that have a poor prospect of survival to breeding, without additional survival costs for the parents. Favorable seasons therefore have a high value in terms of fitness because of the high quality of the chick produced. We suggest that understanding how long-lived animals optimize their provisioning behavior and lifetime reproduction can only be achieved through studies encompassing several contrasted seasons. *Key words:* adult mass, breeding effort, chick quality, *Diomedea chlororhynchos*, life history, Procellariiforms, survival, yellow-nosed albatross. [*Behav Ecol* 12:22–30 (2001)]

A central issue in life-history theory is the prediction that parents should balance investment in their offspring against their own chance to reproduce in the future (Stearns, 1976; Williams, 1966). One implication of this prediction is that long-lived species 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 (Charlesworth, 1980; Goodman, 1974). It has been suggested that, to maximize the survival of adults in long-lived species such as seabirds, parental effort should be regulated to a fixed level of investment, independent of the offspring needs (Ricklefs, 1992; Saether et al., 1993). Results of studies on reproductive costs, especially those using an experimental approach, are equivocal, with several studies indicating that survival costs may occur in long-lived species (e.g., see review by Golet et al., 1998). However, long-lived animals such as seabirds often live in highly variable environments, and this variability may partly explain why results on reproductive costs are so varied, even when results of studies on the same species are compared (Golet et al., 1998). Because many trade-offs appear only when food is limited (Stearns, 1992), it has been predicted recently that high environmental variability may favor the selection of a flexible breeding effort (Erikstad et al., 1998). These authors predicted that during poor breeding conditions maximum fitness is achieved by not breeding or

by abandoning the brood and that beyond a certain threshold in breeding conditions there is a steep increase in reproductive effort but a decrease in survival. To verify these predictions, it is necessary to study breeding effort under different levels of resource availability.

Provisioning behavior is generally considered to be a good measure of the breeding effort by parents. In central place foragers such as seabirds, study of the provisioning behavior of adults reveals foraging performances at sea and thus links foraging and life-history traits (Nur, 1987), but also breeding effort and environmental variability (e.g., Croxall et al., 1988). When food is less available in the environment, seabirds are likely to adjust breeding effort by modifying the rate of provisioning of the offspring (Burger and Piatt, 1990), and ultimately they can abandon the brood if the risk to their survival is too great (Drent and Daan, 1980). Conversely, years of high food availability may contribute disproportionately to lifetime reproductive success because under this condition birds are likely to produce offspring of good quality at low survival costs (Erikstad et al., 1998). Procellariiformes (albatrosses and petrels) are typical long-lived animals sharing distinctive life-history attributes including a single-egg clutch, slow reproductive rate, high survival, and slow chick growth (Warham, 1990, 1996). These extreme attributes are believed to reflect the conditions of their marine environment (Lack, 1968; Ricklefs, 1990). However, with their single chick, petrels and albatrosses are unable to adjust their breeding effort by rearing more or fewer offspring. Provisioning is related to food availability, but adults are also likely to regulate provisioning according to the needs of the chick (Kilner and Johnstone, 1997). Several studies have suggested that Procellariiformes cannot modify their provisioning behavior according to the nutritional status of

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their chick, but rather they provision the chick at a fixed rate (Hamer and Hill, 1993, 1994; Ricklefs, 1987, 1992). Other studies suggest that several species may indeed regulate provisioning (Bolton, 1995; Hamer and Thompson, 1997; Weimerskirch et al., 1995, 1997, 1999). However, only one of these studies (Weimerskirch et al., 1999) took place over more than a single season, so knowledge is still lacking on whether regulation abilities vary according to change in food availability. In addition, most studies used methods based on chick weight gains alone, which do not properly address the problem of regulation of provisioning rates (Granadeiro et al., 1999); therefore, monitoring individual behavior of parents is crucial (see, e.g., Weimerskirch, 1998).

Provisioning parameters represent only investment in the chick. The body condition of parents, rarely examined in provisioning studies, is a fundamental parameter that cannot be dissociated from provisioning of the offspring because it represents a degree of self-maintenance and a buffer against the risk of increased mortality due to breeding. Adult condition also plays a crucial role in breeding decisions (Drent and Daan, 1980) as well as in foraging decisions (e.g., Tveera et al., 1998; Weimerskirch, 1998). Patterns of mass changes have been used as an index of reproductive costs and as the outcome of adaptive compromises among different factors (Moreno, 1989). It is of particular interest to understand how long-lived species trade investment in their offspring against their own body condition (McNamara and Houston, 1996). Most studies investigating changes over time in breeding success or provisioning behavior have not simultaneously studied the effect of environmental variability on adult body condition (but see Chastel et al., 1995; Monaghan et al., 1989). Life-history theory would predict that in a long-lived seabird adult, body condition should be less affected than provisioning rates by a reduction of food availability. Investigating how adults adjust provisioning and body condition when environmental condition and food availability vary can test this prediction. Furthermore, no information is generally available on the survival of adults, yet adult survival is a key parameter when measuring costs of reproduction.

In this study we examined over several years, but also within two contrasted seasons, the degree of variation of a series of indices of breeding effort (individual provisioning parameters, quality of fledging, survival, and mass of adults) in a long-lived seabird, the yellow-nosed albatross, *Diomedea chlororhynchus*. This is the first time that all these parameters have been studied simultaneously over several years in a long-lived species. The purpose of the study was to assess the extent of variability of these indices between seasons and within a season and thus to examine the flexibility of breeding effort in a long-lived seabird, as well as to test the prediction by Erikstad et al. (1998) that under poor environmental conditions adults should stop breeding, but that beyond a certain threshold in breeding conditions they should increase reproductive effort at a cost for survival.

## METHODS

The study was carried out at Pointe d'Entrecasteaux, Amsterdam Island (37°50' S, 77°30' E), between January 1991 and April 1997, during the chick rearing period. Chicks hatch in early December, are left alone on the nest in late December, and fledge from the first days of April (Jouventin et al., 1983). The study was carried out in two adjoining colonies. One, with about 200 nests, had been used for long-term population studies ("long-term colony") since 1981 (see Weimerskirch et al., 1987) and a second, with about 120 nests, was used from 1990 onward to study the provisioning behavior ("provisioning colony").

The study of provisioning by individual parents was carried out in 1991, 1992, 1993, 1996, and 1997. In the provisioning colony adult birds were banded with a metal band, a plastic, colored band, and one member of the pair was marked with a spot of picric acid on the breast to allow identification at a distance. From mid-January to mid-February 1991, 1992, and 1993, two people continuously observed 28–42 nests from dawn to dusk (no adult return under darkness) to monitor the visits of the individual parent birds to the chick. The times of arrival and departure of the adults were noted continuously, yielding the duration of individual foraging trips. We weighed all chicks with a 5-kg spring balance accurate to 1% at 0500 h and at 1900 h. Whenever feeding was observed, the chick was also weighed within an hour of the departure of the parent. No negative impact of weighing chicks frequently was noted; they do not regurgitate food when accustomed to handling since hatching. As chicks lose mass on the nest from respiration and defecation, the difference in mass between the morning weighing and mass after a feed is not exactly the mass of the feed (Ricklefs et al., 1985). We therefore calculated the average rate of mass loss over time according to meal size and derived a value of expected mass loss during the time elapsed between the last weighing and the delivery of the meal. To estimate the net mass of the meal, we added the values of expected mass loss before the meal was delivered to the observed mass gain.

In early January 1996 and 1997, we replaced five nests with artificial nests (Francis Scientific Instruments, Caxton, UK) incorporating an automated system for weighing albatross chicks at 15-min intervals (Prince and Walton, 1984). Both the adults associated with each automated nest were fitted with a 9-g VHF transmitter (ATS, Isanti, Minnesota, USA) taped on the back feathers. In addition to the parents with automated nests, we fitted 12 and 20 adults rearing chicks from 18 and 25 nests with similar VHF transmitters in 1996 and 1997, respectively. An automatic recording station, comprising a receiver, a data logger (R4000 and DCCII, ATS, Isanti, MN) and an omni-directional antenna were installed in a hut 200 m from the colony. The automatic recording station continuously scanned the different frequencies. Each frequency was searched for 10 s, so every frequency was monitored every 4–5 min. The data from the automated nests and from the automatic receiving and recording station were downloaded every 15–20 days using a laptop computer. The information downloaded from the automatic recording station gives a list of frequencies, each representing an individual for a particular time, with a number of pulses. From these data the time of arrival and durations of the stay on land and at sea were calculated. The simultaneous analysis of data from the automated nest and automatic recording station permitted us to attribute each mass increase of the chick, corresponding to a meal, to one of the two parents. The automated nests and the logging and receiving station worked from early January till fledging of the last chicks in mid-April. We calculated the body condition of chicks before and after they had received a meal from the data for growth of the chicks at automated nests. Body condition was defined as the residual of the nonlinear regression of chick mass on time. Because chick mass growth in Procellariiformes is complex, characterized by a period of increase to peak mass followed by a period of mass decrease, it cannot be described entirely by classical growth curves (Warham, 1990). To calculate the age and mass for the asymptote, we modeled the chick growth using third-degree polynomial equations (SigmaPlot, SPSS Inc., Chicago). In addition to the five chicks at automated nests, samples of 74 and 71 chicks were weighed regularly throughout the chick-rearing period in 1996 and 1997, respectively, and the wing length measured at the same time. In addition, on 20

March 1993 and 1995, we recorded the body mass and wing length of a sample of chicks. We calculated the provisioning rate as the quantity of food delivered daily to the chick by the two parents (in grams per day), hence  $2 \times (1/\text{average duration of foraging trips}) \times \text{meal size}$ . To compare values of meal size or duration of foraging trips between years, we used for each year the period between mid-January and mid-February when information was available every season. Although the field methodology was not the same in 1991–1993 and in 1996–1997, the duration of foraging trips is directly comparable. For meal size, to allow comparisons between the two periods, we used the same calculation method as described in the previous paragraph.

In the provisioning colony, between 1991 and 1997 each year, we weighed samples of adults just after they had delivered a meal during the study period of provisioning. Each individual was only weighed once a year, allowing comparison between groups through ANOVA. Some individuals may have contributed to the data set over several years, but this probably is not a serious potential source of pseudoreplication because a relatively small number of birds was sampled randomly every year in a large colony.

During a particular year or fortnight, in some cases several values of meal size and duration of foraging trips were obtained from the same individual. To account for this, for overall comparisons between years we used nested ANOVA with year as the topmost fixed level and individual birds as the nested random levels. We performed post-hoc tests using Fisher's least-significant difference (LSD) test. For comparison within season and year, we used average values for each level to avoid duplicate data for the same individual for the same categorical variables in ANOVA and Student's *t* tests.

We estimated annual adult survival from a group of 202 adult breeding birds, individually marked with stainless-steel bands recaptured between 1990 and 1998 in the long-term colony (see Weimerskirch et al., 1987, for details of recapture procedures). The data set was first tested for heterogeneity with Release software (Burnham et al., 1987). The goodness-of-fit results (test 2 and test 3) were not significant ( $\chi^2_{20} = 29.5$ ,  $p = .0791$ ), indicating no heterogeneity in the data set. The effect of time (*t*) on survival (*S*) and capture rates (*P*), with average sea surface temperature anomalies as a covariant were modeled using Surge 4.0 (Lebreton et al., 1992). We selected the most parsimonious model using Akaike's Information Criterion and tested for significance using likelihood ratio tests (Lebreton et al., 1992).

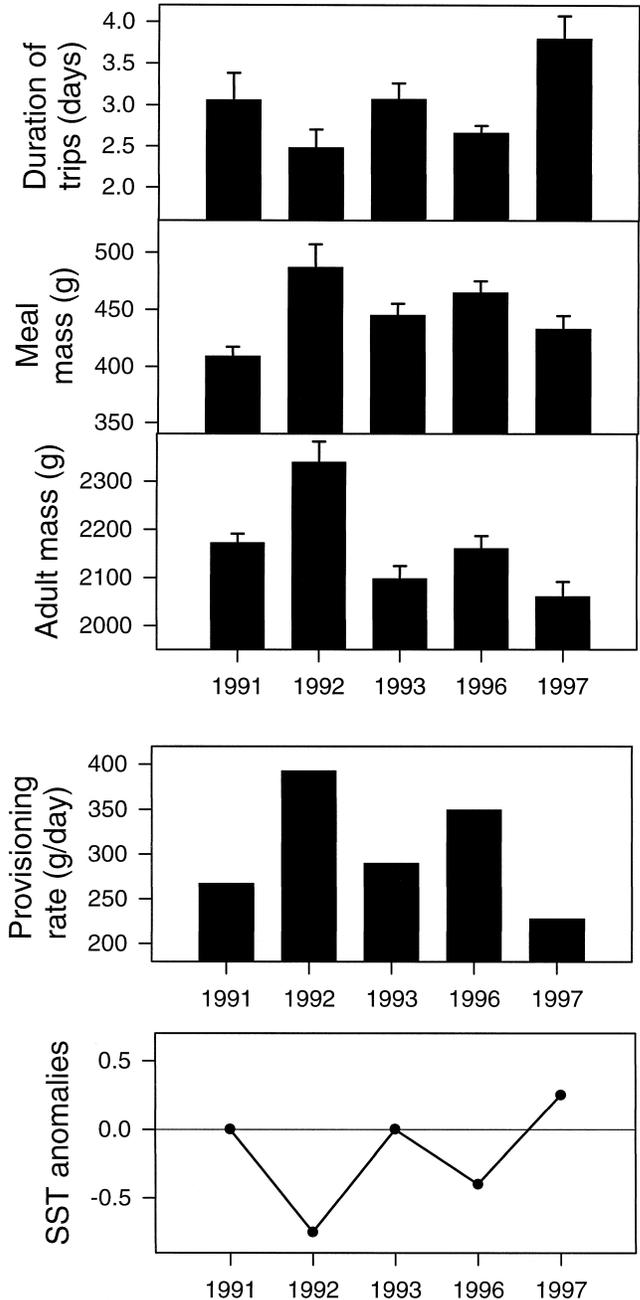
For analysis of reproductive costs, we compared the proportions of birds surviving to the next season for parents rearing a chick and for parents that stopped breeding just after hatching during two successive seasons. To do this, we searched for birds banded as breeders in the provisioning colony in 1996 and 1997 in the same colony and in the neighboring colonies (Jouventin et al. 1983) during the next two breeding seasons in October, just after egg laying.

The sea surface temperature (SST) anomalies were provided by IGOSS (International Global Ocean Service System). They are estimated using monthly SSTs blended from ship, buoy, and bias-corrected satellite data (Reynolds and Smith, 1994). We used average SST anomalies for January–March each season. Negative values of SST indicate that the waters were colder than the average value recorded since 1982. Statistical analyses were performed using SYSTAT 7.0 (Wilkinson, 1996).

## RESULTS

### Annual variation in provisioning parameters, adult mass, and mass of fledglings

The mass of meals delivered to chicks differed between years (nested ANOVA,  $F_{4,854} = 2.98$ ,  $p = .0182$ ). In 1992 it was sig-



**Figure 1**  
Average provisioning parameters and adult mass of yellow-nosed albatrosses and sea-surface temperature anomalies recorded around Amsterdam Island for 5 years.

nificantly higher than in 1991, 1993, and 1997, and in 1996 it was higher than in 1991 and 1992 (Fisher LSD post-hoc tests; Figure 1). There were significant differences between years in the duration of foraging trips (nested ANOVA,  $F_{4,1000} = 7.13$ ,  $p < .0001$ ), those in 1997 being significantly longer than in 1992, 1993, and 1996 (Figure 1). This difference was mainly the result of the occurrence of particularly long foraging trips in 1997 compared to the other years. The resulting provisioning rate varied from 227 g/day in 1997 to 392 g/day in 1992 (Figure 1).

The mass of adults after they had delivered a meal differed between years (ANOVA,  $F_{6,384} = 6.30$ ,  $p < .0001$ ). In 1992 adult mass after meal delivery was significantly higher than

**Table 1**

Sea surface temperature (SST) anomalies, annual adult survival and recapture rates, chick mass before fledging, and adult mass of yellow-nosed albatrosses measured during 7 successive years

Year	Mean SST anomalies	Adult survival	Recapture rate	Chick mass before fledging <sup>a</sup> (g)	Adult mass, Jan–Feb (g)
1991	0	0.870 ± 0.036			2174 ± 207 (122)
1992	-0.75	0.778 ± 0.043	0.958 ± 0.023		2340 ± 243 (32)
1993	0	0.862 ± 0.044	0.795 ± 0.046	2626 ± 493 (123)	2099 ± 220 (93)
1994	+0.25	0.824 ± 0.0429	0.761 ± 0.0474	2758 ± 568 (44)	2175 ± 232 (30)
1995	+0.38	0.905 ± 0.037	0.839 ± 0.041		2180 ± 198 (30)
1996	-0.4	0.875 ± 0.038	0.793 ± 0.437	2949 ± 445 (74)	2161 ± 211 (67)
1997	+0.25	0.920 ± 0.021	0.870 ± 0.362	2512 ± 436 (71)	2061 ± 179 (36)

Values in parentheses refer to sample sizes; survival, recapture rates, and adult mass are given with ± 1 SD.

<sup>a</sup> Measured on 18–20 March every year.

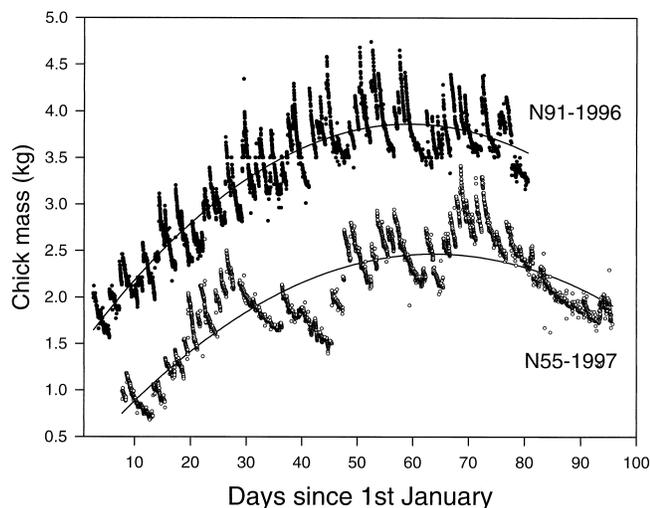
any other year, and in 1997 it was lower than in any other year except 1993 (Figure 1).

The 1992 season, and to a lesser extent 1996, were characterized by high average negative SST anomalies compared to other years; waters were colder in January–March 1992 than in any other year between 1991 and 1997 around Amsterdam Island (Figure 1, Table 1). The 1991 and 1993 seasons were standard years, whereas 1997 (and 1994 and 1995) showed positive anomalies (Figure 1, Table 1). When examining the relationships between SST anomalies and provisioning parameters or adult mass, we found a significant relationship only for the duration of foraging trips and for the provisioning rate (Spearman rank correlation,  $r_s = -.975$ ,  $p < .05$  and  $r_s = -.975$ ,  $p < .05$ , respectively; Figure 1, Table 1).

The mass of chicks before fledging differed between years (Table 1; ANOVA,  $F_{3,308} = 11.40$ ,  $p < .0001$ ). It was lower in 1997 and higher in 1996 than in 1993 and 1994.

#### Annual variation in adult survival

There was no significant time dependence in the survival rates (comparison of models  $St Pt$  and  $S Pt$ :  $\chi^2_5 = 6.2$ ,  $p > .1$ ),

**Figure 2**

Change in mass of two chicks recorded every 15 min throughout the fledging period during 1996 and 1997, with polynomial growth curve for each individual.

indicating that there was no significant variation in survival rates over time (Table 1). Because recapture rates were dependent on time ( $St Pt$  compared to  $St P$ :  $\chi^2_5 = 14.4$ ,  $p < .1$ ), the model with time-dependent recapture rates was preferred (AIC = 1038.8). The time dependence in recapture rate was not correlated with the SST anomalies used as covariate: Akaike's Information Criterion (1046.8) was higher when compared to the previous model, indicating that recapture rates were not related to SST anomalies.

#### Chick growth, fledging success, and return rates of adults in 1996 and 1997

The changes in mass recorded every 15 min at automated nests for one chick in 1996 and one chick in 1997 show the typical alternation of periods of fasting, characterized by slow mass loss, and sudden mass increases, corresponding to the feeds delivered by adults (Figure 2). There were significant differences between 1996 and 1997 in growth parameters of five chicks measured in this way each year (Table 2). In 1996 chicks attained a higher asymptotic mass at an earlier date, and fledged with a higher mass, slightly but not significantly earlier than in 1997 (Table 2).

Values for larger samples of chicks ( $n = 111$  chicks weighed in 1996 and 80 in 1997) measured at intervals of 10–15 days confirmed that in 1996 chicks grew more rapidly, attained higher peak mass, and fledged at higher mass than in 1997, even though they were of similar mass at the end of brooding in late December (Figure 3, upper panel). There was no significant difference between 1996 and 1997 in the wing length of the chick on 20 March (ANOVA,  $F_{1,143} = 0.34$ ,  $p = .5607$ ). Fledging success was similar between the two seasons (Table 2). The return rate of adults that fledged a chick was similar to that of adults that stopped breeding (after a breeding failure) after hatching in 1996 as well as in 1997 (Table 2).

#### Seasonal variation in provisioning parameters

In 1996 and 1997 there was an effect of fortnight but not of year on the size of the meal delivered (Figure 4; two-way ANOVA, effect of fortnight,  $F_{5,88} = 4.66$ ,  $p = .0008$ ; effect of year,  $F_{1,86} = 2.68$ ,  $p = .1051$ ; interaction,  $F_{5,86} = 1.13$ ,  $p = .3494$ ). During both years meal size increased during the chick-rearing period until the first fortnight of March, then declined (Figure 4). For the duration of foraging trips, there was an effect of fortnight and of year, with significant interaction effects (Figure 4; two-way ANOVA: effect of fortnight,  $F_{5,174} =$

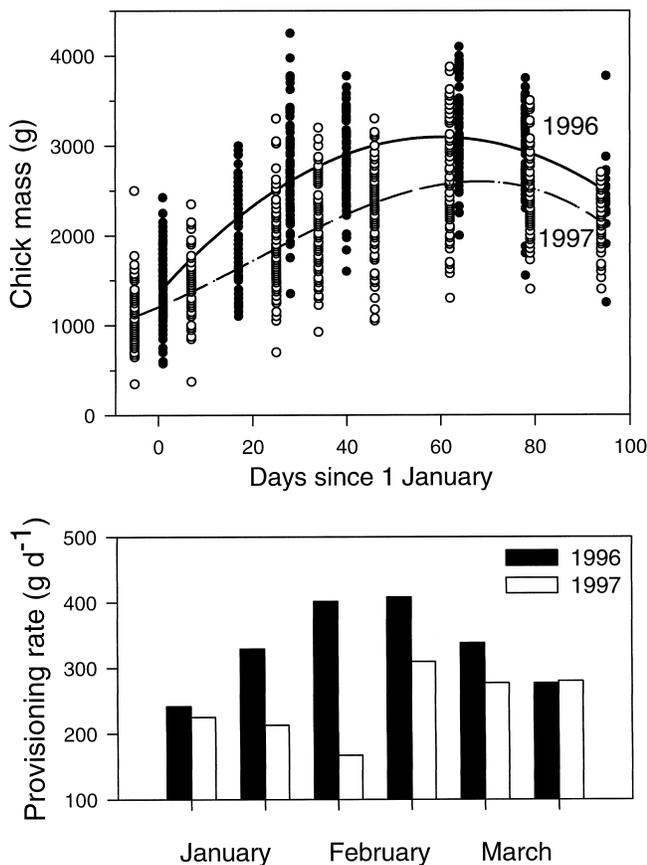
Table 2

Parameters for growth of chicks reared on automated nests, fledging success, and recapture rates for adults the next season

	1996	1997	Comparison between years	
			test	<i>p</i>
Growth parameters of chicks				
Asymptotic mass (g)	3373 ± 470 (2837–3856)	2591 ± 539 (1932–3245)	$t = 2.446$	.0401
Date at asymptotic mass	5 March ± 4.5 days (27 Feb–9 March)	18 March ± 8.8 days (7–28 March)	$t = 2.940$	.0260
Mass at fledging (g)	2694 ± 384 (2350–3240)	2058 ± 476 (1630–2650)	$t = 2.323$	.0487
Date of fledging	31 March ± 5.7 days (21 March–4 April)	5 April ± 2.9 days (2–10 April)	$t = 1.967$	.0846
% Fledging success (of chicks left unattended)	0.89 (82)	0.901 (81)	$\chi^2_1 = 0.05$	.826
Recapture rates				
% Adults rearing a chick	78.8	79.5	$\chi^2_1 = 0.014$	.924
% Adults failing during incubation/brooding <sup>a</sup>	76.1	79.0	$\chi^2_1 = 0.117$	.733
2 categories of adults compared	$\chi^2_1 = 0.179, p = .673$	$\chi^2_1 = 0.05, p = .846$		

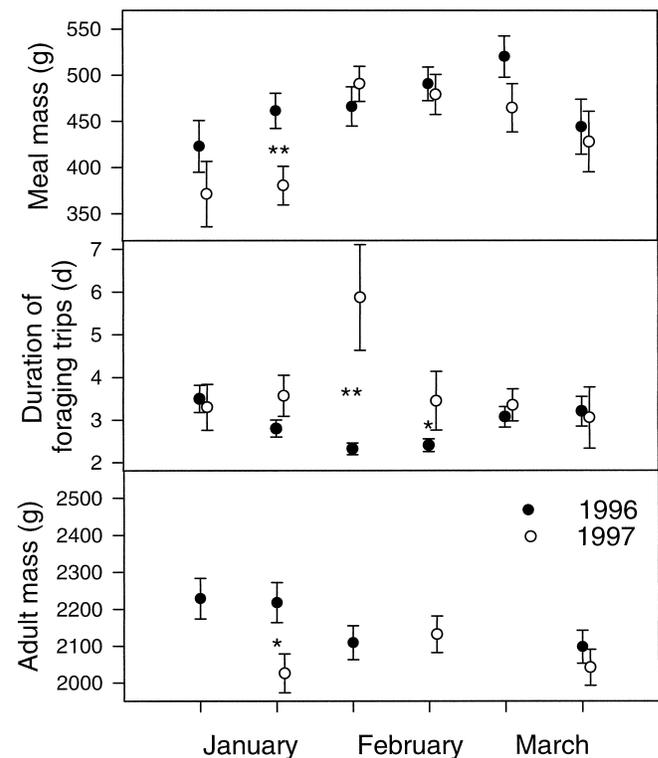
Growth parameters for 5 chicks reared on automatic nests, 1996 and 1997, mean ± 1 SD; range in parentheses.

<sup>a</sup> Failure through the first month after hatching.



**Figure 3** Upper panel, mass of chicks recorded throughout the chick rearing periods and modeled curve based on a third-degree polynomial equation in 1996 ( $y = 1390 + 50.5x + 0.25x^2 - 0.002x^3$ ) and in 1997 ( $y = 1240 + 22.4x + 0.25x^2 - 0.004x^3$ ); lower panel, change in provisioning rate throughout the chick rearing period in 1996 and 1997.

3.66,  $p = .0035$ ; effect of year,  $F_{1,174} = 12.51, p = .0005$ , interaction effect,  $F_{5,174} = 8.88, p < .0001$ ). In 1996 the duration of foraging trips was longer in January than in February (Figure 4) and in 1997 it was much longer during the first fortnight of February than in the rest of the season (Figure 4). Foraging trips were longer in February 1997 than in February 1996 (Figures 3 and 4). As a result, the provisioning rate in 1996 increased until the chick attained peak mass at the end of February, then declined during March, whereas in 1997



**Figure 4** Seasonal variation in meal mass, duration of foraging trips, and adult mass recorded in 1996 and 1997.

provisioning rate was lowest during the second fortnight of January and first of February, and returned to similar values to those of 1996 in March (Figure 3, lower panel).

In 1996 and 1997 the mass of adults birds did not change significantly with the period (Figure 4; 1996,  $F_{3,63} = 1.90$ ,  $p = .1383$ ; 1997,  $F_{2,33} = 1.09$ ,  $p = .3461$ ). In the second fortnight of January adults were heavier in 1996 than in 1997 ( $t = 2.49$ ,  $df = 27$ ,  $p = .0192$ ), whereas during the second fortnight of March there was no significant difference between the two years ( $t = 0.83$ ,  $df = 28$ ,  $p = .412$ ).

### Regulation of provisioning in 1996 and 1997

There was a tendency for meal sizes to increase with the duration of foraging trips in 1996 ( $r = .1234$ ,  $p = .0482$ ,  $n = 260$ ) but not in 1997 ( $r = .0398$ ,  $p = .705$ ,  $n = 93$ ). In 1996 the size of meal delivered was inversely related to the body condition of chicks before they received a meal ( $r = -.3146$ ,  $p < .0001$ ,  $n = 260$ ), whereas there was no such relationship in 1997 ( $r = -.0878$ ,  $p = .3007$ ,  $n = 141$ ). In 1996 the condition of the chick after it received a meal was not significantly related to the duration of the next foraging trip of the adult ( $r = .1166$ ,  $p = .6912$ ,  $n = 244$ ). Conversely, in 1997 adults leaving a chick in good condition tended to spend more time at sea ( $r = .3620$ ,  $p = .0045$ ,  $n = 90$ ).

## DISCUSSION

### Annual and seasonal variations

Interannual variability within ecosystems is a well-recognized phenomenon. It originates from cyclic or stochastic variations in oceanographic conditions due to environmental perturbations. SST anomalies have been used widely to describe oceanographic conditions. Although it is not well documented in subtropical waters such as around Amsterdam Island, variations in SST are known to directly affect the distribution and abundance of marine organisms such as krill, squid, or fish (e.g., Deacon, 1977) and therefore the distribution of top predators such as seabirds (e.g., Hunt, 1990) and their foraging performance. For example, negative correlations between SST and reproductive performance or body condition of seabirds have been found in other studies (e.g., Guinet et al., 1998; Springer, 1992). In this study the negative correlation between SST anomalies and foraging performance of yellow-nosed albatrosses suggests that SST anomalies are a good indicator of food availability for this subtropical predator.

Seabird parameters are thought to vary nonlinearly with food availability (i.e., to attain peak values at a certain level of food availability; Cairns, 1987). Parameters such as provisioning are believed to attain peaks under moderate conditions (Cairns, 1987). The results of our study show that foraging and provisioning parameters of yellow-nosed albatrosses varied extensively between years. The year 1992, and to a lesser extent 1996, appeared particularly favorable because parents were able to perform relatively short foraging trips and at the same time to provide large meals, and adults were much heavier than in other years. This situation occurred when subtropical waters were abnormally cold around Amsterdam Island. During the 1990–1993 period, the catch per unit effort of the tuna fishery operating in the Amsterdam Island area was very high in 1992 compared to the other years (Ardill, 1995), suggesting that SST anomalies might represent a reasonable index of resource availability. In contrast, the 1997 season appeared particularly unfavorable because provisioning rate was the lowest ever recorded, and adults as well as fledging chicks were significantly lighter than during the other seasons. The season 1997 was characterized by the occurrence of warmer

water around Amsterdam Island. During other years when provisioning parameters were recorded, there were no noticeable sea surface anomalies.

The environmental perturbation that occurred in 1997 was limited in duration, lasting during the second fortnight of January and the first fortnight of February only. This unfavorable episode resulted in low provisioning rates and consequently in a delay in the growth of chicks that parents were unable to compensate for when environmental conditions improved. As a result, chicks fledged with a lower mass in 1997, yet had similar wing length. This shows that low food availability can occur during only a fraction of the breeding season and can remain undetected if provisioning parameters are recorded only over a short period that does not encompass the perturbation.

These results indicate that environmental variability in subtropical waters has a profound effect on breeding effort of yellow-nosed albatrosses. Breeding effort appears particularly variable in this species in terms of provisioning parameters, but varies less in terms of adult condition, with no effect on survival.

### Regulation of provisioning abilities

Considering the two components of provisioning rate, the duration of foraging trips appears much more sensitive to change in environmental conditions, while meal mass differs less. Similar results have been obtained in yellow-nosed albatrosses when foraging costs are experimentally increased (Weimerskirch et al., 2000b). Yellow-nosed albatrosses have a specific foraging strategy in which they forage in oceanic waters at an average distance of 350 km and do not concentrate on a specific oceanographic sector and do not return to the same area from one trip to the next (Weimerskirch, unpublished satellite tracking data). They probably maximize to a great extent the mass of meals, as expected for central place foragers (Bryant and Turner, 1982; Cuthill and Kacelnik, 1990; Lessels and Stephens, 1983), and foraging success is best represented by the duration of foraging trips.

There has been much debate about whether Procellariiformes could modify their provisioning behavior according to the chick's needs; several studies suggest that they are unable to do so (Hamer and Hill, 1993; Ricklefs 1987, 1992) and that they provision at a fixed rate (Ricklefs and Schew, 1994). In these studies the individual behavior of adults was not recorded, which may not allow the problem of regulation of provisioning rates to be addressed adequately (see Granadeiro et al., 1999). In our study the differences observed in provisioning strategies between two contrasted seasons, 1996 and 1997, give an indication of the way yellow-nosed albatrosses are able to adjust their provisioning effort. When environmental conditions are favorable (1996), parents can deliver larger meals to chicks that are in poor condition, but this is not the case when food availability is low. This suggests an ability to regulate provisioning according to the chick's needs, but only when conditions are favorable. An alternative explanation is that when food availability is high, the chick could be restrained by its swallowing capacities, and that when it is in good condition it cannot swallow the entire meal mass (see Hamer and Hill, 1994; Weimerskirch et al., 1997). Conversely, during years of low food availability, chicks could be in a chronic state of underfeeding and able to swallow the adult's entire stomach content, which would moreover be smaller under these environmental conditions. When environmental conditions are poor, adults modify the duration of the foraging trips according to the condition of the chick after it has received a meal, whereas this is not the case when conditions are favorable. Thus, when conditions are poor at sea, adults

spend more time at sea, probably to recover some of their own body condition after having left a chick in good condition. Yellow-nosed albatrosses spend more time at sea when they leave the colony in poor condition (Weimerskirch et al., 2000b).

The results of this study indicate that, as in several other species of petrel and albatross (Bolton, 1995; Weimerskirch et al., 1995, 1997), the adult yellow-nosed albatross can regulate provisioning according to the nutritional status of the chick, but only when conditions are favorable. The contrasting results obtained with Procellariiformes suggest that different species may differ in their ability to regulate provisioning according to the needs of the chick, and it has been suggested that this may arise from differences in the foraging strategies of the species (Weimerskirch et al., 1997). Our study indicates that the situation is even more complex because regulatory ability not only varies between species, but that for the same species it varies according to the environmental conditions and the food availability encountered during the breeding season (see also Granadeiro et al., 1998; Weimerskirch et al., 1997, 1999). Studies investigating regulatory abilities should therefore work at the individual level, especially over contrasted periods of resource availability. Our study also confirms the general idea that trade-offs appear only when food is limited (Stearns, 1992). The variability of provisioning rates according to food availability results in variable chick growth and mass of chicks at fledging, whereas wing length or fledging success did not vary between contrasted seasons.

#### Role of adult mass in breeding effort

There is a good concordance between changes in the mass of adults and their rate of provisioning: adults are heavier when they provision their chick at a high rate and lighter when provisioning rates are low. This suggests that both the levels of self-feeding and of chick provisioning were affected by food availability. However, adult body mass was less variable than provisioning parameters when environmental conditions changed. During unfavorable years, adults were only slightly lighter (4%) than during standard years, whereas the provisioning rate was 23% lower. This reduction in body mass is likely the result of food stress (see review in Merkle and Barclay, 1996) due to the lower food availability, as suggested by the simultaneous lower provisioning rate. Birds are probably forced to tap into their reserves to provision their chick. It is not an adaptive response to either reduce metabolic expenditure of flight or to use the energy released by mass loss for the chick (Norberg, 1981) because it occurs only during the years or fortnights of low food availability, whereas a flight adaptation hypothesis for mass loss predicts that patterns should be same from one year to the next (Merkle and Barclay, 1996). The low mass reached during an unfavorable period still includes a large amount of body reserves. Indeed, the threshold mass of yellow-nosed albatrosses that induces the cessation of a breeding attempt (Chaurand and Weimerskirch, 1994) is on average 1750 g (Weimerskirch, 1999). Thus, even during the worst period of 1997, adults were still on average 300 g heavier than the lower threshold mass, having thus drawn only part of their body reserves. This amount of body reserves can be considered as a "safety margin" that is retained at the expense of provisioning rate and indicates that birds preferentially allocate resources to the maintenance of their own body condition at the expense of investment in the chick.

During standard years the safety margin represents an extensive amount of reserves—on average 23% of the threshold mass. This safety margin is probably used to meet temporary food shortage (Cairns, 1987), possibly to adjust their provi-

sioning rate (Weimerskirch, 1998, 1999), as suggested by the temporary decline in body mass during the perturbation in 1997. Moreover, the mass at a particular time influences the duration of the next foraging trip; birds in poor condition spend more time foraging than birds in good condition (Weimerskirch et al., 2000b). When foraging costs are experimentally increased, adults also reduce their body mass temporarily (Weimerskirch et al., 2000b). This is what might be expected from a long-lived species, seeking to reduce the risk incurred through increased breeding effort when food is scarce by keeping a significant amount of body reserves, even when conditions are unfavorable. Yellow-nosed albatrosses appear to work with a much wider safety margin than smaller seabirds, either because they are larger or because they are longer lived (Weimerskirch, 1999). Although we cannot easily separate the two effects, it is clear that it is only in extreme circumstances that adult seabirds die because of low food availability (Weimerskirch, 1999). Increased mortality is more likely to be observed in species that have a narrow safety margin (i.e., small species), and even in this case remains limited to catastrophic situations (Vader et al., 1990). Mortality due to low food availability is much less likely in a large species such as an albatross.

Conversely, during the exceptionally good season when they provisioned chicks at a very high rate, parents were 8% heavier compared to standard years, delivered heavier meals, and their provisioning rate increased by 22%. Specifically, adults were 31% heavier than the lower threshold mass. This represents an extensive extra load and indicates that birds are able to carry more mass, either as food in the stomach or as body stores, than during standard years. This is surprising because it is generally predicted that the amount of body reserves should be similar under conditions of medium and high food availability and possibly lower when feeding conditions are poor (Montevecchi, 1993). Indeed, it is expected that birds would not accumulate additional body reserves unless they have a functional role, mainly because the additional load could reduce flight efficiency (Lima, 1986; see also Cuthill and Kacelnik, 1990). In this species the benefits of carrying extra loads of body reserves probably outweigh the ecological costs of fat storage (Witter and Cuthill, 1993). Several factors may favor this, such as the lower cost of extra loads in species using dynamic soaring flight compared to a flapping flight (Pennycuik, 1989), as well as the absence of predation on these larger seabirds (Witter and Cuthill, 1993). The benefit of extra body reserves is probably to allow this albatross to cover foraging costs during unfavorable periods.

#### Fitness consequences of environmental variability

In Southern Hemisphere Procellariiformes fledging a single offspring, breeding success is most often reduced through loss of eggs or newly hatched chicks (Weimerskirch, unpublished data). Once chicks have been left unattended, fledging success is generally high. In our study fledging success was similar during the two contrasted seasons, 1996 and 1997. However, the quality of the chick produced varied greatly from one year to the next. During good seasons chicks are fledged with a high mass, confirming that reproduction during good years has a large value with respect to fitness compared to bad years (Erikstad et al., 1998). Conversely, Erikstad et al. (1998) predicted that during unfavorable years maximum fitness is achieved either by not breeding or by abandoning the brood. Yellow-nosed albatrosses still continue to invest in their chick despite unfavorable conditions (e.g., in 1997), but they produce a poor quality offspring at fledging. This probably has important consequences in terms of fitness. Lower mass at fledging means a low prospect of survival till breeding in seabirds (Magrath, 1991; Sagar and Horning, 1998; Weimerskirch

et al., 2000a). There is no evidence that changes in adult survival are related to environmental variability, and there is no indication of a survival cost of rearing a chick during good or poor years. This is in agreement with the prediction that survival should not be affected by reproductive costs in long-lived adult animals (Williams, 1966). The absence of reproductive costs due to the variable breeding effort of the species and its extensive safety margin probably explains why adults do not desert a chick with a low prospect of survival. Periods of low food availability may be short or at least not last the complete fledging period, as indicated by the 1997 season. Therefore, because food availability may improve at any time and because adults are not at risk themselves, they continue provisioning the chick even at low rates. However, this contrasts with the prediction of Erikstad et al. (1998) that birds should stop breeding when conditions are unfavorable. Their assumptions were based on empirical data from smaller, shorter lived seabirds such as puffins or kittiwakes (Erikstad et al., 1997; Jacobsen et al., 1995). Smaller size confers a smaller safety margin (Weimerskirch, 1999), and the shorter life span reduces the residual reproductive value of the individuals, making large Procellariiformes more “prudent” parents (sensu Drent and Daan, 1980). The available studies suggest that small species are prone to desert the chick when conditions become unfavorable (puffins: Johnsen et al., 1994; terns: Monaghan et al., 1992; small petrels: Weimerskirch et al., 1999).

In conclusion, the results of this study indicate that understanding how long-lived seabirds optimize their provisioning behavior and lifetime reproduction can only be achieved through studies encompassing several contrasted seasons. The results of previous studies investigating the problem of regulation of provisioning rates in Procellariiformes have probably been so varied and contradictory not only because they were carried out on different species of different size and different life-history traits, but also because almost all have been carried out during a single breeding season when it was not known whether individuals were under food stress or not. Understanding how seabirds optimize their breeding effort will also help predict how climatic changes will affect populations of predators in the marine environment.

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