POPULATION ECOLOGY - ORIGINAL PAPER

Long- and short-term influence of environment on recruitment in a species with highly delayed maturity

Marie Nevoux · Henri Weimerskirch · Christophe Barbraud

Abstract Short-term effects of environmental perturbations on various life history traits are reasonably well documented in birds and mammals. But, in the present context of global climate change, there is a need to consider potential long-term effects of natal conditions to better understand and predict the consequences of these changes on population dynamics. The environmental conditions affecting offspring during their early development may determine their lifetime reproductive performance, and therefore the number of recruits produced by a cohort. In this study, we attempted to link recruitment to natal and recent (previous year) conditions in the long-lived black-browed albatross (*Thalassarche melanophrys*) at Kerguelen Islands. The environmental variability was described using both climatic variables over breeding (sea surface temperature anomaly) and non-breeding grounds (Southern Oscillation index), and variables related to the colony (breeding success and colony size). Immature survival was linked to the breeding success of the colony in the year of birth, which was expected to reflect the average seasonal parental investment. At the cohort level, this initial mortality event may act as a selective filter shaping the number, and presumably the quality (breeding frequency, breeding success probability), of the individuals that recruit into the breeding population. The decision to start breeding was strongly structured by the age of the individuals and adjusted according to recent conditions. An effect of natal conditions was not detected on this parameter, supporting the selection hypothesis. Recruitment, as a whole, was thus influenced by a combination of long- and short-term environmental impacts. Our results highlight the complexity of the influence of environmental factors on such long-lived species, due to the time-lag (associated with a delayed maturity) between the impact of natal conditions on individuals and their repercussion on the breeding population.

Keywords Black-browed albatross · Breeding decision · Natal conditions · Environmental variability · Immature survival

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Introduction

Environmental variability, via the regulation of resources available for organisms, is considered as one of the main parameters involved in population regulation (Lack 1966; Sæther 1997). Numerous studies have recently highlighted a widespread influence of climate, in relation to recent global change, on the distribution, the phenology and the demography of populations (Walther et al. 2002). Although short-term effects (from one season to another) are generally well documented, long-term effects (e.g. from birth to an event occurring several years later) of environmental perturbations are often more complex and thus difficult to appreciate. Estimating the consequences of these long-term effects on population dynamics is essential to better understand and predict responses to ongoing changes. The environmental conditions affecting offspring during their

early development may fix some physiological or structural traits (Lindström 1999) affecting post-fledging survival and reproductive success (Olsson 1997; Sæther 1997; Lindström 1999; Thompson and Ollason 2001; Cam et al. 2003; Sedinger et al. 2004), and consequently the lifetime reproductive performance of a cohort as a whole (Lindström 1999; Gaillard et al. 2000). Inter-cohort differences in individuals' performances could also be levelled out during the first years of life by a variety of behavioural mechanisms such as learning, delayed breeding or selection (Greig et al. 1983; Weimerskirch 1992). It would be interesting to explore how long the influence of natal conditions could persist throughout individuals' lives, by studying long-term effects of environmental conditions in long-lived species. This question is often logistically difficult to investigate in such species due to a lengthy immature stage when individuals are generally not observable (Pradel et al. 1997; Gaillard et al. 1998; Oro and Pradel 2000; Reed et al. 2003; Cam et al. 2005; Crespin et al. 2006) and long-term field studies are required to link early environmental condition to future fitness components. Recent developments in capture-mark-recapture (CMR) analyses provide a relevant approach to estimate recruitment parameters in species where pre-breeders cannot be observed (Fujiwara and Caswell 2002; Lebreton et al. 2003). The effect of external covariates on demographic rates can be assessed with ultra-structured models.

A detailed 26-year individual-based study conducted at Kerguelen Islands (Southern Indian Ocean) on the black-browed albatross (*Thalassarche melanophrys*) offers the opportunity to track the influence of natal conditions throughout a cohort's life. Influences of climatic indices on some life history traits have been reported in this population (Pinaud and Weimerskirch 2002; Nevoux et al. 2007; Rolland et al. 2008), suggesting a certain sensitivity to environmental conditions. In this study, we investigated the potential persistence of effects associated with natal conditions until adulthood. We attempted to explain the inter-annual fluctuation in recruitment by natal and recent (previous year) conditions to test for long- and short-term effects, respectively. The environmental variability was described using both climatic variables related to breeding (sea surface temperature anomaly; SSTA) and non-breeding periods (Southern Oscillation index; SOI), and variables related to the colony (breeding success and colony size).

We predicted that conditions during growth and at fledging would affect immature survival as well as the probability of starting to breed. Good environmental conditions should allow breeders to produce high-quality fledglings which would have a high probability of surviving the winter period and then enter the breeding part of the population several years later. In addition, we suspect the recent environment to be a major element affecting the decision to start breeding by controlling the resources available for new recruits (food, nest site, mate,…).

Materials and methods

Study species, area and data

The black-browed albatross is a large Procellariiform inhabiting the Southern Ocean and breeding on Subantarctic islands during the austral summer (Marchant and Higgins 1990). In this long-lived seabird with an average age at first breeding of 8.9 years (Weimerskirch et al. 1997) the immature stage lasts several years before recruitment. Adults reproduce once a year, laying a single egg without replacement clutches (Marchant and Higgins 1990).

The study took place at Cañon des Sourcils Noirs (49°40′S–70°15′E), Kerguelen Islands, Southern Indian Ocean. In a large colony of about a 1,000 pairs, a fixed area of ∼200 (minimum 114, maximum 265) nests delimited by physical borders (cliff faces and streams) was monitored each year from the 1979–1980 season (hereafter "1980"). During the breeding season, each nest was checked 3 times: during early incubation in October, at hatching in late December and before fledging in late March, all pair members were identified by their metal ring and their breeding success (fledging an offspring or not) was determined. Each year, all unringed breeding individuals found in the study area and all chicks were ringed just before fledging with a stainless steel band. Regular observations outside the study colony suggested that very few individuals (less than ten) born in the study colony were breeding either in the main colony or in an adjacent colony (2 km distant). The sex of individuals was not known as the species is monomorphic. In summer, satellite tracking revealed that birds from this population foraged invariably in the north-eastern and south-eastern parts of the peri-insular Kerguelen shelf (Weimerskirch et al. 1997; Pinaud and Weimerskirch 2002), feeding on fish, squid (Cherel et al. 2000) and on offal from fisheries (Weimerskirch et al. 1988). In winter, birds migrate off southern Australia, as indicated by band recoveries (Weimerskirch et al. 1985), stable isotope analyses (Cherel et al. 2000), and geolocator studies (Weimerskirch et al., unpublished data).

The food available for organisms is a key resource regulating population dynamics, but this resource is generally very difficult to quantify in marine ecosystems. As a result, climatic indices are generally used as proxies of the environmental variability affecting these ecosystems because they affect primary production and then the whole trophic web (Stenseth et al. 2003). From the literature, we do not expect a significant impact of climate on seabirds other than through food resources (Stenseth et al. 2003).

However, we cannot rule out the possibility that climatic factors affect the target species via some other variables given the uncertainties between food resources and climatic/oceanographic factors. As our black-browed albatross population was distributed across two distinct oceanographic systems over the year, we selected environmental variables over two geographic areas according to this seasonal distribution. During summer, the foraging ground of our population is restricted to a small and precisely known area over the Kerguelen shelf, enabling us to use fine-scale SSTA [SSTA; data available from the Integrated Global Ocean Service System (Reynolds and Smith 1994, IGOSS—http://ingrid.ldeo.columbia.edu/(plotaxislength)540+def/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv1/.monthly/.ssta/)] over this particular area to describe fine-scale climatic conditions [see Pinaud and Weimerskirch (2002) and Rolland et al. (2008) for a description of the area focussed on]. Warm sea surface temperatures appeared to enhance food productivity in this particular oceanographic system (Blain et al. 2001), and have been correlated to good breeding success in the black-browed albatross colony (Pinaud and Weimerskirch 2002; Nevoux et al. 2007). SSTA was used to test for a short-term effect of environmental conditions on both immature survival and the decision to start breeding, and for a long-term effect on the decision to start breeding; it was not expected to affect birds during the non-breeding period. During winter, the distribution of black-browed albatrosses from Kerguelen off southern Australia covers a too large-scale area to allow a relevant use of local indices such as SSTA. We rather selected the global SOI [SOI; data available from the Australian Bureau of Meteorology (ABM—ftp://ftp.bom.gov.au/anon/home/ncc/www/sco/soi/soiplaintext.html] used to describe global environmental variability across the tropical Pacific Ocean in association with the El Niño/La Niña oscillation. A positive SOI, characteristic of La Niña events, is described by cold anomalies off Peru and is correlated with warm temperatures off southern Australia (Kwok and Comiso 2002); consequently, low marine productivity is expected in this oligotrophic area (Wilson and Adamec 2002). This index has been negatively related to the survival of young individuals breeding in this Kerguelen colony (Nevoux et al. 2007). It was used to test for an effect of winter conditions on immature survival probability and on the probability of starting to breed, taking into consideration both an effect of natal conditions (i.e. during the first winter; t_0) and an effect of the conditions during the winter preceding the first breeding event (t_{-1}). We considered a direct spatio-temporal effect of SOI on these traits (no lag), to coincide with the presence of birds during the non-breeding period off southern Australia; SOI is not expected to affect birds during the breeding period. Both SSTA and SOI were summarised over a 4-month period: January-April (rearing period) and June–September (wintering period); no significant linear trend was detected in these variables during the study [SSTA$_{(1982–2005)}$: $F_{22,1} = 1.17$, $P = 0.444$ and SOI$_{(1980–2005)}$: $F_{24,1} = 0.00$, $P = 0.985$].

We also considered some non-climatic variables related to the environment in the breeding colony, which may potentially influence the recruitment process. The number of breeding pairs may affect the accessibility to breeding sites for newcomers, i.e. the probability of starting to breed (Forchhammer et al. 2001; Crespin et al. 2006). Colony size was assessed (from 1987) using an annual census of the number of active breeding sites from a fixed vantage point in the colony. This ground count method provides accurate and precise estimates in low vegetation areas (Robertson et al. 2008) which was the case in this colony. Colony size might also affect immature survival, but we did not investigate this effect because it could only be tested in a very short time period ($n = 5$ years). The breeding success of the colony, defined as the number of young fledged per breeding pair, can be viewed as an index of the average seasonal parental investment, which may influence the quality of the fledglings produced and consequently immature survival. The breeding success of the colony was also considered as major information about the quality of the colony, as it is known to affect settlement and the decision to start breeding in some colonial seabirds (Danchin et al. 1998; Frederiksen and Bregnballe 2001). The breeding success is dependent on the environment and it is known to be correlated to SSTA in this population (Nevoux et al. 2007). So, if both SSTA and breeding success explained a significant part of the variability on vital rates in our models, this would indicate an effect of climatic condition, but it would not be possible to draw a conclusion about the potential effect of parental investment on the focal trait. If the breeding success was the only variable selected, we would expect parental investment to be the main effect driving the observed correlation or that another climatic variable not tested for affected breeding success.

Modelling the demographic parameters and effects of covariates

Recruitment was divided into juvenile survival probability and probability of breeding for the first time. These two parameters were estimated using two groups of individuals: known-age individuals (banded as chicks; g_1) used to estimate immature survival and recruitment; unknown-age individuals (banded as adults; g_2) used to help stabilize estimates of adult survival and recapture probabilities, which in turn would help estimate the pre-breeding parameters. Analyses were conducted using a CMR model

with two states (Lebreton and Pradel 2002): one immature state (imm), and one adult state starting at first reproduction (ad). This leads to the general time-dependent model:

$$p((\text{imm, ad}) \times g \times t) \quad S((\text{imm, ad}) \times g \times t) \quad \Psi((\text{imm, ad}) \times g \times t) \quad (1)$$

where the capture probability (p), the survival probability (S) and the probability of transition from one state to the other (Ψ) varied with the state (imm and ad), the group (g) and time (t).

As is generally the case for models with unobservable states, constraints on the general model are needed to make the parameters identifiable (Kendall and Nichols 2002; Lebreton et al. 2003). These constraints correspond to biologically reasonable assumptions. Among g_1, less than 5% of the birds banded as fledglings were recaptured in the colony before their first breeding attempt. Consequently, these few observations of pre-breeders were deleted ($n = 162$ events). The immature state is assumed to be unobservable, birds are banded as fledglings but they are never seen again as immature [$p(\text{imm}) = 0$]. In addition, we know that recruitment never occurred before 5 years of age (Fig. 1): no adult could be observed in the colony before 5 years of age in g_1 [$p(\text{ad} \times g_1 \times a_{1-4}) = 0$, where a denotes age]. By definition, the local apparent immature survival was estimated over the 5 years of the immature period [$S(\text{imm} \times a_{0-4})$]. Mature pre-breeders (older than 4 years) and adults had the same survival probabilities [$S(\text{imm} \times a_{5+}) = S(\text{ad})$]. We assumed that there was no temporary emigration in adults and the transition from adult to immature (or to a non-observable non-breeder state) was fixed at zero ($\Psi_{\text{ad}\rightarrow\text{min}} = 0$). The probability of starting to breed in g_1 was described by the transition from immature to adult state ($\Psi_{(\text{imm}\rightarrow)}(g_1)$). This transition was

then structured by age and was allowed to vary across time and cohorts. Transition to the adult state did not occur before the age of 5 years ($\Psi_{(\text{imm}\rightarrow\text{ad})}(g_1 \times a_{1-4}) = 0$) and we searched for the maximum age at first breeding (a_{max}) where all recruitment had occurred ($\Psi_{(\text{imm}\rightarrow\text{ad})}(g_1 \times a_{\text{max}}) = 1$). This transition did not exist in g_2 because only adult individuals were considered ($\Psi_{(\text{imm}\rightarrow\text{ad})}(g_2) = 0$). In the black-browed albatross the average age at first breeding was 8.9 years (Weimerskirch et al. 1987) and the observed distribution of the age at first breeding (Fig. 1) revealed that 99% of the recruitment occurred between 5 and 15 years of age in this population. In long-lived species, the difficulty in obtaining data over sufficiently long periods restricts the use of this CMR approach. At the end of the time interval, individuals from the last cohorts were too young to start breeding, i.e. a proportion of the immature individuals remained unobservable and may be artificially considered dead in models, thereby underestimating immature survival. To avoid this bias, we restrained the dataset to the only cohorts that had entirely recruited at the end of the study period. We assumed that all individuals born at least 15 years before 2005 (last year of the study period) had started to breed if alive, corresponding to the first 11 cohorts (coh_{1-11}) of the study born between 1980 and 1990 ($n = 1{,}003$ and $n = 799$ individuals for g_1 and g_2, respectively). Analyses were performed with the M-Surge software (Choquet et al. 2004). There are no formal goodness-of-fit (GOF) tests available for multi-state models with an unobservable state. Following Lebreton et al. (2003), we suppressed the first capture event to focus on adults, leading to a standard single-state model:

$$p(g \times t) \, S(g \times t) \quad (2)$$

for which the fit was assessed using GOF tests for the Cormack-Jolly-Seber model with the U-Care software (Choquet et al. 2005).

Model selection among time-dependent models was performed using a quasi-likelihood Akaïke's information criterion (QAIC; Burnham and Anderson 1998) that integrates the correction from the over-dispersion coefficient (see Results). The smaller the QAIC, the better the model, with two models considered to be different when the difference in their QAIC values (ΔQAIC) is >2 (Lebreton et al. 1992).

External covariates allowed us to test whether oceanographic or colony-related conditions might explain some of the variability in the demographic parameters. To assess the significance of the contribution of a given covariate to the model, we performed analysis of deviance tests (Anodev) between the model with the covariate, the relative time-dependent and constant models (Skalski et al. 1993; Grosbois et al. 2008). As SSTA and census datasets started 2 and 7 years later than the period during which juvenile

Fig. 1 Observed age at first breeding of black-browed albatrosses at Kerguelen Islands: frequency (*bars*) and cumulative frequency (*solid line*) of age at first breeding

survival was estimated (from 1980), we performed Anodev tests using, as reference models, a global time dependent model and a constant model for the occasions where covariates were tested. All covariates were standardized over the study period.

Results

Goodness of fit

The GOF test, applied to the single-state model (model 2), provided evidence of a global lack of fit of the model to the data ($\chi^2 = 411.01$, $df = 159$, $P = 0.006$; Table 1), due to a strong transient effect (test 3.SR) on g_1 and a trap-happiness effect (test 2.CT) on g_2 and to a lesser extent on g_1. Use of an artificial age-class for capture and survival is recommended to account for trap-dependence and transience in adults and to disentangle the first occasion where individuals were recorded as adults from the following ones (Pradel 1993). In g_2, with a typical capture history 2202002, we used this approach to correct for trap-dependence [$p(\text{ad} \times g_2 \times m \times t)$, where m denotes trap-dependence]. In g_1, the addition of the pre-breeding state (unobservable, except at birth) leads to a capture history such as 1000002202002. Because the age at first breeding was highly variable, the first adult event could not be modelled with an age-dependent effect in this group. The final GOF with trap-dependence on g_2 ($\chi^2 = 200.42$, $df = 137$, $P = 0.008$) returned a relatively small variance-inflation factor ($\hat{c} = 1.463$), compatible with overdispersed data (Lebreton et al. 1992). Our initial constrained model was:

$$p(\text{ad} \times g_1 \times t, \text{ad} \times g_2 \times m \times t)\, S(\text{imm} \times g_1 \times a_0,\ \text{ad} \times t)$$
$$\Psi_{(\text{imm} \to \text{ad})}(g_1 \times a_{5-a\,\text{max}} \times t).$$

$$(3)$$

Model selection

Pooling the probability of recapturing adult birds from g_1 with those of the second age-class from g_2 (Table 2, model 4) was better supported by the data than a time-dependent model (model 3). Capture probability increased during the first part of the study, and was on average 0.695, SE = 0.012 over the whole period. The apparent survival probability over the first 5 years of life seemed to vary over time (model 4 vs. 5; Fig. 2a). By contrast, a constant model was preferred to a time-dependent model to describe adult survival (model 6 vs. 4; Fig. 2a). On average, the immature survival probability was 0.281, SE = 0.021 over the first 5 years of life and the annual adult survival probability was 0.910, SE = 0.004. The local probability of starting to breed did not seem to differ between cohorts (model 7) but was highly structured by age (model 8). The maximum age at first breeding a_{max} was 14 years old, so the transition $\Psi_{(\text{imm} \to \text{ad})}$ was fixed at 1 from that age (model 9; Fig. 2b). The age-dependent probability of starting to breed was not described by a linear (model 10) but by a quadratic model (model 11; Fig. 2b), increasing from 5 to 11 years and decreasing in older individuals. Adding an additive effect of time on this last model (model 11) did not enable the detection of any inter-annual variability in this parameter, potentially due to large SEs (Fig. 3b).

Models with covariates

We did not find any evidence for an impact of climatic conditions on immature survival (Table 2, models 13 and 14). The average breeding success of the study colony the year of birth was positively correlated to the immature survival (model 15, slope = 0.502, SE = 0.091, $R^2 = 0.52$, and Fig. 3a). We did not detect an effect of natal conditions on the probability of starting to breed (models 16–18). By contrast, SOI during the winter preceding the return of immatures to the colony (model 18) was positively correlated to the probability of starting to breed (model 19, slope = 0.505, SE = 0.131, $R^2 = 0.52$, and Fig. 3b). Oceanographic conditions off Kerguelen Islands at the beginning of the breeding season did not appear to explain a significant part of the variance in the decision to start breeding (model 20). Similarly, neither the breeding success of the colony the previous year (model 21) nor the size of the breeding population the

Table 1 Decomposition of the goodness of fit test on the single-state Cormack–Jolly–Seber model for known and unknown-age individuals (group 1 and group 2, respectively)

	3.SR	3.SM	2.CT	2.CL	Sum of tests
Group 1					
χ^2	44.75	9.04	23.9	8.25	85.94
df	16	15	14	11	56
P	<0.001	0.875	0.047	0.691	0.006
Group 2					
χ^2	17.33	29.91	210.59	67.24	325.07
df	22	28	22	31	103
P	0.745	0.368	<0.001	<0.001	<0.001

Only components 3.SR and 2.CT have a simple interpretation, with component 3.SR testing the null hypothesis of no difference in the probability of being later re-encountered between the "new" and "old" individuals, and component 2.CT testing the null hypothesis of no difference in the probability of being re-encountered at $t + 1$ between those encountered and not encountered on occasion t conditional on presence on both occasions

Table 2 Modelling capture probability (p), survival probability (S) and probability of starting to breed [transition from immature (*imm*) to adult (*ad*)] and the effects of covariates on these parameters ($\hat{c} = 1.463$)

ID	Capture	Immature survival	Adult survival	Transition (imm to ad)	np	Dev	ΔQAIC	P_{Anodev}
Time-dependent models initial model								
Eq. 3	$g_1 \times a_{5+} \times t, g_2 \times m \times t$	t	t	$a_{5+} \times t$	120	10,956.9	55.4	
Modelling capture probability								
1	$g_1 \times a_{5+} \times t, g_2 \times m + t$	t	t	$a_{5+} \times t$	100	11,017.0	56.5	
2	$g_1 \times a_{5+}, g_2 \times m \times t$	t	t	$a_{5+} \times t$	80	11,071.6	52.7	
4	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	t	$a_{5+} \times t$	99	11,000.5	43.2	
Modelling survival probability								
5	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	c	t	$a_{5+} \times t$	92	11,046.6	62.7	
6	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	$a_{5+} \times t$	78	11,047.6	33.4	
Modelling recruitment probability								
7	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	$a_{5+} \times coh$	69	11,158.6	91.2	
8	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	a_{5-25}	78	11,021.3	15.4	
9	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	$a_{5-13}, a_{14} = 1$	67	11,044.6	9.3	
10	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	$a_{5-13} \times T, a_{14} = 1$	60	11,081.8	20.7	
11	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	$a_{5-13} \times T^2, a_{14} = 1$	61	11,081.8	9.3	
12	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	$(a_{5-13} \times T^2) + t, a_{14} = 1$	78	11,030.5	21.7	
Models with covariates modelling immature survival								
13	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	SOI	c	$(a_{5-13} \times T^2), a_{14} = 1$	53	11,111.6	27.1	0.119
14	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	SSTA	c	$(a_{5-13} \times T^2), a_{14} = 1$	54	11,099.8	15.1	0.118
15	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	BS	c	$(a_{5-13} \times T^2), a_{14} = 1$	53	11,094.0	21.0	0.013
Modelling recruitment (initial conditions)								
16	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	$a_{5+} \times coh \times SOI, a_{14} = 1$	60	11,163.6	76.7	1.000
17	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	$a_{5+} \times coh \times SSTA, a_{14} = 1$	60	11,163.4	76.5	0.555
18	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	$a_{5+} \times coh \times BS, a_{14} = 1$	62	11,162.8	80.1	0.286
Modelling recruitment (present conditions)								
19	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	$(a_{5-13} \times T^2) + SOI, a_{14} = 1$	62	11,045.6	0.0	<0.001
20	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	$(a_{5-13} \times T^2) + SSTA, a_{14} = 1$	62	11,061.2	10.7	0.461
21	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	$(a_{5-13} \times T^2) + BS, a_{14} = 1$	62	11,061.1	10.6	0.437
22	$(g_1 \times a_{5+} = g_2 \times m_2) \times t, g_2 \times m_1 \times t$	t	c	$(a_{5-13} \times T^2) + n, a_{14} = 1$	64	11,060.2	14.0	0.564

np Number of parameters estimated, *Dev* deviance, *ΔQAIC* difference in the quasi-likelihood Akaike's information criterion values, *Anodev* test on covariates, g_1 known-age individuals, g_2 unknown-age individuals, a_{5+} individuals older than 5 years pooled together (one age class), a_{5-13} age effect between 5 and 13 years (nine age classes), *t* time, *c* constant, *coh* cohort, *T* linear trend, T^2 quadratic trend, *SOI* winter Southern Oscillation index, *SSTA* summer sea surface temperature anomaly, *BS* breeding success of the colony, *n* number of breeding pairs on the colony, × interaction, + additive effect

current year seemed to affect the decision to start breeding (model 22).

Discussion

In this study, the inter-cohort variability in immature survival probability could be linked to natal conditions. We did not detect any long-term consequence of natal conditions on the age-specific probability of starting to breed for the first time. Although the influence of the natal environment did not persist throughout the immature stage,

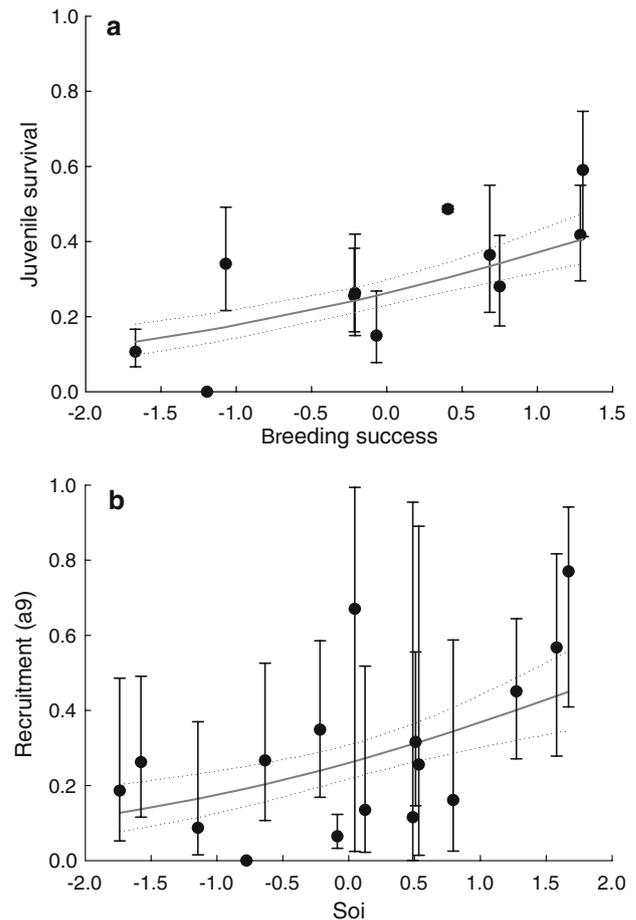recent conditions may be one of the main parameters driving the decision to start breeding.

Parameter estimates

Few estimates of immature survival are available in the literature for species with similar life histories. Similar multi-state CMR approaches gave a juvenile survival of 0.77 in the tropicbird (*Phaethon rubricauda*; Schreiber et al. 2004), whereas the survival over the first 2 years of life was estimated to be 0.376 in the roseate tern (*Sterna dougalli*; Lebreton et al. 2003), 0.576 in the common
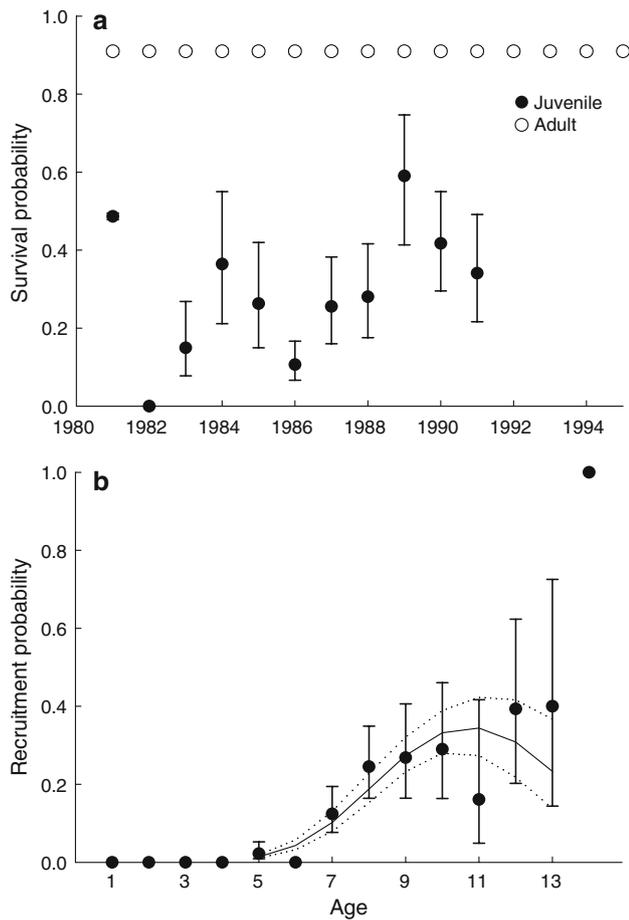
Fig. 2 Estimates of survival probability and probability of starting to breed in the black-browed albatross at Kerguelen Islands from the selected time-dependent model. **a** Adult survival probability [±95% confidence interval (CI); Table 2, model 10], and immature survival probability for cohorts 1–11 (±95% CI; model 10). **b** Age-dependent probability of starting to breed. Estimates for the age-dependent model (*filled circles* ±95% CI; model 7) and the selected model with a quadratic effect on age (*solid line* ±95% CI: *dotted lines*; model 10)

Fig. 3 Relationships between immature survival probability and the probability of starting to breed in the black-browed albatross at Kerguelen Islands and external covariates. **a** Immature survival from the time-dependent model (*filled circles* ±95% CI; Table 2, model 10) and immature survival modelled as a function of the breeding success in the year of birth (*solid line* ±95% CI: *dotted lines*; model 14, $P_{Anodev} = 0.013$, $R^2 = 0.52$). **b** Probability of starting to breed from the time-dependent model (*filled circles* ±95% CI; model 11) and probability of starting to breed modelled as a function of the Southern Oscillation index (*solid line* ±95% CI: *dotted lines*; model 18, $P_{Anodev} < 0.001$, $R^2 = 0.56$). The relationship is shown for birds aged 9 years for illustration

guillemot (*Uria aalge;* Crespin et al. 2006) and variable from 0.09 to 0.76 in the greater snow goose (*Chen caerulescens atlanticus;* Reed et al. 2003). By comparison, in our albatross population, the apparent annual survival probability and the apparent survival over the first 2 years of life would be respectively 0.776 ($\sqrt[5]{immature survival}$) and 0.602 ($\sqrt[5]{immature survival}^2$), in accordance with previous findings for delayed-maturity species. In the black-browed albatross population from Kerguelen, Weimerskirch and Jouventin (1997) observed that 13.7% of the chicks banded between 1980 and 1990 returned to breed in the colony. With 10 additional years of data, we observed a return rate equal to 17.4% for the same cohorts. This difference came from the highly delayed age at first breeding, with some birds born in the late 1980s that only recruited in recent years. Using models assuming a

probability of recapturing individuals lower than 1 to estimate immature survival probability and the age-specific probability of starting to breed, we estimated that 0.183 of the chicks recruited to the colony (i.e. this is the probability of surviving up to age 5 years and to start breeding at age 5 years or not to breed at age 5 years and to survive to age 6 years and to start breeding at age 6 years…). The small difference observed between the two approaches, related to the high recapture rate obtained in this population, suggests that our CMR models produced reasonable estimates of the immature survival probability and the probability of starting to breed.

Immature survival

The annual breeding success of the colony, used as a proxy of the average parental investment, was positively correlated to the local immature survival probability, explaining 52% of the inter-cohort variability in this parameter. Parental investment is partly related to the environmental conditions and the food resources. For example in years with suitable conditions parents may invest more in rearing their offspring (McGinley et al. 1987). Not being able to detect a significant contribution of SSTA to this trait suggests that it may be the ability of parents to convert the resource available into "offspring product" that matters to produce high-quality fledglings able to survive the immature period, or that another climatic variable not tested for affected breeding success. In a recent study, we tested the impact of fisheries on immature survival and probability of starting to breed, but no significant impact was detected on these two traits (Rolland et al. 2009). We did not detect an influence of the climatic conditions encountered during the first winter on immature survival although the majority of the mortality is expected to occur during the first winter in birds (Newton 1998). Winter survival might be more strongly related to the initial condition of a fledgling rather than to the severity of environmental conditions (Naef-Daenzer et al. 2001), supporting the role of parental investment described above. As a consequence, natal conditions faced by chicks during their early development would have considerable repercussions for future fitness and parental investment may be viewed as a source of inter-cohort heterogeneity in immature survival. Nevertheless, our approach only gives information on annual trends and it would be interesting to investigate how the expected differences in parental quality may affect intra-cohort heterogeneity in immature survival.

Decision to start breeding

In this study, we were not able to detect a delayed effect of natal conditions on the age-specific probability of starting to breed, as also reported by Reed et al. (2003) in the greater snow goose. Because of the very long period of immaturity, the importance of initial conditions may be gradually weakened during the immature stage, leading to undetectable inter-cohort differences in the timing of the recruitment of individuals in the colony. This result may also indicate that initial inter-cohort differences could be masked by the increasing importance of key factors controlling the decision to start breeding such as age, body mass or mate availability. In the meantime, the recent climatic conditions seemed to play a major role in the decision to start breeding. The inter-annual variability in the probability of starting to breed was positively related to the recent winter conditions. A similar result has only been

demonstrated recently in the common guillemot (Crespin et al. 2006). Long-lived species may only start to reproduce once they have reached a sufficient body condition to face the increased costs of reproduction without decreasing their own chance of survival (Weimerskirch 1992). In this study, we found a direct relationship between climatic conditions during the last winter and the probability of starting to breed, which seems to support this hypothesis. The underlying mechanisms remain unclear as previous findings on this black-browed albatross population highlighted a negative impact of the winter SOI on the survival of first-time breeders (Nevoux et al. 2007). This opposite response to winter SOI might suggest that immature and adult birds do not winter in the same region or do not rely on the same resources. To our knowledge, there are no data available to test this hypothesis. Alternatively, this difference might be explained by the hypothesis of compensatory recruitment, where a reservoir of non-breeders would act as a buffer against environmental stress (Porter and Coulson 1987; Klomp and Furness 1992; Votier et al. 2008). Younger breeders weakened by a first breeding investment may suffer from high mortality rates during positive SOI phases, whereas immature individuals, experiencing no cost of reproduction could be more capable of dealing with taxing environmental conditions and better able to recruit in newly vacated sites. In this colony the number of free nests did not appear to limit recruitment, but the low quality and/or attractiveness of these vacant nests may prevent first-time breeder occupation. Where compensatory recruitment occurs, density dependence may be difficult to detect as the observed number of breeders does not decrease (Votier et al. 2008). In that case, our measure of colony size may not be appropriate to detect density dependence as it included new recruits in the current number of breeders.

Several studies have reported a long-term influence of natal conditions on the recruitment of immature individuals (Forchhammer et al. 2001; Thompson and Ollason 2001; Cam et al. 2003; Sedinger et al. 2004; Van De Pol et al. 2006), and our results support the same conclusion. The analysis of the recruitment as a two-step process permitted us to highlight that the natal conditions experienced by a given cohort primarily affected the immature survival, that is to say the number of individuals that would recruit. The decision to start breeding refers to the timing when these individuals would effectively recruit. It was strongly structured by the age of individuals and adjusted according to recent conditions. A long-term effect of natal conditions has not been detected on this parameter, nor on adult survival and breeding success in this population (cohort effects; Nevoux et al. 2007), suggesting that the influence of natal conditions did not persist throughout the long-lasting immature stage in surviving individuals. Immature mortality, directed by this initial background, may act as a

strong selective filter by retaining the best performers among cohorts (Cam and Monnat 2000; Daunt et al. 2007), which could be coupled to the progressive homogenisation of an individual's skills through learning (Greig et al. 1983; Weimerskirch 1992) at the cohort level. Recruitment, as a whole process, was thus influenced by a combination of long- and short-term environmental impacts. In the present context of a changing environment, our results highlight the complex combination of natal and recent environmental impacts in this albatross population. They also indicate the difficulty in taking into account and modelling the influence of environmental variability on population dynamics in such long-lived species due to the time-lag associated with a delayed maturity between the impact of natal conditions on individuals and their repercussion, 5 to 15 years later, in the breeding population.

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