

Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird

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Summary

1. Our understanding of demographic processes is mainly based on analyses of traits from the adult component of populations. Early-life demographic traits are poorly known mainly for methodological reasons. Yet, survival of juvenile and immature individuals is critical for the recruitment into the population and thus for the whole population dynamic, especially for long-lived species. This bias currently restrains our ability to fully understand population dynamics of long-lived species and life-history theory.
2. The goal of this study was to estimate the early-life demographic parameters of a long-lived species with a long immature period (9–10 years), to test for sex and age effects on these parameters and to identify the environmental factors encountered during the period of immaturity that may influence survival and recruitment.
3. Using capture–mark–recapture multievent models allowing us to deal with uncertain and unobservable individual states, we analysed a long-term data set of wandering albatrosses to estimate both age- and sex-specific early-life survival and recruitment. We investigated environmental factors potentially driving these demographic traits using climatic and fisheries covariates and tested for density dependence.
4. Our study provides for the first time an estimate of annual survival during the first 2 years at sea for an albatross species (0.801 ± 0.014). Both age and sex affected early-life survival and recruitment processes of this long-lived seabird species. Early-life survival and recruitment were highly variable across years although the sensitivity of young birds to environmental variability decreased with age. Early-life survival was negatively associated with sea surface temperature, and recruitment rate was positively related to both Southern Annular Mode and sea surface temperature. We found strong evidence for density-dependent mortality of juveniles. Population size explained 41% of the variation of this parameter over the study period.
5. These results indicate that early-life survival and recruitment were strongly age and sex dependent in a dimorphic long-lived species. In addition, early-life demographic parameters were affected by natal environmental conditions and by environmental conditions faced during the period of immaturity. Finally, our results constitute one of the first demonstrations of density dependence on juvenile survival in seabirds, with major consequences for our understanding of population dynamics in seabirds.

Key-words: capture–mark–recapture, *Diomedea exulans*, juvenile vital rates, population dynamics, wandering albatross

Introduction

Demographic processes have strong implications for both theoretical and applied research through life-history theory on one hand and conservation biology and ecosystem

management on the other hand. So far, most demographic studies focused on the vital rates of the adult component of populations (e.g. adult survival, fertility), whereas the vital rates of the immature component (e.g. juvenile survival, recruitment) have been manifestly less studied (Clutton-Brock, Albon & Guinness 1985; Quinn & Peterson 1996; Gaillard *et al.* 2000; Coulson *et al.*

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2001), particularly in seabirds (Nevoux, Weimerskirch & Barbraud 2010). Yet, in long-lived species, younger age classes represent up to half of the total population and account for a large contribution to the total reproductive value and demographic stochasticity (Sæther *et al.* 2013). Thus, variations in vital rates of younger age classes are likely to have a high influence on the whole population dynamics and the rate of evolutionary change in long-lived species (Sæther *et al.* 2013). In addition, there is increasing evidence that conditions experienced in early life may have long-term individual fitness consequences with important demographic and evolutionary effects (Lindström 1999; Gaillard *et al.* 2000; Metcalfe & Monaghan 2001; Monaghan 2008; Cam & Aubry 2011). Hence, our knowledge bias towards the adult compartment of populations currently restrains our ability to fully understand population dynamics of long-lived species and life-history theory.

The lack of quantitative knowledge on demographic traits in the early life of long-lived species is mainly due to methodological limitations. First, in most taxa such as insects, fishes or amphibians, juveniles are so small that they cannot easily be individually monitored. Only large vertebrates such as birds or mammals have sufficient size at independence to be tracked individually allowing estimation of juvenile survival. But even in this case, studying survival after young become independent from their parents is challenging since immature survival is typically low (Newton 1989) and highly sensitive to environmental variability (Gaillard & Yoccoz 2003) so that large sample sizes need to be monitored. Furthermore, juvenile mortality is commonly confounded with permanent dispersal unless considerable large-scale monitoring effort is undertaken, which is often not the case due to logistical constraints. Finally, although sex could affect both dispersal behaviour (Clobert *et al.* 2001) and survival probability (Clutton-Brock, Albon & Guinness 1985), few studies controlled for offspring sex when estimating vital rates of younger age classes because of difficulties in determining offspring sex at independence before convenient molecular methods became available (Maness & Anderson 2013).

At the interface between evolutionary and ecological processes, demographic traits in early life may be affected both by natal conditions though parental care (Clutton-Brock 1991; Cam, Monnat & Hines 2003) and environmental variability encountered after independence (Sedinger, Flint & Lindberg 1995; Gaillard, Festa-Bianchet & Yoccoz 1998; Votier *et al.* 2008). Today, it is not clear whether environmental conditions between fledging and recruitment override the influence of conditions experienced during development. It is difficult to disentangle these two processes which probably interact with age (Cam & Aubry 2011). Identifying factors driving demographic traits in wild populations is especially challenging since it requires long-term data series without the possibility to control environmental parameters as for experimental studies. Furthermore, extrinsic factors such as climatic

or anthropogenic variables may interact with intrinsic population processes, for example density-dependent effects (e.g. Martínez-Padilla *et al.* 2014). Although intrinsic mechanisms may have a central role for the population dynamic of birds, affecting vital rates of the adult component (Barbraud & Weimerskirch 2003), density-dependent effects on early-life demographic traits have been little studied, especially for seabirds.

Although marine top predators such as seabirds and pinnipeds are convenient species for population demographic studies because they breed on discrete units, colonies, where large numbers of individuals can be tracked year after year given their high site fidelity, the study of their early-life demographic parameters implies coping with additional difficulties. Most seabirds do not breed until at least 3 years (Furness & Monaghan 1987; Gaston 2004), and for most species, juveniles are unavailable for detection remaining permanently at sea for several years before returning to breeding colonies (Warham 1990; Croxall & Rothery 1991). Consequently, our knowledge of vital rates in juvenile seabirds is very limited and was defined as a priority for seabird research (Lewison *et al.* 2012). Additionally, the status of the world's seabirds has deteriorated rapidly over recent decades and has now become the most threatened group among birds (IUCN 2012). Thus, conservation management of seabirds requires new studies including the consideration of early-life stages (e.g. Finkelstein *et al.* 2010).

Here, we estimate the early-life demographic parameters of a seabird and investigate the environmental factors encountered during the period of immaturity that may influence survival and recruitment. We analysed mark-recapture data of 9685 known-age Wandering albatrosses (*Diomedea exulans*). In this long-lived species, the immature period is particularly long, lasting around 9–10 years (Weimerskirch 1992). Using capture-mark-recapture multievent models (Pradel 2005) that allows dealing with unobservable states and age-related recapture probability in early life, we estimated early-life survival distinguishing the juvenile stage corresponding to the first 2 years at sea from later observable immature stages, as well as recruitment probability. Our models included both age and sex effects which are important factors to understand the demographic processes in long-lived species including wandering albatrosses (Barbraud & Weimerskirch 2012). We used climatic covariates and fisheries covariates to describe environmental conditions encountered by young animals and tested for density dependence on early-life demographic parameters.

Hypothesis and predictions

Prediction 1

According to the canalization theory, which predicts a stronger buffering against environmental stochasticity in the vital rates to which the population growth rate is the

most sensitive (Gaillard & Yoccoz 2003), we expect juvenile survival to be more variable than adult survival and juvenile survival to be more affected by environmental variability.

Prediction 2

The theory predicts that when sexual size dimorphism occurs in birds and mammals, the larger sex may be more susceptible to food shortage after independence causing sex difference in juvenile mortality (Clutton-Brock, Albon & Guinness 1985; Kalmbach & Benito 2007). Wandering albatrosses present strong sexual size dimorphism when adult and at fledging, with males being in average 4% larger and 23% heavier than females, and juvenile males present faster growth rates and increased nutritional requirements than juvenile females (Weimerskirch, Barbraud & Lys 2000). We thus expect that juvenile survival was sex specific, with lower survival probability for males.

Prediction 3

Wandering albatrosses suffer additional mortality through bycatch in longline fisheries (Brothers, Cooper & Lokkeborg 1999), and immature individuals appear to be captured in larger proportion than adults (Morant, Brooke & Abrams 1983; Gales, Brothers & Reid 1998). In addition, earlier studies on wandering albatross populations have established negative relationships between population abundance and longline fishing effort (Croxall *et al.* 1990; Weimerskirch, Brothers & Jouventin 1997). We thus expect a negative effect of fishing effort on early-life survival.

Prediction 4

Juvenile seabirds are known to be less efficient foragers than adults and may be less able to compete with adults (Porter & Sealy 1982; Wunderle 1991; Daunt *et al.* 2007). In addition, for wandering albatrosses, decreasing age of recruitment has been reported simultaneously to declining breeding population size (Weimerskirch, Brothers & Jouventin 1997), suggesting density-dependent recruitment as observed in others species when compensatory recruitment occurs after important breeder mortality (Pradel *et al.* 1997; Votier *et al.* 2008). We thus expect negative density dependence for early-life survival and annual recruitment rate.

Materials and methods

STUDY SPECIES AND SITE

We studied the wandering albatross population of Possession Island in the Crozet Archipelago (46°S; 52°E), southern Indian Ocean, from 1965 to 2012. Monitoring started in 1960, but all chicks were ringed each year with a stainless steel band just

before fledging from 1965. The breeding cycle of this quasi-biennial species lasts almost 1 year, with pair formation in December, laying in early January, hatching of the egg in April and fledging of the chick in November (Tickell 2000). Clutch size is limited to one egg without replacement laying. There is no post-fledging care, and the fledglings leave the colony alone remaining at sea continuously for the following 2–7 years (Weimerskirch 1992). Juvenile wandering albatrosses remain in the tropical and subtropical waters of the Indian Ocean with males moving more to the east than females (Weimerskirch *et al.* 2014). After 2 years at sea, their range shifts southward, and young immature birds start to return to their natal colony before starting to breed when 6 years old at the earliest (Weimerskirch 1992 and unpublished data). This population showed important changes in population size over the study period: with 500 breeding pairs in the 1960s, it declined steeply in the 1970s to reach 260 pairs in the mid-1980s, increased progressively to 380 pairs in the 2000s and declined slowly since then (Delord *et al.* 2008).

FIELD METHODOLOGY

From early to mid-December, pre-breeding adults are checked over the whole island. From mid-January (just after egg laying is resumed) to mid-February, at least three visits are made every 10 days to identify the two members of each pair and their breeding status. All new individuals are ringed with a uniquely numbered stainless steel band. In mid-April, June and August, nests are checked and the chick status recorded (alive/dead). During all visits, non-breeding individuals (mainly immatures) are searched for and their identity determined (from ring number) when possible. From mid-September to mid-October, fledglings are ringed. Chicks that died on the colony between ringing and fledging are noted during the first checks of the following breeding cycle and were excluded from our data set (0.3% of all individuals). Sex assignment methodology is given in supplementary materials (Appendix S1, Supporting information).

GENERAL MODEL

Individual encounter histories were modelled using a multievent approach. The model consisted in seven states, one immature state and six adult states (Fig. 1), and five events. To consider individuals during the period of immaturity, we defined the pre-recruitment (PrR) state after which immature birds can recruit, that is lay an egg for the first time into the breeding population. Adult birds can transit towards successful breeder (SB) state, when the chick fledged; failed breeder (FB) state, when the chick died before fledging; or recruited non-breeder (NB) state, when individuals that have recruited in the population (i.e. bred at least once) were observed as non-breeders at the colony. To model the sabbatical years spent continuously at sea, we added three unobservable states (Kendall & Nichols 2002; Lebreton & Pradel 2002) corresponding to the three previous adult states defined as follows: post-successful breeder (PSB), post-failed breeder (PFB) and post-non-breeder (PNB). Thus, adults, which are at sea (i.e. not at colonies for a whole year), are distinguished based on their most recent breeding state; last time, they were on a colony. In our study, state assignment was not always certain since between 1966 and 1986, state assessment was unknown for a number of breeders; some individuals were classified as breeders, but the success or failure was not always ascertained. Multievent models

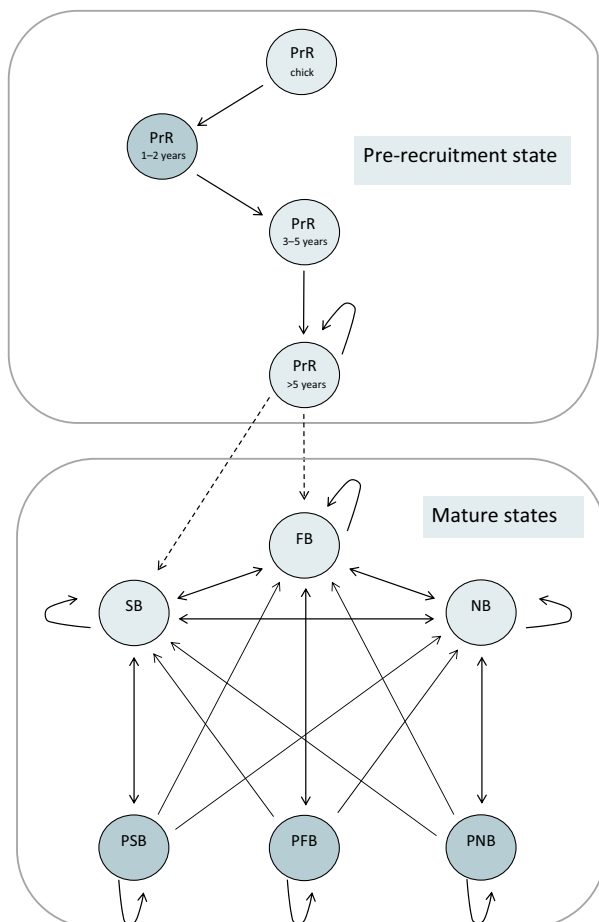


Fig. 1. Life cycle graph representing transitions between observable (white) and unobservable states (grey). As all birds are ringed as chicks, individuals start in the pre-recruitment state (PrR). After fledging, all birds remain at least 2 years continuously at sea and are thus unobservable. Pre-recruitment state becomes observable from 3 years old when birds start to return at the colony. Starting at 6 years old, birds can transition into the breeding part of the population. This transition corresponds to recruitment and it is represented by the dashed arrows. Then, mature birds irrespectively of age can make the transition between mature states: successful breeder (SB), failed breeder (FB), observable recruited non-breeder (NB), post-successful breeder (PSB), post-failed breeder (PFB) and post-observable recruited non-breeder (PNB).

allowed us to deal with state uncertainty by assessing the likelihood of an individual state given the events (i.e. observations) (Pradel 2005). We considered five events, that is five types of observation in the field, 0 = 'not observed', 1 = 'seen as non-breeder', 2 = 'seen as a FB', 3 = 'seen as a SB' and 4 = 'seen as a breeder but successful status not ascertained'. Details of the parameterization of the general model can be found in Appendix S2.

ENVIRONMENTAL COVARIATES

We used previous knowledge on seabird and wandering albatross ecology to select candidate covariates. Selected covariates included a large-scale climate index, the Southern Annular Mode (SAM), and a local climate index, the Sea Surface Temperature

Anomaly (SSTA). Both have been linked to seabird demography (Barbraud *et al.* 2012), including in the wandering albatross (Weimerskirch *et al.* 2012). Long-term effects of environmental conditions were assessed both with the natal climatic conditions and with the breeding success of the colony (as a proxy for natal environmental conditions). Natal climatic conditions were considered during the chick-rearing period (April–November), when parental investment, potentially affected by environmental fluctuations, could have a high impact on chick condition and future fitness components (Cam, Monnat & Hines 2003). Parental investment and foraging areas are sex dependent in the wandering albatross (Weimerskirch, Barbraud & Lys 2000). Thus, for natal SSTA, we distinguished the SSTA on the males' foraging grounds (SSTAm-a), the SSTA on the females' foraging grounds (SSTAfe) and the SSTA on the foraging grounds of both sexes (SSTAm + fe) (see Fig. S2). The impact of fishery activities on early-life survival was assessed using the numbers of hooks set as a proxy of fishing effort. To test for an effect of population density on pre-recruitment survival and recruitment, we used the number of breeding pairs observed annually at Possession Island as a covariate. More details on environmental covariates and their modelling are available in supplementary materials (Appendix S3). To make inference about temporal variability in early survival, we distinguished process variance from sampling variance as described in Appendix S4.

Results

Goodness-of-fit tests ($\chi^2 = 1003.4$, d.f. = 749, $P < 0.001$ for females and $\chi^2 = 1263.8$, d.f. = 898, $P < 0.001$ for males) indicated that the general JMV model did not fit the data correctly (see Appendix S5 and Table S1 for detailed comments). We thus used a variance inflation factor ($\hat{c} = 1.37$) for model selection. As the general model included age effects, our model selection is conservative since these age effects accounted for a part of the variation not captured by the JMV model. Results indicated that early-life survival and recruitment probability were influenced by both age and sex (Table S2), showing high variability across years although the sensitivity of young birds decreased with age. Our study suggests that these variations could be explained both by climate and by population density.

In early life, both sexes showed a progressive increase in survival until 9–13 years, followed by a strong decrease after this age (Fig. 2). The annual average juvenile survival during the first 2 years of life was 0.801 ± 0.014 (0.770 ± 0.020 for males and 0.829 ± 0.025 for females), with consistent variations between cohorts over the study period following a quadratic pattern for both sexes (Fig. 3). For the 3–8 age class, sex differences in annual survival were reversed with males having higher survival than females (Fig. 2). The 3- to 8-year-old immature survival was not related to birth cohort (Table S2, M8 vs. M6, $\Delta\text{QAIC} = 60$) but showed interannual variations which were similar between sexes (Table S2, M7 vs. M8, $\Delta\text{QAIC} = 70$). Between 9 and 13 years old, survival probability reached 0.980 ± 0.008 without difference between sexes and remained stable over the study period (Table

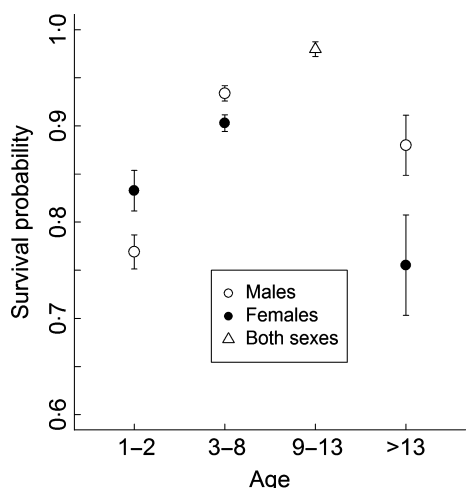


Fig. 2. Pre-recruitment survival estimates (\pm SE) as a function of age and sex for the wandering albatross population of Crozet. Open and filled dots correspond to males and females, respectively. Open triangles correspond to the sex-independent parameter according to model selection. Estimates came from model 4 (Table S2).

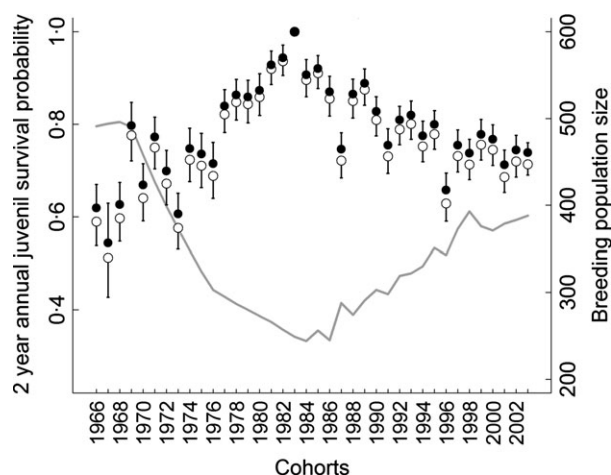


Fig. 3. Cohort-specific first 2-year annual juvenile survival and breeding population size (grey line, expressed as the number of breeding pair) from 1966 to 2002 of the wandering albatross population of Crozet. Open and filled dots correspond to males and females, respectively. Survival estimates (\pm SE) came from model 10 (Table S2).

S2, M3 vs. M4, Δ QAIC = 1.5), after 13-year-old survival of individuals that had not yet recruited declined to 0.876 ± 0.036 for males and 0.768 ± 0.061 for females.

Model selection suggested that in early life, survival temporal variability stabilized progressively with age. Time effect was strongly supported for the juvenile stage (Δ QAIC = 153), weakly supported for the 3- to 8-year-old class (Δ QAIC = 2), and not supported for older individuals. In accordance with this result, relative process variance decreased gradually with age (Table 1). Variation of juvenile survival was strongly related to natal environmental conditions. Breeding population size

Table 1. Relative process variances and SD of first 2-year juvenile survival and immature survival parameters for wandering albatrosses from Crozet Island from 1965 to 2012

Age class	Estimate	Relative process variance	Relative process SD
1–2 years	0.801 ± 0.016	0.058	0.240
3–8 years	0.918 ± 0.007	0.013	0.116
9–13 years	0.980 ± 0.009	–0.111	0

at the year of birth was negatively related to juvenile survival, explaining 41% of the variation of this parameter over the study period (Table 2, M1, Fig. 3). Additionally, we found an additive negative effect of SSTA on the male adults foraging grounds on juvenile survival which explained 6% of the total variation (Fig. S4a). Neither the SSTA on the female foraging grounds nor the global SSTA on the foraging grounds of both sexes was significantly related to juvenile survival (Table 2, $F_{\text{test}_{\text{cst/co}/t}} = 1.39$ and 1.45, respectively, P -value > 0.20). None of the other covariates had a statistically significant effect on juvenile survival (Table 2, P -value > 0.15). The best model for the 3- to 8-year-old class retained a significant but weak effect of SSTA (Table 2, $F_{\text{test}_{\text{cst/co}/t}} = 3.10$, P -value = 0.05). This climatic covariate was negatively related to 3- to 8-year-old survival and explained 8% of the total variation (Table 2, M12). We did not find evidence for an impact of any other covariates on the 9- to 13-year-old class survival. Due to small sample sizes, we could not test whether survival variations for the oldest age class were time or covariate dependent.

Concerning recruitment, females bred earlier than males. At 9 years old, the probability to be recruited was 80% for females, whereas it was only 50% for males (Fig. S3). Nevertheless, the probability to be recruited at age 15 was very similar between sexes reaching 95%. Both sexes showed increasing recruitment probability from 6- to 9-10-year-old and a decrease in recruitment probability at older ages (Fig. 4). Constraining the recruitment probability to be constant after 10 years improved significantly our model reducing the AIC of 14 points, probably due to large SEs resulting from the smaller sample size of these ages. To assess the relationships between recruitment and the covariates, we used this more parsimonious model structure. Results suggest that recruitment was not limited by population density since recruitment probability was positively correlated with breeding population size (Table 2, M25, slope = 0.33 ± 0.03). SSTA was positively related to the probability to start to breed, explaining 28% of the variation of recruitment rate (Table 2, M28). We found an additive positive effect of SAM (Fig. S4c). However, SAM presented a linear temporal trend as did our estimated recruitment rate between 1982 and 2000 (Fig. 5). After removing the linear trend from SAM using the residual regression technique and reanalyzing the

Table 2. Testing for the effects of covariates on pre-recruitment survival and recruitment probability for wandering albatrosses from Crozet Island from 1965 to 2012. Results include the relative deviance corrected by the overdispersion factor (QDev), the statistic $F_{\text{test}_{\text{cst}/\text{co}/t}}$ testing the null hypothesis that the focal climatic covariate has no effect on survival, the percentage of variation explained by the covariates (r^2) and the slope \pm SE. All covariates were standardized. * indicates one-sided tests (P -value/2) since we expected bycatch to increase with fishing effort and thus to be negatively related to survival. Models with statistically significant covariate effects at the level of 5% are in bold characters

No.	Pre-recruitment survival	QDev	F	P -value	r^2	Slope
1- to 2-year old class						
1	N	80328-01	25-63	< 0-001	0-41	-0-41 \pm 0-05
2	N + SAM	80326-95	0-35	0-71	0-41	
3	N + SSTA	80327-35	0-22	0-80	0-41	
4	N + fishing effort	80326-74	0-42	0-33*	0-41	
5	N + SAMnatal	80327-79	0-07	0-93	0-41	
6	N + SSTAfe	80323-96	1-39	0-26	0-43	
7	N + SSTAma	80315-15	4-78	0-01	0-47	-0-21 \pm 0-06
8	N + SSTAfe + ma	80323-76	1-45	0-24	0-43	
9	N + BS	80322-80	1-80	0-17	0-43	
3- to 8-year-old class						
10	N	80289-82	1-26	0-29	0-03	
11	SAM	80290-89	0-72	0-49	0-02	
12	SSTA	80286-39	3-10	0-05	0-08	-0-20 \pm 0-07
13	Fishing effort	80290-51	0-91	0-20*	0-02	
14	N + SAMnatal	80292-09	0-70	0-50	0-03	
15	N + SSTAfe	80292-31	0-12	0-89	<0-01	
16	N + SSTAma	80292-35	0-01	0-99	<0-01	
17	N + SSTAfe + ma	80292-10	0-67	0-52	0-03	
18	N + BS	80292-35	0-01	0-99	<0-01	
9- to 13-year-old class						
19	N	80214-07	0-67	0-42	0-02	
20	SAM	80213-79	1-45	0-24	0-04	
21	SSTA	80214-04	0-76	0-39	0-02	
22	Fishing effort	80213-40	2-52	0-06*	0-07	
23	N + SAMnatal	80214-25	0-16	0-85	<0-01	
24	N + SSTAfe	80214-26	0-13	0-87	<0-01	
25	N + SSTAma	80213-71	1-30	0-30	0-07	
26	N + SSTAfe + ma	80214-31	0-05	0-95	<0-01	
27	N + BS	80214-13	0-39	0-68	0-02	
No.	Recruitment	QDev	F	P -value	r^2	Slope
28	SSTA	80245-87	11-59	< 0-001	0-28	0-28 \pm 0-05
29	SAM	80276-66	3-10	< 0-001	0-10	0-16 \pm 0-05
30	detrendedSAM	80276-55	0-02	1	0-01	
31	N	80224-75	12-28	< 0-001	0-41	0-33 \pm 0-03
32	N + SAMnatal	80292-34	<0-01	1	<0-01	
33	N + SSTAfe	80292-23	0-03	1	<0-01	
34	N + SSTAma	80292-36	0	1	0	
35	N + SSTAfe + ma	80291-70	0-17	1	<0-01	
36	N + BS	80292-33	<0-01	1	<0-01	

relationship between recruitment rate and this climatic covariate, the SAM effect was no longer significant (Table 2, M24, $F_{\text{test}_{\text{cst}/\text{co}/t}} = 0-02$, P -value = 1).

Discussion

This study demonstrated that sex, population density and climatic conditions can strongly influence survival during early life, and to a lesser extent recruitment, of a long-lived marine top predator. In addition, it provides for the first time an estimate of juvenile survival (during the first 2 years at sea) for an albatross species.

EARLY-LIFE SURVIVAL

Previous studies in mammals and birds suggested that most of the mortality between fledging and recruitment occurs during the first months of life (Gaillard *et al.* 2000; Naef-Daenzer, Widmer & Nuber 2001; Martin *et al.* 2007; Riotte-Lambert & Weimerskirch 2013). This pattern has been linked to progressive improvement of flight abilities and foraging skills in early life (Marchetti & Price 1989; Thornton & Clutton-Brock 2011). In wandering albatrosses, juvenile survival over the first 2 years of life was 0-64 (annual survival of 0-801), which is one of the highest

Fig. 4. Estimates of age-specific probability of recruitment for females (a) and males (b) of the wandering albatross population of Crozet. Estimates (\pm SE) came from model 15 (Table S2).

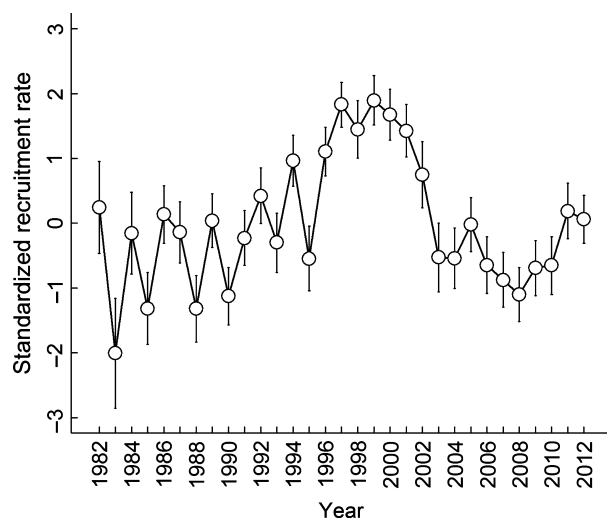
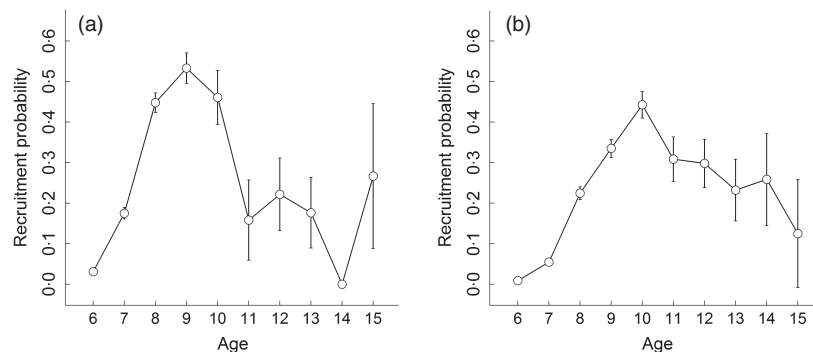


Fig. 5. Recruitment rate between 1982 and 2012 of the wandering albatross population of Crozet. The proportions of new recruits are expressed as standardized difference from the average recruitment rate. Estimates (\pm SE) came from model 19 (Table S2).

values of early-life survival estimated for a bird species, but still lower than adult survival. Given that long-distance natal dispersal is very rare in this highly philopatric species (Inchausti & Weimerskirch 2002; Charmantier *et al.* 2011), we are confident that our apparent survival estimates are close to the true survival probabilities.

As predicted, we found that juvenile survival was highest for females. Male wandering albatrosses that are structurally larger and heavier than females could be more sensitive to starvation during this critical step of independence due to their higher food requirements for self-maintenance (Clutton-Brock, Albon & Guinness 1985). Males of larger size at fledging are those that better survive, whereas females in better body condition survive better (Weimerskirch, Barbraud & Lys 2000). However, after the juvenile stage, the sex difference in survival was surprisingly reversed. Different hypotheses could explain this pattern. First, it could be the result of a selective process. Indeed, sex-specific juvenile mortality potentially removed disproportionately low-quality individuals according to genders during the first year at sea,

providing more high-quality males than females in older age classes. Nevertheless, this hypothesis suggests that such survival shifts between sexes during early life would be regularly observed in wild populations, which is not currently supported by the literature. On the other hand, immature birds show sex-specific distributions at sea with male wandering albatrosses from Possession Island moving more to the east of the southern Indian Ocean than females (Weimerskirch *et al.* 2014). Thus, environmental conditions experienced by immature individuals could be different between sexes, and females may experience less favourable climatic and trophic conditions than males. Non-exclusively, immature females could be more exposed to longline fisheries with associated bycatch mortality due to different overlap with fisheries or different susceptibility (Barbraud & Weimerskirch 2012), as it has been suggested to explain higher male survival in adults due to their differential overlapping distribution with fisheries at sea (Weimerskirch, Brothers & Jouventin 1997).

Early-life survival increased with age and reached adult survival value at 9 years. As predicted by the environmental canalization theory (Gaillard & Yoccoz 2003), survival stabilized progressively against temporal variability with ageing. In 3- to 8-year-old individuals, immature survival appeared less variable than juvenile survival and we did not detect a delayed effect of natal conditions on immature survival. However, we observed a decrease in immature survival after 13 years old. This decrease may be due to individual heterogeneity (Vaupel & Yashin 1985; Cam & Aubry 2011). Birds that have not yet recruited after 13 years are probably individuals of lower quality. Although very few studies estimated age-specific survival during early life in interaction with breeding status by distinguishing non-recruited from recruited individuals, declining survival associated with late recruitment could be a common pattern in long-lived species.

In contrast with adult survival which was not affected by climatic covariates (Rolland, Weimerskirch & Barbraud 2010), we detected significant correlations between environmental covariates and survival of young birds. Juvenile survival appeared highly related to conditions at sea during chick rearing. We found that SSTA on the males' foraging grounds during breeding was negatively

related to future juvenile survival. SSTA anomalies are widely used as an indicator of food availability for seabirds, and high SSTA may negatively affect food resources favouring more stable density stratification of the water column associated with a strong decrease in net primary production (Behrenfeld *et al.* 2006). Thus, during positive SSTA years, breeders may face low abundance of food resources. This would reduce food provisioning to the chick, which may be in poorer body condition at fledging, compromising their survival. Concordant results have been provided in the yellow-nosed albatross *Thalassarche carteri*. In this species, positive SSTA has been related to increasing foraging trip duration, affecting negatively the provisioning rate of adults to their chick, with negative effects on chick body condition at fledging (Weimerskirch, Zimmermann & Prince 2001). Additionally, the ability of wandering albatrosses to increase their foraging effort may be limited by the unpredictability of their foraging success due to the extreme scattered distribution of their food resources (Weimerskirch, Gault & Chérel 2005). Male wandering albatrosses provision more food to their offspring than females (Weimerskirch, Barbraud & Lys 2000). Our study supported the main role of male parental investment since the relationship between SSTA and juvenile survival was only found for adult males' foraging grounds. Early-life survival seemed to be more affected by natal environmental conditions since we did not detect an influence of the climatic conditions encountered during the first year of life at sea on juvenile survival. As found in other long-lived species, survival in early life might be more strongly related to the initial conditions rather than to the severity of environmental conditions after independence (Gaillard *et al.* 2000; Reid *et al.* 2003; Beuplet *et al.* 2005).

Three- to eight-year-old immature survival was negatively related to SSTA on their foraging grounds. This effect was again consistent with the literature since most of the relationships between SSTA and seabird demographic parameters in the Southern Ocean are negative owing to unfavourable effect of warm water temperature on food resources (Barbraud *et al.* 2012). Finally, the effect of SSTA on 1- to 2-year-old and 3- to 8-year-old individuals was similar with no significant difference between slope estimates (z -test = 0.128, $P = 0.898$).

Contrary to expected, we found no effect of longline fishing effort on juvenile and immature survival variations. Barbraud *et al.* (2012) reported that 24% of studies ($n = 33$) investigating the effects of fisheries activities in the Southern Ocean on seabird demography focusing mainly on the mature state found no significant relationship. Several hypotheses could explain this surprising result. First, our assumption of proportionality between bycatch rates and fishing effort may be false. This could be due to the implementation of mitigation measures to reduce albatross bycatch in longline fisheries, in which case fishing effort would become independent of bycatch rates. However, preventive measures to reduce seabird

mortality in longline fisheries occurred mainly in Antarctic and sub-Antarctic waters, whereas young albatrosses remained in subtropical waters and thus did not benefit from mitigation measures. Secondly, we cannot exclude that our analysis using fishing effort data was biased due to the varying quality of fishing effort data that we could not control. Finally, young albatrosses could interact less with fishing vessels than previously expected. In contrast to our results, studies conducted on the adult component of this population reported a negative relationship between survival and fishing effort (Rolland, Weimerskirch & Barbraud 2010). Young albatrosses might be excluded from longline fishing vessels by older individuals since they are probably less competitive (Morant, Brooke & Abrams 1983; Weimerskirch, Brothers & Jouventin 1997).

RECRUITMENT

As documented in other species, the recruitment process seemed highly influenced by current environmental condition without persistent observable effects of natal conditions (Reid *et al.* 2003; Stauffer, Rotella & Garrott 2013). In contrast to survival, the highest recruitment rate was associated with warmer sea surface temperatures during the previous year. This relatively strong relationship ($r^2 = 28\%$) was difficult to interpret since it is generally expected that positive SSTA depress food resources and thus affect negatively the demographic traits, and studies that reported negative relationships between SSTA and survival reported the same effect on recruitment probabilities (Votier *et al.* 2008; Oro *et al.* 2010). Yet, similarly to our findings, studies on the black-browed albatross *Thalassarche melanophrys* found opposite associations between survival and recruitment for the same climatic variable (Nevoux, Weimerskirch & Barbraud 2007, 2010).

Although wandering albatrosses are sexually mature at age 6 years (Hector, Croxall & Follett 1986), and some breed at this age in our population, most individuals recruit several years later. As suggested for survival, decreasing recruitment probabilities beyond 10 years old were probably the result of individual heterogeneity with accumulating low-quality non-recruited birds at later age.

DENSITY DEPENDENCE

Density-dependent mortality has been found in terrestrial mammals and birds (Durell *et al.* 2000; Gaillard *et al.* 2000) but was rarely documented in seabirds and marine mammals (Frederiksen & Bregnballe 2000; Barbraud & Weimerskirch 2003; Rotella *et al.* 2009). Although adult survival and reproductive parameters (i.e. breeding and success probability) in this albatross population appeared density independent (Rolland 2009), our study suggested that juvenile survival was strongly density dependent with a clear negative relationship between breeding population

size the year of birth and juvenile survival. These results support the paradigm of Eberhardt (Eberhardt 2002), suggesting that in long-lived species, juvenile survival is the first parameter affected by increasing population density. The effect of breeding population was restricted to very early life since immature survival was not affected, and was nearly two times stronger than the effect of natal SSTA (significant difference between slope estimates: z -test = 3.123, $P = 0.002$). Two different processes may explain density dependence in this species. First, juvenile survival could be affected by parental investment variations depending on intraspecific competition for food during the breeding season. In seabirds, foraging competition among breeders may be important, affecting colony distribution (Furness & Birkhead 1984) and foraging trip duration (Lewis *et al.* 2001). In long-lived species, life-history theory predicts that breeders minimize their energetic costs to preserve future breeding attempts (Stearns 1992). Thus, in cases when increasing breeding population size implies a higher foraging effort, parents may shunt this additional cost on their chick, reducing chick food supply, with negative consequences on the chick condition at fledging and its subsequent survival probability. In agreement with this expectation, Gaston, Chapdelaine & Noble (1983) showed that mass at fledging of thick-billed murre *Uria lomvia* chicks was negatively related to colony size. An alternative, but non-exclusive, hypothesis is that juvenile albatrosses may suffer from direct competition during early life at sea. Recent studies on spatial ecology at sea revealed that offshore competition among seabirds may be an active process with strong consequences on populations, and juveniles could be more affected by competition than older birds (Navarro *et al.* 2010). Indeed, juveniles are known to be less efficient foragers than adults suggesting that they may be less competitive (Daunt *et al.* 2007; Riotte-Lambert & Weimerskirch 2013). For wandering albatrosses, the overall range of juvenile at sea is mainly situated in subtropical waters at lower latitudes than the adult range (Weimerskirch *et al.* 2014). These differences in spatial distribution may be the result of selective pressures to avoid competition.

Results did not support density dependence for recruitment rate. Indeed, we found a positive relationship between annual variation in the number of recruits and the breeding population size. Thus, it appears the effects of density dependence are limited to the first step in the sequence of changes in vital rates as population density increases as proposed by Eberhardt (2002). In colonial birds, a negative influence of breeders' density on recruitment probability was reported in a handful of species (Pradel *et al.* 1997; Tavecchia *et al.* 2007). Thus, it is likely that the population size of wandering albatrosses of Crozet was below the threshold for which density-dependent recruitment may occur. Indeed, present numbers (350 pairs) are much lower than the original population size in the 1960s (500 pairs) (Delord *et al.* 2008).

CONCLUSION

To conclude, we found that early-life demographic traits were sex specific, highly sensitive to environmental variability and stabilized progressively with ageing, as predicted by the life-history theory. Our study provided strong evidence for density dependence in juvenile survival in a pelagic seabird. This result has important consequences for our understanding of population dynamics in seabirds. Indeed, the effects of population density and climate factors on juvenile survival are generally not considered explicitly into projection population models for seabirds and other long-lived species (e.g. Finkelstein *et al.* 2010), whereas our results demonstrate that the juvenile compartment may be strongly impacted by population density and climate fluctuations. Including the effects of density into projection population models will have important consequences on the projected population growth rates and trajectories (Caswell 2001). Furthermore, the mechanisms proposed here to explain this density effect are not restricted to albatross species suggesting that density-dependent juvenile mortality may occur across a higher number of seabird species than currently suspected.

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Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.p62h7> (Fay *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Sex assignment.

Appendix S2. Parameterization of the general model.

Appendix S3. Environmental covariates.

Appendix S4. Estimation of temporal variation.

Appendix S5. Goodness-of-fit and model selection.

Table S1. Results from the GOF tests performed on the adult component of the dataset with known states.

Table S2. Pre-recruitment survival and recruitment modelling as a function of age (a), sex, cohort (c) and time (t) of the wandering albatross population of Crozet Island from 1965 to 2012.

Fig. S1. Graph summarizing selected environmental covariate: sea surface temperature anomaly (SSTA), southern annular mode (SAM), Breeding success of the colony (BS), Breeding population size (N) and Fishing effort (Fisheries), and the early life demographic parameters potentially affected: survival (ϕ) and recruitment probabilities (ψ).

Fig. S2. Distribution area from which SSTA and fishing effort values were extracted for (a) juvenile (1–2 years), (b) immature (>2 years), (c) parents of both sexes and (d) parents distinguishing male range (solid square) from female range (dashed square).

Fig. S3. Estimated cumulated probability to be recruited according to age and sex for the wandering albatross population of Crozet.

Fig. S4. Relationships between early life survival and recruitment probabilities in the wandering albatross population of Crozet and environmental covariates.