

Demographic and population responses of an apex predator to climate and its prey: a long-term study of South Polar Skuas

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Abstract. Ecologists widely acknowledge that a complex interplay of endogenous (density-dependent) and exogenous (density-independent) factors impact demographic processes. Individuals respond differently to those forces, ultimately shaping the dynamics of wild populations. Most comprehensive studies disentangling simultaneously the effects of density dependence, climate, and prey abundance while taking into account age structure were conducted in terrestrial ecosystems. However, studies on marine populations are lacking. Here we provide insight into the mechanisms affecting four vital rates of an apex Antarctic marine predator population, the South Polar Skua *Catharacta maccormicki*, by combining a nearly half-century longitudinal time series of individual life histories and abundance data, with climatic and prey abundance covariates. Using multistate capture–mark–recapture models, we estimated age classes effects on survival, breeding, successful breeding with one or two chicks and successful breeding with two chicks probabilities, and assessed the different effects of population size, climate, and prey abundance on each age-specific demographic parameter. We found evidence for strong age effects in the four vital rates studied. Vital rates at younger ages were lower than those of older age classes for all parameters. Results clearly evidenced direct and indirect influences of local climate (summer sea ice concentration), of available prey resources (penguins), and of intrinsic factors (size of the breeding population). More covariate effects were found on reproductive rates than on survival, and younger age classes were more sensitive than the older ones. Results from a deterministic age-structured density-dependent matrix population model indicated greater effects of prey abundance and sea ice concentration on the total population size than on the breeding population size. Both total population size and the number of breeders were strongly affected by low values of sea ice concentration. Overall, our results highlight the greater sensitivity of reproductive traits and of younger age classes to prey abundance, climate variability, and density dependence in a marine apex predator, with important consequences on the total population size but with limited effects on the breeding population size. We discuss the mechanisms by which climate variability, prey abundance, and population size may affect differentially age-specific vital rates, and the potential population consequences of future environmental changes.

Key words: Adélie Penguin *Pygoscelis adeliae*; age structure; Antarctica; capture–mark–recapture; *Catharacta maccormicki*; density dependence; deterministic density-dependent matrix population model; Emperor Penguin *Aptenodytes forsteri*; food availability; multistate model; sea ice concentration.

INTRODUCTION

Population dynamics depends on a complex interplay of endogenous (density-dependent) and exogenous (density-independent) factors (Bjørnstad and Grenfell 2001). Negative density dependence tends to keep populations near equilibrium through population density feedbacks on demographic rates (e.g., survival, reproduction and recruitment), resulting in variation of the population growth rate that, in turn, drives the population

abundance. Density-independence encompasses demographic stochasticity and exogenous factors such as environmental variability (weather, food...) and predation (Berryman 1999, Grange et al. 2015), which act as limiting factors.

Demographic responses to these factors differ among individuals according to age (Charlesworth 1980, Pardo et al. 2013, Oro et al. 2014). Studies on wild populations have reported an increase of survival and reproductive rates from early ages to intermediate age (Forslund and Pärt 1995, Gaillard and Yoccoz 2003). This improvement of demographic performances could result from three non-mutually exclusive processes: the progressive

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disappearance of phenotypes (the selection hypothesis), an increase in parental investment in older individuals (the restraint hypothesis), and an improvement of foraging, migration or reproductive skills required to breed and to cope with environmental constraints (the constraint hypothesis; Williams 1957, Curio 1983, Newton 1998, Rebke et al. 2010). In intermediate age classes, demographic performances of individuals stabilize or immediately decline after the age of primiparity (Jones et al. 2008). The decline in demographic performances may originate from two non-exclusive sources (Williams 1957, Hamilton 1966): senescence, i.e., the natural decline of physiological functions with age (Monaghan 2008), or the consequences of a trade-off between investment in current or early reproduction and subsequent reproduction and survival (Stearns 1989). Following the terminal investment theory, reproductive effort of elderly could also increase (McNamara et al. 2009). In addition to age-related variations in demographic traits, individuals may differentially respond to environmental variations according to their age, young and old individuals being generally more sensitive to environmental variation (Stearns and Kawecki 1994, Gaillard et al. 2000, Coulson et al. 2001, Gaillard and Yoccoz 2003, Oro et al. 2010, Pardo et al. 2013).

However, it remains difficult to quantify the relative effect of these factors on the full life cycle of a species because it requires long-term data for climate, and the resources and demographic information, which are often laborious and difficult to acquire (Coulson et al. 2001, Clutton-Brock and Sheldon 2010), particularly in marine ecosystems (Stenseth et al. 2002, Zabel et al. 2006). The relevant covariates could also be difficult to gather due to logistical limitations or lack of relevant knowledge, often constraining studies to use indirect measures intended to represent the relevant processes, i.e., proxies (Frederiksen et al. 2007). In marine ecosystems, the local variation in food abundance is often approximated indirectly through oceanographic physical variables such as sea surface temperature (Frederiksen et al. 2007), large-scale stock estimates from fisheries (Cury et al. 2011), or industrial fishing effort and catches (Rolland et al. 2009).

To address this gap of knowledge, we present here a comprehensive demographic study to understand how age-related effects of density dependence, climate variation, and prey abundance affect the full life cycle of an apex marine predator, the South Polar Skua (*Catharacta maccormicki* (Saunders, 1983) generic assignment Carlos 2016), using a 52-yr longitudinal capture–recapture data set. In polar ecosystems, skuas are top predators and scavengers that play an important role in ecosystem functioning (Votier et al. 2007, Dawson et al. 2011, Schmidt et al. 2012, Barraquand et al. 2014). However, their demographic and population responses to fluctuations in climate and prey abundance remain poorly understood, especially in Antarctic ecosystems. A previous study on the same population analyzed the sensitivity of the breeding population growth rate to density

dependence, local climate conditions and prey abundance using a time series analysis (Pacoureau et al. 2018). They found evidence of a direct negative density-dependent regulation of the breeding population and suggested territorial behavior as a limiting mechanism of the breeding population. Various forms of relationships between breeding population size and climate and prey factors were detected by Pacoureau et al. (2018), as well as lagged effects. Although this study provided significant insight into the factors driving the population dynamics, such a time series approach based on abundance data did not allow the identification of the underlying demographic processes involved.

Building on these earlier findings, our main objectives are twofold. First, using longitudinal individual data, we characterize the functional age-specific responses of the population vital rates to intrinsic and extrinsic factors. Specifically we aim (1) to estimate age-class effects on four demographic parameters (survival probability, probability of breeding, probability of a successful breeding with one or two chicks, and probability of a successful breeding with two chicks), and (2) to assess the different effects of population size, climate, and prey abundance on these age-class specific demographic parameters. Second, at the population level, we develop an age-structured density-dependent matrix population model (Caswell 2001), which explicitly includes the functional relationships between demographic rates and influential covariates. Based on previous knowledge of this population and from the existing literature, we test three predictions.

HYPOTHESES AND PREDICTIONS

Prediction 1

As predicted by theory and typically observed in long-lived species, we expected vital rates of younger age classes of South Polar Skuas to be lower than those of older age classes either due to inexperience, poor foraging skills, and/or a progressive selection of “high-quality” (or “less frail”) individuals, and a decrease in survival and/or breeding performances in the latest age class.

Prediction 2

As the population growth is a function of all vital rates, different combinations of survival and fecundity patterns can lead to the same population growth rate. Pacoureau et al. (2018) found a lagged linear effect of local climate with warmer spring air temperature on breeding population size of South Polar Skua. It could be evidenced by a linear relationship with one vital rate, for example juvenile survival or rates related to breeding success and thus subsequent recruitment of individuals. A U-shaped response of the number of breeding South Polar Skuas to sea ice concentration with a lag was also outlined. It was proposed that sea ice conditions could

act indirectly via the population dynamic of their main prey, Adélie Penguins *Pygoscelis adeliae*, showing the exact reverse response to this same environmental factor. We thus expected that this relationship could be explained by (1) quadratic relationships between sea ice concentration (SIC) and one or more vital rates (breeding success parameters or juvenile survival), or (2) an opposite relationship (positive and negative) between sea ice concentration and two or more vital rates (e.g., a strong positive relationship between juvenile survival and a strong negative relationship between breeding success with sea ice concentration could lead to an increase of the number of young individuals at both extreme values of sea ice concentration). The availability of another prey item, dead Emperor Penguin chicks *Aptenodytes forsteri*, impacted positively the breeding population size but without lag, thus possibly affecting directly breeding probability of South Polar Skuas.

Prediction 3

We expected negative density dependence to occur in this population primarily because South Polar Skuas show strong territorial behavior as territories include both breeding and feeding grounds (Jouventin and Guillotin 1979, Ainley et al. 1990). Two previous studies using time series analyses have suggested regulation of this population (Lande et al. 2002, Pacoureaux et al. 2018). We thus expected a negative relationship between breeding probability and population size. Since sibling competition and egg and chick predation by conspecifics has also been reported in South Polar Skuas (Procter 1975, Young and Millar 2003), we could also expect a negative relationship with population size and breeding success parameters.

METHODS

We conducted a comprehensive demographic study of the effect of the environment on the vital rates and population size of South Polar Skuas. First, our aim was to understand the effects of density-dependent and density-independent processes on the vital rates by accounting for the age of individuals. To do so, we analyzed a longitudinal individual data set using statistical capture–recapture models and determined the best age structure for each vital rate. Second, we investigated potential influence of covariates (density dependence, climate, prey abundance). Finally, we constructed a life cycle structured by age classes and incorporated the effect of the influential covariates on the vital rates into a structured matrix population to project the population size of South Polar Skuas.

Study species

The South Polar Skua generally breeds in colonies in Antarctica and is highly territorial during breeding with

strong site tenacity and mate fidelity (Young 1963, 1972, Jouventin and Guillotin 1979, Ainley et al. 1990, Pietz and Parmelee 1994). South polar skuas were studied on the Pointe Géologie archipelago, Terre Adélie, Antarctica (66°40' S, 140°01' E), where they regularly breed on 15 islands. Pair formation starts in October and usually two eggs (one in late nesting pairs) are laid at intervals of 2–4 d in mid-November. Hatching of the eggs occurs in late-December and chicks fledge 50 d after (Young 1963). Parents feed their chicks until chicks leave the nesting territory (Spellerberg 1971a) at the end of the breeding season between late March and mid April (Le Morvan et al. 1967). Individuals start to breed when 3 yr old at the earliest. Most females start breeding between 5 and 7 yr and slightly later for males (Ainley et al. 1990). At Pointe Géologie, South Polar Skuas feed almost exclusively on penguins. Eggs and chicks of Adélie Penguins constitute the main food resources during the breeding season (Jouventin and Guillotin 1979, Micol and Jouventin 2001, Cherel 2008, Weimerskirch et al. 2015, Carravieri et al. 2017). After arriving on the breeding grounds in October, South Polar Skuas feed regularly on dead Emperor Penguin chicks that are available at the surface of sea ice occupied by the penguin colony during the breeding season (Pryor 1968). After the breeding season, adults from Pointe Géologie migrate directly to winter off eastern Japan at latitudes of 35° to 45° N, without marked stopovers (Weimerskirch et al. 2015).

Longitudinal data sets

Every year since 1963/1964 (named the 1963 breeding season), all islands of the archipelago were visited regularly by foot on fast ice or by boat after break up of fast ice, and South Polar Skua territories were recorded and counted. We considered a pair to have established a territory when its members vigorously defended an area against the intrusion of an observer. Chicks just before fledging and unbanded individuals (breeders and non-breeders) found in territories and their surroundings were captured and banded with a stainless steel band and a plastic band engraved with a unique alphanumeric code. We used plastic bands to facilitate individual identification at distance using binoculars. Every breeding season, from mid October to mid April, nesting territories were visited every two weeks (4–12 visits per territory) and each partner of a breeding pair was identified at the time of the visits. Breeding status was determined by checking the nest contents during each visit for the presence of eggs or young chicks, and nest surroundings for the presence of chicks. To ascertain breeding status, the territories were searched intensively. A group of non-breeding individuals (“clubs”), a common feature of *Stercorariidae* (Furness 1987), of ~30–50 individuals found at the same place all years in the study area was also checked, with the same survey intensity as for breeding individuals, for individual identification of

banded birds. We considered observations of individuals banded as chicks in Pointe Géologie ($n = 1,567$) during the period 1963–2014, allowing us to know the age at recaptures with precision. Until recently, very few individuals were sexed and thus we do not have information on sex for most individuals. Therefore, sex was not taken into account in this study.

A capture–recapture model to estimate the vital rates

To estimate demographic parameters simultaneously, and the effects of age, population size and covariates while taking into account imperfect detectability of marked individuals at the study site, we used multistate capture–mark–recapture models (MSCMR; Brownie et al. 1993, Lebreton and Pradel 2002). We estimated the following demographic parameters: apparent survival probability (ϕ), probability of return to the colony for immature individuals (r), probability of breeding (β), probability of successful breeding (at least one chick fledged, γ), probability of successful breeding with two chicks (δ), and the recapture probability (p).

To do so, we constructed a MSCMR model including seven states (immature [I], immature that have returned to the colony at least once [IR], non-breeder [NB], successful breeder with one fledged chick [SB1], or two fledged chicks [SB2], the failed breeder [FB], and the dead state [†]). Immature individuals are birds that have not laid an egg into the breeding population. Immature individuals can return to the colony with probability r and then have the probabilities of breeding defined above (i.e., the non-breeder state, the successful breeder state with one fledged chick or two fledged chicks, the failed breeder state when the egg(s) laid did not hatch and/or the chick(s) died before fledging. Capture histories were coded considering five events corresponding to field observations: 0, not observed; 1, seen as NB; 2, seen as FB; 3, seen as SB1; 4, seen as SB2.

First we developed a general age-dependent model where all mathematical parameters were identifiable (see Appendix S1). To ensure that the starting (general) model adequately fitted the data, goodness-of-fit tests were performed for multistate models (Pradel et al. 2003) using the software U-Care, version 2.3.2 (Choquet et al. 2009a). We ran the test on the JollyMoVe (JMV; Brownie et al. 1993) umbrella model for multistate data. The goodness-of-fit test ($\chi^2 = 1,135.45$, $df = 488$, $P < 0.001$) indicated the data poorly fitted the general model (see Appendix S2 and Appendix S2: Table S1). The lack of fit was mainly due to a transient effect and to trap dependence. Accounting for an age effect on survival and heterogeneity in recapture probability in our general model resulted in an improvement to model fit ($\chi^2 = 571.25$, $df = 409$, $P < 0.001$), partly taking account of the variance not captured by the JollyMoVe model. Since the corrected test was still statistically significant, we thus used a variance inflation factor ($\hat{c} = 1.4$), estimated from the goodness-of-fit chi-square

statistic of the global model divided by its degrees of freedom, in the model selection procedure. The variance inflation factor was taken into account by correcting the Akaike information criterion corrected for sample size (AIC_c) for overdispersion in the data (Burnham and Anderson 2002).

Second, we performed a preliminary model selection to define a simplified model so as to investigate age effects on demographic parameters and recapture probability. Model selection was performed with a modified version of the quasi- AIC_c corrected for small sample sizes ($QAIC_c$; Akaike 1974). Two models were considered to differ when the $QAIC_c$ difference was greater than 2 ($\Delta QAIC_c > 2$; Burnham and Anderson 2002). When $\Delta QAIC_c < 2$, we selected the model with the smallest deviance. All estimates and $QAIC_c$ values were computed using program E-Surge v1.9.0 (Choquet et al. 2009b). We reduced the general full age-dependent model by determining groups of age classes with similar values using a threshold methodology (Berman et al. 2009, Pardo et al. 2013, see Appendix S3 and Appendix S3: Table S1). This gave the best simplified model described in Table 1.

Testing for a differential impact of environmental, prey and population size variations with age

We tested the age-specific effects of covariates separately on the four vital rates (ϕ , β , γ , and δ) with a correlative approach to assess their potential influence. For each vital rate, we used the selected model structure describing the age-dependent variations to which each covariate effect was added separately in interaction with age classes. We selected eight candidate covariates based on previous knowledge on seabird and South Polar Skua ecology. These covariates included the potential climatic, prey, and population size effects in both the breeding and wintering areas of South Polar Skuas: South Polar Skua population size, number of dead chicks of Emperor Penguins, number of breeding pairs of Adélie Penguins, sea ice concentration during spring and summer, air

TABLE 1. Best simplified multistate capture–mark–recapture model.

Parameter	Age class
Survival probability, ϕ	[1:2].[3:28]
Return probability, r	[1:28]
Breeding probability, β	[1:3].[4:6].[7:28]
Breeding success probability, γ	[1:3].[4:6].[7:28]
Probability of fledging two chicks, δ	[1:3].[4:7].[8:28]
Recapture probability, p	
Group 1	[1→13].[14:28]
Group 2	[1→13].[14:28]

Notes: [$i : j$] indicates that age classes were grouped from age i to age j . [$i \rightarrow j$] indicates that age classes were separated between age i and age j . The two groups in recapture probability indicate the effect of heterogeneity.

temperature during spring and summer, and sea surface temperature anomalies in the wintering area (see Appendix S4 for description of covariates). Analyzing the effects of covariates on demographic parameters was restricted to the period 1988–2014 because some covariates were not available before 1988.

Different sets of covariates were tested on each age class of each demographic parameter to evaluate their influence (see Appendix S5 and Appendix S5: Table S1). For early survival of individuals during their first two years of life, we tested covariates representing natal climatic conditions (i.e., all covariates except those of spring). For survival of individuals older than two years old and other demographic parameters all the covariates were tested –except for the breeding probability where summer covariates were not tested as they represented the period after establishment of territory and copulation.

As a first step, we tested for the presence of density dependence in each demographic parameter. In a second step each covariate was tested in addition to density dependence if the effect of the latter was significant. If several covariates were selected, a third step consisted of adding them in a final model and testing their interactions.

All relationships between covariates and vital rates were fitted using a logit link function: $\text{logit}(\theta) = \alpha_0 + \alpha_1 \times x_t$, where θ is a demographic parameter of a certain age class, α_0 is an intercept parameter, α_1 is a slope parameter, and x_t is the value of the covariate at time t . For climatic covariates (sea ice concentration, air temperature, and sea surface temperature) we also fitted quadratic regressions, also using a logit link, to test for optimum type responses of vital rates. We then performed an analysis of deviance (ANODEV), which assesses the fit of a covariate model relative to that of both the constant and the time-dependent models, to test the significance of each relationship. ANODEV significance values were corrected with the Benjamini-Hochberg procedure to control for false discovery rate as the number of covariates tested was high (see

Appendix S5). To assess the relative importance of each selected covariate relative to a given demographic parameter, we calculated the partial derivatives of vital rates with respect to each selected covariate in a sensitivity analysis (see Appendix S6).

The environment-dependent age-structured population model

In order to evaluate the influence of covariates at the population level, we used a deterministic density-dependent age-structured post-breeding matrix (Caswell 2001) to project the population for a large range of values of selected covariates.

We constructed a life cycle derived from the best age-class description for each vital rate obtained from our capture–recapture analysis (see previous section and *Results*). It consisted of eight age classes: four immature classes (fledging F1, first year J2, second year J3, third year J4) and four mature classes (fourth year A5, sixth year A6, seventh year A7, eight years old or older A8⁺) (Fig. 1). The population is projected from year t to $t + 1$ using the equation $\mathbf{n}_{t+1} = \mathbf{A}[\mathbf{n}_t, \mathbf{C}_t] \mathbf{n}_t$, where \mathbf{n}_t is vector including the number of individuals in each age class and $\mathbf{A}[\mathbf{n}_t, \mathbf{C}_t]$ is the density-dependent population projection matrix at time t , which contains the demographic rates as a function of population size \mathbf{n}_t and climate and prey population size covariates \mathbf{C}_t . The population reached a single equilibrium as only the fecundity was a function of the population size using the inverse of the sigmoidal logistic function (Neubert and Caswell 2000).

Parameters in the projection matrix were survival from fledging to 2 yr old (ϕ_1), survival of individuals older than 2 yr old (ϕ_2), and the fecundity of each mature age classes. Fecundity (F_i) for each age class (i) was calculated as the product of breeding probability β_i , clutch size (probability of successful breeding γ_i multiplied by one plus the probability of successful breeding with two chicks δ_i), the survival probability during the first year ϕ_1 , and assuming a 1:1 sex ratio.

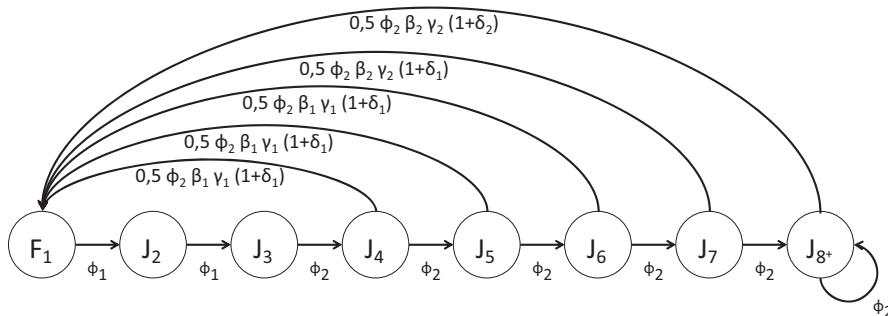


FIG. 1. Life-time cycle graph for the South Polar Skua at Pointe Géologie. The eight age classes include four immature classes (fledging J1, first year J2, second year J3, third year J4) and four mature classes (fourth year A5, sixth year A6, seventh year A7, eight years old or older A8⁺). Variables are ϕ_i , survival probability at year i ; β_i , breeding probability at year i ; γ_i , probability of successful breeding with one or two chicks at year i ; δ_i , probability of successful breeding with two chicks at year i .

Vital rates with no significant relationship with a covariate were included as their mean value. When a vital rate had a significant relationship with one or more covariates, its yearly value was projected using the functional relationship estimated on the logit scale (see *Testing for a differential impact of environmental, prey, and population size variations with age*).

We projected the total population and the number of South Polar Skuas at equilibrium for a large range of values of selected covariates. Matrix parameterization and modeling was performed in MATLAB (Matlab version 9.4.0.813654 2018 and Symbolic Math Toolbox 8.1; Appendix S7). Each population was projected with 1,000 time steps, and initial distribution of individuals in each age class was randomly sampled and multiplied by 100 to get a biologically coherent size of initial population. Ten different simulations of the initial distribution of each class were performed to ensure that the populations in each given condition reached the same equilibrium.

RESULTS

Age-specific demographic patterns and temporal trends (Prediction 1)

Recapture probability was best modeled by two classes of heterogeneity showing the same pattern with a progressive increase of recapture probability from 1 to 13 yr old followed by constant rates at 0.930 ± 0.011 and 0.296 ± 0.038 (mean \pm SE; Appendix S1: Table S2). Apparent survival was constant for ≥ 3 yr olds and averaged 0.908 ± 0.005 , and was lower for 1 and 2 yr olds (0.756 ± 0.015 ; Appendix S2: Table S1 and Table 2, Fig. 1). Two age classes best described age variation in probability to breed and to breed successfully: one

TABLE 2. Age-class-specific demographic parameter estimates and standard errors based on the selected model for South Polar Skuas in Terre Adélie from 1963 to 2014.

Parameter and age class	Mean	Standard error
ϕ		
1–2 yr old	0.756	0.016
3–28 yr old	0.910	0.005
r		
1–28 yr old	0.124	0.009
β		
4–6 yr old	0.369	0.037
7–28 yr old	0.881	0.010
γ		
4–6 yr old	0.522	0.053
7–28 yr old	0.657	0.013
δ		
4–7 yr old	0.200	0.040
8–28 yr old	0.279	0.016

Note: Parameters are defined in Table 1.

between 4 and 6 yr old where probabilities were, respectively, 0.369 ± 0.037 and 0.522 ± 0.053 , and one for individuals older than 7 yr old with, respectively, 0.881 ± 0.009 and 0.657 ± 0.013 (Appendix S2: Table S1 and Table 2). The probability to fledge two chicks was also best described by two age classes, between 4 and 7 yr old with a probability of 0.200 ± 0.040 , and after 8 yr old with a probability of 0.279 ± 0.016 (Appendix S2: Table S1 and Table 2).

Positive temporal trends were found in apparent survival of both age classes (Appendix S5: Tables S2 and S3). Apparent survival increased non-linearly in young individuals with a quadratic function (more deviance explained by the quadratic model and positive quadratic parameter estimate), and linearly for older ones (similar deviance explained by both models and quadratic parameter estimate not different from 0). For the 7–28 age class, there was a negative temporal trend in breeding probability (more deviance explained by the quadratic model) whereas a negative temporal trend in breeding success probability was linear (Appendix S5: Tables S2 and S3). No linear or quadratic temporal trend was found in covariates (see Appendix S5: Fig. S1).

Effects of population size, climate, and prey conditions (Predictions 2 and 3)

The detailed results of univariate ANODEV tests of density dependence and the covariates for each age class and for each demographic parameter can be found in the Appendix S8 (Appendix S8: Tables S1–S8). A summary with the retained models for each age class and for each demographic parameter is shown in Table 3. Estimates of selected age-specific covariate effects on demographic traits are shown in Appendix S9 (Appendix S9: Table S1).

Density dependence was found in survival of both age classes but did not remain when accounting for the temporal trend in survival and after removing the trend in the covariate. For survival probability, only the survival of 1–2 yr old individuals was influenced by natal conditions (Appendix S8: Table S1). Both linear and quadratic effects of SIC in summer on survival of 1–2 yr old individuals were selected (Appendix S8: Table S1). However, the quadratic relationship on high values of SIC poorly fitted to the survival estimates (Appendix S8: Fig. S1), probably due to the structural constraint of the quadratic equation. Therefore, we retained a linear effect of SIC in summer, which indicated that survival increased with increasing SIC (Fig. 2a). SIC in summer explained 31% of the proportion of deviance explained (relative to the constant and time-dependent models) in the survival of individuals during their first two years of life after fledging (Table 3).

Breeding probabilities of young individuals seemed to be unaffected by climate and prey covariates, and the density-dependent effect did not persist when accounting for the temporal trend and after removing the trend in

TABLE 3. Retained models testing for covariate effects on each vital rate and age class for South Polar Skuas between 1 and 28 yr old.

Vital rate and age class	Hypothesis of the retained model	Interaction	k	Dev	ANODEV	P	R^2
ϕ							
1–2 yr old	linear effect of summer sea ice concentration		38	13,621.94	10.567 _(1,24)	0.017 (0.003)	0.31
3–28 yr old	no effect						
β							
4–6 yr old	no effect						
7–28 yr old	additive linear effect of density dependence and linear effect of the number of Adélie Penguin breeding pairs	no	39	13,620.14	7.928 _(2,23)	0.019 (0.002)	0.41
γ							
4–6 yr old	additive linear effect of the number of Adélie Penguin breeding pairs and linear effect of summer sea ice concentration	no	39	13,631.32	7.525 _(2,23)	0.003 (0.003)	0.40
7–28 yr old	linear effect of the number of Adélie Penguin breeding pairs		38	13,559.44	15.846 _(1,24)	0.007 (0.001)	0.40
δ							
4–7 yr old	no effect						
8–28 yr old	no effect						

Notes: k , number of parameters estimated, Dev, deviance. ANODEV is the F statistic ($F_{(df1,df2)}$), R^2 is the proportion of deviance explained by the covariate. P is the Benjamini-Hochberg adjusted P value (with uncorrected values into brackets). Parameters are defined in Table 1.

the number of breeding pairs. However, the breeding probability of individuals >7 yr old decreased with increasing breeding population size (Fig. 2b), even in the presence of temporal trends (Appendix S8: Table S4).

In addition, when testing additively the effects of density dependence and of other covariates on the breeding probability of individuals >7 yr old, all additive models were selected but only the linear effect of the number of Adélie Penguin breeding pairs had a significant effect (the 95% confidence interval of the slope of the relationship with this covariate did not include 0; Fig. 1c).

This final model explained 41% of the proportion of deviance in the breeding probability for individuals >7 yr (Table 3). A model including an interaction between both covariates did not explain significantly any extra variance compared with the model including only the additive effects (the 95% confidence interval of the interaction parameter included 0 and the ANODEV between the model with and without the interaction parameter was nonsignificant, $F_{test}^{cst/cov+interac}/t_{(1,24)} = 0.008$, $P = 0.93$).

The breeding success probability of both age classes was strongly negatively impacted by the number of Adélie Penguin breeding pairs (Table 4; Fig. 2d, f). Individuals between 4 and 6 yr old had less chance to breed successfully when SIC during summer was high (Fig. 2e). We retained the linear effect of SIC during summer because it was selected by ANODEV in the final model over the quadratic regression and was simpler, but the linear and quadratic regression gave very

similar results. The model including an effect of the number of Adélie Penguin breeding pairs and of SIC during summer explained 40% of the proportion of deviance in breeding success in young individuals (Table 3), but no interaction between effects was found (the 95% confidence interval of the interaction parameter included 0 and the ANODEV between the model with and without the interaction parameter was nonsignificant, $F_{test}^{cst/cov+interac}/t_{(1,24)} = 1.596$, $P = 0.22$). The number of Adélie Penguin breeding pairs explained 40% of the variance in breeding success of older individuals (Appendix S8: Table S6 and Table 3).

No covariate effect was detected on the probability to raise two chicks successfully (Appendix S8: Tables S7 and S8).

The sensitivity analysis showed that survival and breeding success of young individuals were most sensitive to sea ice concentration (Table 4). Breeding success probability of young and older individuals showed a similar response to fluctuations in the number of breeding pairs of Adélie Penguins. The strength of the effects of density dependence and of the number of breeding pairs of Adélie Penguins was much smaller on the breeding probability.

Population prediction

The total number of breeding pairs of South Polar Skuas and the total number of individuals at equilibrium are shown on Fig. 4 as a function of Adélie Penguin abundance and SIC in summer. The total population at

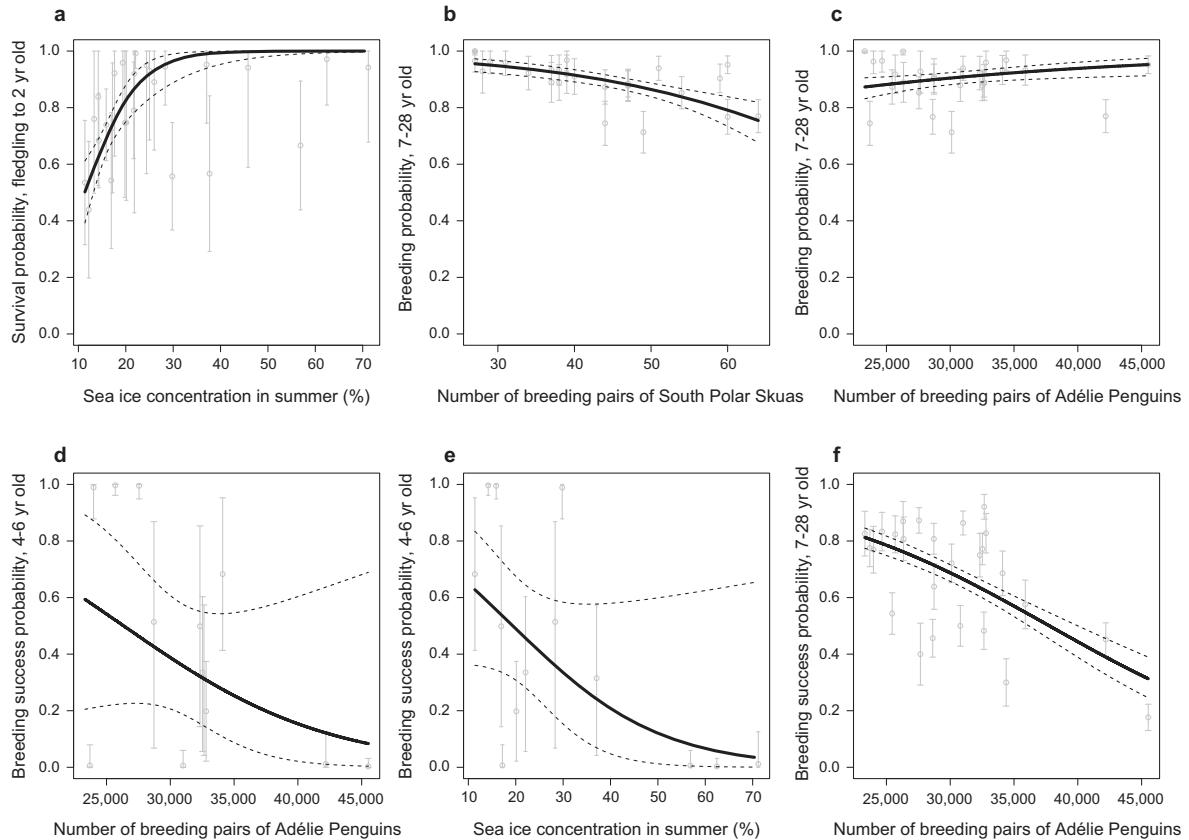


FIG. 2. Retained covariate effects on each vital rate and age class for South Polar Skuas between 1 and 28 yr old. Solid line represents the modeled relationship obtained from the covariate model. Dashed lines represent the 95% confidence interval calculated with the Delta method (Dorfman 1938, Ver Hoef 2012). Points represent time-dependent survival estimates obtained from the time-dependent model. Error bars are standard errors. (a) Survival probability of South Polar Skuas from fledging to 2 yr old as a linear function of sea ice concentration (SIC) in summer. (b) Breeding probability of South Polar Skuas older than 7 yr as a linear function of the number of breeding pairs of South Polar Skuas. (c) Breeding probability of South Polar Skuas older than 7 yr as a linear function of the number of Adélie Penguin breeding pairs. (d) Breeding success probability of South Polar Skuas from 4 to 6 yr old as a linear function of the number of Adélie Penguin breeding pairs. (e) Breeding success probability of South Polar Skuas from 4 to 6 yr as a linear function of SIC in summer. (f) Breeding success probability of South Polar Skuas older than 7 yr as a linear function of the number of Adélie Penguin breeding pairs.

equilibrium reached its optimum value on relatively low numbers of Adélie Penguin breeding pairs (20,000–30,000) and on medium values of SIC in summer (between 25 and 45%), and stayed high when SIC in summer increased. Both the breeding population (number of breeding individuals) and the total population of South Polar Skuas went extinct when SIC in summer was lower than 10% and when the number of Adélie Penguin breeding pairs was >45,000. Taking the mean SIC in summer and the mean number of Adélie Penguin breeding pairs during the last 10 yr of the study, the total population at equilibrium was at 820 individuals, including 196 breeding individuals.

DISCUSSION

Our comprehensive demographic study including the simultaneous effects of age classes, density dependence, prey, and climate indicated that all age classes

and all life history traits of an apex predator did not equally respond to the same environmental variations (Fig. 4). Our results showed an improvement of all vital rates with age. Our results highlight the greater sensitivity of reproductive traits and of younger age classes to prey abundance (Adélie Penguins), climate variability (sea ice concentration) and density dependence in a marine apex predator, with important consequences on the total population size but with limited effects on the breeding population size. The effect on the number of Adélie Penguin breeding pairs was weak on the breeding population size of South Polar Skuas, except on extreme values, and the effect of SIC in summer was in general stronger. Population size affected directly, and probably indirectly, the demography of this highly territorial predator. However, demographic parameters were overall more sensitive to climatic and prey fluctuations than to breeding population size variations.

TABLE 4. Sensitivities of the demographic parameters to the covariates for which a significant effect was detected for South Polar Skuas between 1 and 28 yr old.

Vital rate	Age class	Sensitivity to covariates		
		Density dependence	Number of Adélie Penguin breeding pairs	Summer sea ice concentration
ϕ	1–2 yr old			0.46
β	7–28 yr old	–0.05	0.02	
γ	4–6 yr old		–0.17	–0.26
γ	7–28 yr old		–0.12	

Note: Parameters are described in Table 1.

Early life vs. adult life-history traits (Prediction 1)

The South Polar Skua population in Pointe Géologie showed typical life history traits characteristic of long-lived organisms, with a high and weakly variable adult survival and a low and variable fecundity (Stearns 1992, Gaillard et al. 2000, Gaillard and Yoccoz 2003). As expected by life history theory, birds experienced a lower survival rate during their first two years of life after fledging, and a higher and more stable survival rate from age 3 onward, falling into the range of other *Stercorariidae* (Burton 1968, Wood 1971, Furness 1987, Ainley et al. 1990, Pietz and Parmelee 1994, Julien et al. 2013). Studies in mammals and birds have reported an increase in breeding performances with age attributed to lower experience, lower reproductive effort or higher proportion of lower-quality individuals in young ages (Gaillard et al. 2000, Penteriani et al. 2003, Rebke et al. 2010). We found the same pattern with young individuals being poorer reproductive performers than older ones. The breeding probability of old individuals was twice as high than for younger ones and breeding individuals older than 7 yr produced an average of 0.84 fledglings per year, against 0.63 for younger breeders, which is consistent with the other populations and closely related species (Young 1963, 1994, Spellerberg 1971a, Wood 1971, Ainley et al. 1990).

Contrary to our prediction, no decrease in demographic rates was found for old individuals. Although our main aim was not to test for senescence patterns, three hypotheses may explain this result. First, our approach to model age classes specific variations in demographic parameters was based on threshold models and further modeling using nonlinear models such as quadratic, Weibull, or Gompertz models, more suited to test for senescence (Gaillard et al. 2004, Nussey et al. 2008), would be required. Second, senescence patterns may not be detected due to the sample sizes of older age classes with an insufficient proportion of mature birds reaching the age when senescence may become important. Third, individual heterogeneity was not taken into account when modeling adult survival. Unobserved

individual heterogeneity affects the detection of senescence in wild populations because frail individuals disappear progressively as they age (Cam et al. 2002, Péron et al. 2010). Age-dependent variation in vital rates has been suggested to vary between females and males but we do not have information on sex for most individuals, so our estimates are averaged between females and males.

Age-specific impact of environmental and prey covariates (Prediction 2)

As in other seabirds (Nevoux et al. 2007, Rolland et al. 2008, Pardo et al. 2013), we found that this population were impacted by environmental factors but that these factors did not affect all fitness components in the same way (Fig. 3). The strongest environmental influence was on juvenile survival and on breeding success of young individuals. Our sensitivity analysis suggested that sea ice concentration was the strongest factor impacting vital rates of South Polar Skuas and was restricted to younger age classes (survival and breeding success). Adélie Penguin abundance mainly affected breeding success of all age classes, and to a lower extent the breeding probability of the older age class. As expected, adult survival was unaffected by environmental and prey factors.

High sea ice concentration in summer affected positively the survival of individuals during their first two years of life. South Polar Skuas feed mainly on eggs and chicks of Adélie Penguins at Pointe Géologie, which are known to be ice obligate (Croxall et al. 2002, Ainley et al. 2005, Forcada and Trathan 2009). During heavy ice years, foraging trips of breeding Adélie Penguins during the incubation and the guard phase are prolonged due to decreased prey accessibility (Spée et al. 2010, Ropert-Coudert et al. 2014). As a consequence, breeding success decreases due to (1) an increased abandonment of eggs and young chicks by the nest-attending parent if its partner spends too much time foraging at sea and (2) an increase in chick mortality due to undernourishment (Wilson et al. 2001, Emmerson and Southwell 2008, Spée et al. 2010, Ropert-Coudert et al. 2014). We therefore strongly suspect a positive influence of a food surplus during these heavy ice years on South Polar Skua yearlings' body condition, potentially improving their post-fledging survival. Remarkably, high South Polar Skua juvenile survival occurred when sea ice concentration in summer was higher than $\approx 30\%$, corresponding to the sea ice concentration threshold from which Adélie Penguin breeding success start to respond negatively in Pointe Géologie (Barbraud et al. 2015).

The number of breeding Adélie Penguins was negatively related to South Polar Skua breeding success for both age classes. This result appears counterintuitive at first, because we expected improved performance with increased food availability. Oro et al. (2014) reported in a long-lived seabird (Audouin's Gull, *Larus audouinii*) that food availability per capita shaped reproductive

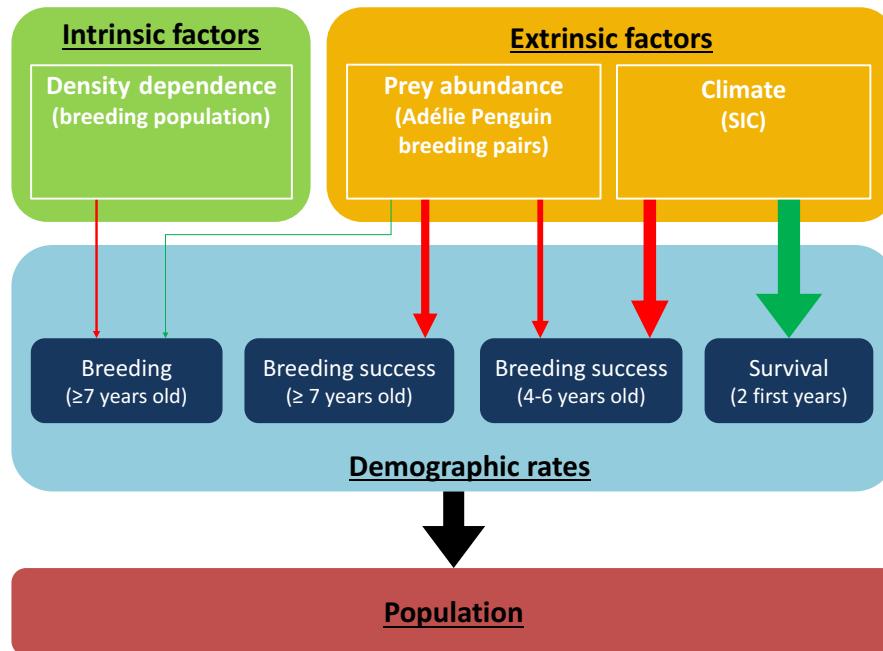


FIG. 3. Diagram summarizing the influential intrinsic (density dependence) and extrinsic (prey abundance, local climate) factors on South Polar Skua vital rates. The thickness of the arrow refers to the sensitivity of the vital rate to the factor. The color of the arrow refers to a positive effect (green) or a negative effect (red). The relationships that were not statistically significant are not shown. The thickness of the lines in the figure refers to the magnitude of the sensitivity of a covariate to a vital rate.

performance of individuals differently according to their ages (better performance for middle-aged individuals in contrast with inexperienced and senescent ones). During “poor years” when resource availability per capita is smaller, only high-quality individuals may breed due to more intense intraspecific competition, making the age pattern less marked. This is consistent with the greater sensitivity of breeding success to environmental parameters in young South Polar Skuas compared to older ones, with younger individuals probably suffering more from competition due to their inexperience. In the study of Oro et al. (2014), all breeding parameters were positively related to food availability but in our study there were opposite responses of breeding probability (positive for old individuals) and breeding success (negative for both age classes). Thus, it seemed that even a higher quantity of prey at the beginning of the breeding period could not benefit all the individuals. However, some of these breeding pairs could be less demanding on the quality of their breeding sites (e.g., nest sites more exposed to snow accumulation and runoff water from ice and snow melting, no Adélie Penguin colonies in the territories) as observed in Pointe Géologie (all authors, *personal observations*). As the breeding population increases, especially during years with high numbers of breeding Adélie Penguins, so does the proportion of low-quality individuals (inexperienced or with a lower competitive ability) relegated to poorer sites (Dhondt et al. 1992, McPeck et al. 2001, Kokko et al. 2004, Grünkorn et al. 2014). Under the habitat heterogeneity hypothesis (Dhondt et al.

1992), hence with territories varying in quality, this could result in a higher rate of failure for the population, even if reproductive success does not decrease in all territories (Sutherland 1996, Rodenhouse et al. 1997, Newton 1998, Gill et al. 2001, Casado et al. 2008).

Fig. 2e suggested that the breeding success of young individuals was null on very high values of sea ice concentration in summer (>55%). During these years, Adélie Penguin breeding failure might be such that young skuas could not complete the rearing of their chicks due to the low availability of food exacerbated by competition with older individuals. Breeding success parameters for young individuals were difficult to estimate, probably due to the low number of individuals successfully reproducing in this age class. This could have prevented us from detecting an interaction between the effects of the number of Adélie Penguin breeding pairs and the SIC in summer on the reproductive success of young breeders.

Density dependence (Prediction 3)

Two forms of density-dependent processes have been proposed in birds: regulation by intraspecific competition for (limiting) resources (Charnov et al. 1976) and site-dependent regulation through territorial behavior (direct interference) (Rodenhouse et al. 1997). Evidence for site-dependent regulation has been previously reported for several territorial bird species (e.g., Bald Eagle, *Haliaeetus leucocephalus* [Turris and Watts 2014], Brown Skua, *Catharacta lonnbergi* [Phillips et al. 2004],

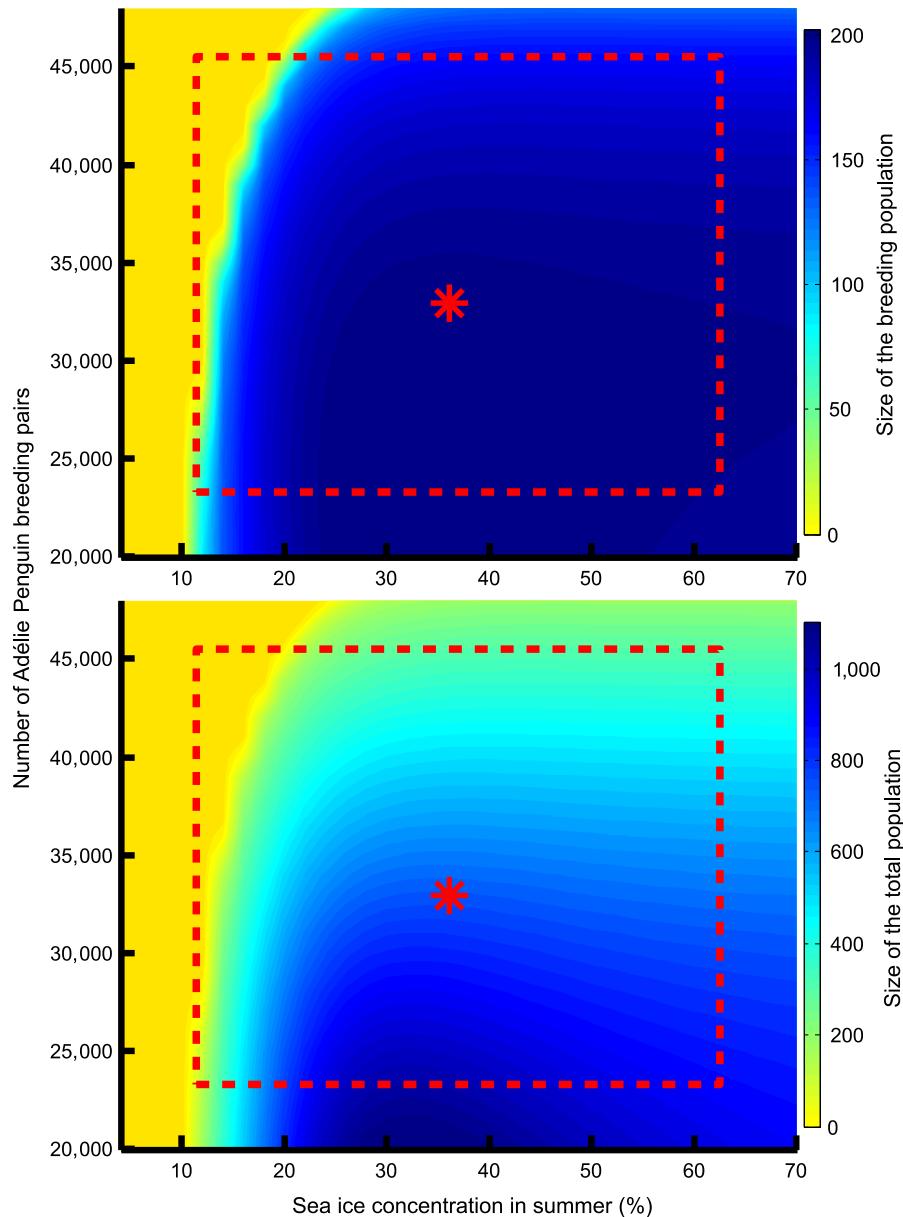


FIG. 4. Prediction of the number of breeding individuals (top) and the total population at equilibrium for different combinations of sea ice concentration in summer (in %) and number of Adélie Penguin breeding pairs. The red star represents the average environmental conditions over the last 10 yr of the study. The red rectangle represents the range of observed environmental conditions during the study period.

Common Guillemot, *Uria aalge* [Kokko et al. 2004], Great Skua, *Catharacta skua* [Furness 2015], Osprey, *Pandion haliaetus* [Bretagnolle et al. 2008]) as well as in mammals (gray wolf, *Canis lupus* [Cubaynes et al. 2014]), and reptiles (side-blotched lizard, *Uta stansburiana* [Calsbeek and Sinervo 2002]).

Skua territories include both breeding and feeding grounds (Adélie Penguin colonies) at Pointe Géologie. As predicted from previous studies at the population level (Lande et al. 2002, Pacoureaux et al. 2018), our results showed a regulation of this South Polar Skua

breeding population. It was evidenced here through a negative feedback on the breeding probability of individuals >7 yr old. The negative density dependence in breeding probability was coherent with the negative temporal trend observed for this demographic trait while the breeding population increased over the study period.

Surprisingly, we did not detect a density-dependent effect on breeding success, despite the negative temporal trend in this vital rate as observed for the breeding probability. Defending a territory against conspecifics is generally costly in terms of time and energy, potentially

limiting energy investment in reproduction, or increasing mortality risks during fights. South Polar Skuas start defend their territory just a few days after arrival on the breeding site, and do not stop until the breeding season is over (Spellerberg 1971*b*). This is this highly territorial behavior that led us to suggest the habitat heterogeneity hypothesis for South Polar Skuas in the previous section, as it is found to be the main operating system in territorial birds of prey (Fernandez et al. 1998). The alternative hypothesis is the individual adjustment (Lack 1954, Ferrer and Donazar 1996), where a decrease in breeding performance of all individuals in colonial species is explained by interference competition. We believe that it could operate in addition to the habitat heterogeneity hypothesis, but probably to a lesser degree in our study system. These two hypotheses have been suggested by Grünkorn et al. (2014) to explain negative density-dependent reproduction in a species sharing many common life history traits with birds of prey, the Raven, *Corvus corax*. Non-breeders (i.e., floaters) constitute a significant part of seabird and skua populations (Katzner et al. 2011, Penteriani et al. 2011) and could also play a significant role in competition. Our population size covariate used to model density dependence (number of breeding pairs) may not be adequate in this case, since it did not include non-breeders. Finally, although we could also have expected density-dependent mortality due to contests for breeding sites resulting in violent fights and direct mortality, those effects were not detected. The low positive temporal trend in survival rates in both juveniles and adults suggest that density dependence is unlikely to affect substantially those rates for the observed densities.

From demographic parameters to population dynamics

The matrix population model allowed modeling the combined effects of the variation in prey abundance, sea ice concentration in summer, and density dependence on population size and structure at equilibrium. The population at equilibrium was maximized with relatively low prey abundance (from 20,000 to 30,000 Adélie Penguin breeding pairs) and sea ice concentration in summer between 25% and 45%. As predicted from a time series analysis of the number of South Polar Skua breeding pairs (Pacoureaux et al. 2018), we found a strong effect of sea ice concentration on the population at equilibrium. A decrease in sea ice concentration in summer will have a considerable repercussion on the population at equilibrium if sea ice concentration falls below $\approx 15\%$. Above this threshold, sea ice concentration had little impact on the population at equilibrium. The absence of an effect of the number of breeding pairs of Adélie Penguins on population growth rate in Pacoureaux et al. (2018) seems more paradoxical. However, this seems supported by the results of the matrix population model (Fig. 4) showing that the variation in the number of Adélie Penguin

breeding pairs has a relatively small effect on the number of breeding South Polar Skuas. Prey had a positive effect on breeding probability of adults but a negative effect on breeding success probability of both adults and young. Therefore, the net effect on the population growth rate may be small and remained undetected in a time series analysis. Contrary to some of our predictions, we did not find a relationship between temperature or the number of dead chicks of Emperor Penguins and demographic rates. By contrast, we identified a new covariate (number of Adélie Penguin breeding pairs) related to demographic parameters and thus population growth rate. A potential explanation for these discrepancies between the time series analysis and the capture-mark-recapture approach is that our capture-mark-recapture analysis was based on marked chicks and ignored the immigrants that came into the Pointe Géologie population to breed. This was not the case for the time series analysis, which was based on the total number of breeding pairs, thus including local recruits and immigrants. Therefore, if immigration rate was positively related to the number of dead Emperor Penguin chicks and to temperature this could explain the decoupling of the relationship between this factor and population growth from that with vital rates (Tavecchia et al. 2016). Another (non-exclusive) hypothesis is that the temperature effect, which was weak in Pacoureaux et al. (2018), was not detected in the present study due to a lack of statistical power for early life demographic parameters.

Average environmental conditions over the last 10 yr of the study period seemed favorable for the South Polar Skua population. However, our population model and counts of breeding pairs suggest that the number of breeding individuals had not reached its full optimum yet (98 breeding pairs predicted compared with a maximum of 80 breeding pairs observed). This difference is probably due to the transient dynamic of the actual population of South Polar Skuas, which has not stabilized yet. Following Intergovernmental Panel on Climate Change (IPCC) forecasts, sea ice concentration will fall approximately 20% during the next century in the vicinity of Pointe Géologie (Jenouvrier et al. 2014). If the reduction in sea ice concentration does not exceed 50%, we do not expect a decrease in the South Polar Skua population size at Pointe Géologie. However, even if the mean decrease of sea ice concentration is above the critical value for South Polar Skuas, we can still expect severe effects on the population size of South Polar Skuas due to the increased frequency of extreme events associated to climate change (Orlowsky and Seneviratne 2012, Cai et al. 2014, Stuecker et al. 2017).

To conclude, our study brings a holistic insight of the underlying processes shaping the population dynamics by linking prey abundance, local climate, and density dependence to multiple vital rates and ultimately their interactions driving the population growth. Our results suggested the presence of inter-individual heterogeneity with differences in individual quality, calling for further

investigation about the interactions between environmental variability and individual quality.

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LITERATURE CITED

- Ainley, D. G., C. A. Ribic, and R. C. Wood. 1990. A demographic study of the South Polar Skua *Catharacta macormicki* at Cape Crozier. *Journal of Animal Ecology* 59:1.
- Ainley, D. G., E. D. Clarke, K. Arrigo, W. R. Fraser, A. Kato, K. J. Barton, and P. R. Wilson. 2005. Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. *Antarctic Science* 17:171–182.
- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19:716–723.
- Barbraud, C., K. Delord, and H. Weimerskirch. 2015. Extreme ecological response of a seabird community to unprecedented sea ice cover. *Royal Society Open Science* 2:140456.
- Barraquand, F., T. T. Høy, J.-A. Henden, M. G. Yoccoz, O. Gilg, N. M. Schmidt, B. Sittler, and R. A. Ims. 2014. Demographic responses of a site-faithful and territorial predator to its fluctuating prey: longtailed skuas and arctic lemmings. *Journal of Animal Ecology* 83:375–387.
- Berman, M., J.-M. Gaillard, and H. Weimerskirch. 2009. Contrasted patterns of age-specific reproduction in long-lived seabirds. *Proceedings of the Royal Society B* 276:375–382.
- Berryman, A. A. 1999. Principles of population dynamics and their application. Stanley Thornes, Cheltenham, UK.
- Bjørnstad, O. N., and B. T. Grenfell. 2001. Noisy clockwork: time series analysis of population fluctuations in animals. *Science* 293:638–643.
- Bretagnolle, V., F. Mougeot, and J.-C. Thibault. 2008. Density dependence in a recovering osprey population: demographic and behavioural processes. *Journal of Animal Ecology* 77:998–1007.
- Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173–1187.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Burton, R. W. 1968. Breeding biology of the brown skua, *Catharacta skua lombergi* (Mathews), at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin* 15:9–28.
- Cai, W., et al. 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change* 4:111–116.
- Calsbeek, R., and B. Sinervo. 2002. The ontogeny of territoriality during maturation. *Oecologia* 132:468–477.
- Cam, E., W. A. Link, E. G. Cooch, J.-Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. *American Naturalist* 159:96–105.
- Carlos, C. J. 2016. How many genera of Stercorariidae are there? *Brazilian Journal of Ornithology* 24:191–195.
- Carravieri, A., Y. Chereil, M. Brault-Favrou, C. Churlaud, L. Peluhet, P. Labadie, H. Budzinski, O. Chastel, and P. Bustamante. 2017. From Antarctica to the subtropics: Contrasted geographical concentrations of selenium, mercury, and persistent organic pollutants in skua chicks (*Catharacta* spp.). *Environmental Pollution* 228:464–473.
- Casado, E., S. Suárez-Seoane, J. Lamelin, and M. Ferrer. 2008. The regulation of brood reduction in Booted Eagles *Hieraaetus pennatus* through habitat heterogeneity. *Ibis* 150:788–798.
- Caswell, H. 2001. Matrix population models. Wiley Online Library, Sunderland, Massachusetts, USA.
- Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge University Press, Cambridge, UK.
- Charnov, E. L., G. H. Orians, and K. Hyatt. 1976. Ecological implications of resource depression. *American Naturalist* 110:247–259.
- Chereil, Y. 2008. Isotopic niches of emperor and Adélie penguins in Adélie Land, Antarctica. *Marine Biology* 154:813–821.
- Choquet, R., J.-D. Lebreton, O. Gimenez, A.-M. Reboulet, and R. Pradel. 2009a. U-CARE: Utilities for performing goodness of fit tests and manipulating capture–recapture data. *Ecography* 32:1071–1074.
- Choquet, R., L. Rouan, and R. Pradel. 2009b. Program E-surge: a software application for fitting multievent models. Pages 845–865 in D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer US, Boston, Massachusetts, USA.
- Clutton-Brock, T., and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution* 25:562–573.
- Coulson, T., E. A. Catchpole, S. D. Albon, B. J. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* 292:1528–1531.
- Croxall, J. P., P. N. Trathan, and E. J. Murphy. 2002. Environmental change and Antarctic seabird populations. *Science* 297:1510–1514.
- Cubaynes, S., D. R. MacNulty, D. R. Stahler, K. A. Quimby, D. W. Smith, and T. Coulson. 2014. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *Journal of Animal Ecology* 83:1344–1356.
- Curio, E. 1983. Why do young birds reproduce less well? *Ibis* 125:400–404.
- Cury, P. M., et al. 2011. Global seabird response to forage fish depletion—one-third for the birds. *Science* 334:1703–1706.
- Dawson, N. M., C. D. Macleod, M. Smith, and N. Ratcliffe. 2011. Interactions with Great Skuas *Stercorarius skua* as a factor in the long-term decline of an Arctic Skua *Stercorarius parasiticus* population. *Ibis* 153:143–153.

- Dhondt, A. A., B. Kempnaers, and F. Adriaensens. 1992. Density-dependent clutch size caused by habitat heterogeneity. *Journal of Animal Ecology* 61:643–648.
- Dorfman, R. 1938. A note on the delta-method for finding variance formulae. *Biometric Bulletin* 1:92.
- Emmerson, L., and C. Southwell. 2008. Sea ice cover and its influence on Adélie Penguin reproductive performance. *Ecology* 89:2096–2102.
- Fernandez, C., P. Azkona, and J. A. Donazar. 1998. Density-dependent effects on productivity in the Griffon Vulture *Gyps fulvus*: the role of interference and habitat heterogeneity. *Ibis* 140:64–69.
- Ferrer, M., and J. A. Donazar. 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles. *Ecology* 77:69–74.
- Forcada, J., and P. N. Trathan. 2009. Penguin responses to climate change in the Southern Ocean. *Global Change Biology* 15:1618–1630.
- Forslund, P., and T. Pärt. 1995. Age and reproduction in birds—hypotheses and tests. *Trends in Ecology & Evolution* 10:374–378.
- Frederiksen, M., M. Edwards, R. Mavor, and S. Wanless. 2007. Regional and annual variation in black-legged kittiwake breeding productivity is related to sea surface temperature. *Marine Ecology Progress Series* 350:137–143.
- Furness, R. W. 1987. The skuas. T. & A. D. Poyser, Calton, UK.
- Furness, R. W. 2015. Density dependence in seabirds: Great Skuas *Stercorarius skua* start to breed at a younger age when conditions are better. *Ringling & Migration* 30:43–50.
- Gaillard, J.-M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84:3294–3306.
- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- Gaillard, J.-M., A. Viallefont, A. Loison, and M. Festa-Bianchet. 2004. Assessing senescence patterns in populations of large mammals. *Animal Biodiversity and Conservation* 27:47–58.
- Gill, J. A., K. Norris, P. M. Potts, T. G. Gunnarsson, P. W. Atkinson, and W. J. Sutherland. 2001. The buffer effect and large-scale population regulation in migratory birds. *Nature* 412:436.
- Grange, S., F. Barnier, P. Duncan, J.-M. Gaillard, M. Valeix, H. Ncube, S. Périquet, and H. Fritz. 2015. Demography of plains zebras (*Equus quagga*) under heavy predation. *Population Ecology* 57:201–214.
- Grünkorn, T., A. Potiek, V. Looft, R. M. Jonker, N. Chakarov, and O. Krüger. 2014. Territory quality affects the relative importance of habitat heterogeneity and interference competition in a long-lived territorial songbird. *Journal of Avian Biology* 45:15–21.
- Hamilton, W. D. 1966. The moulding of senescence by natural selection. *Journal of Theoretical Biology* 12:12–45.
- Jenouvrier, S., M. Holland, J. Stroeve, M. Serreze, C. Barbraud, H. Weimerskirch, and H. Caswell. 2014. Projected continent-wide declines of the emperor penguin under climate change. *Nature Climate Change* 4:715–718.
- Jones, O. R., J.-M. Gaillard, S. Tuljapurkar, J. S. Alho, K. B. Armitage, P. H. Becker, P. Bize, J. Brommer, A. Charmantier, and M. Charpentier. 2008. Senescence rates are determined by ranking on the fast–slow life-history continuum. *Ecology Letters* 11:664–673.
- Jouventin, P., and M. Guillotin. 1979. Socio-écologie du skua Antarctique à Pointe Géologie. *Le Terre et la Vie* 33:109–127.
- Julien, J. R., G. Gauthier, R. I. G. Morrison, and J. Bêty. 2013. Survival rate of the long-tailed Jaeger at Alert, Ellesmere Island, Nunavut. *Condor* 115:543–550.
- Katzner, T. E., J. A. R. Ivy, E. A. Bragin, E. J. Milner-Gulland, and J. A. DeWoody. 2011. Conservation implications of inaccurate estimation of cryptic population size. *Animal Conservation* 14:328–332.
- Kokko, H., M. P. Harris, and S. Wanless. 2004. Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*. *Journal of Animal Ecology* 73:367–376.
- Lack, D. 1954. The natural regulation of animal numbers. The Clarendon Press, Oxford, UK.
- Lande, R., S. Engen, B.-E. Sæther, F. Filli, E. Matthysen, and H. Weimerskirch. 2002. Estimating density dependence from population time series using demographic theory and life-history data. *American Naturalist* 159:321–337.
- Le Morvan, P., J. L. Mougou, and J. Prévost. 1967. *Ecologie du skua antarctique (Stercorarius skua maccormicki) dans l'Archipel de Pointe Géologie (Terre Adélie). Expéditions Polaires Françaises*, Paris, France.
- Lebreton, J. D., and R. Pradel. 2002. Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics* 29:353–369.
- MATLAB. 2018. MATLAB version 9.4.0.813654 and symbolic math toolbox 8.1. The MathWorks, Natick, Massachusetts, USA.
- McNamara, J. M., A. I. Houston, Z. Barta, A. Scheuerlein, and L. Fromhage. 2009. Deterioration, death and the evolution of reproductive restraint in late life. *Proceedings of the Royal Society B* 276:4061–4066.
- McPeck, M. A., N. L. Rodenhouse, R. T. Holmes, and T. W. Sherry. 2001. A general model of site-dependent population regulation: population-level regulation without individual-level interactions. *Oikos* 94:417–424.
- Micol, T., and P. Jouventin. 2001. Long-term population trends in seven Antarctic seabirds at Pointe Géologie (Terre Adélie). *Polar Biology* 24:175–185.
- Monaghan, P. 2008. Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B* 363:1635–1645.
- Neubert, M. G., and H. Caswell. 2000. Density-dependent vital rates and their population dynamic consequences. *Journal of Mathematical Biology* 41:103–121.
- Nevoux, M., H. Weimerskirch, and C. Barbraud. 2007. Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. *Journal of Animal Ecology* 76:159–167.
- Newton, I. 1998. Population limitation in birds. Academic Press, London, UK.
- Nussey, D. H., T. Coulson, M. Festa-Bianchet, and J.-M. Gaillard. 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. *Functional Ecology* 22:393–406.
- Orlowsky, B., and S. I. Seneviratne. 2012. Global changes in extreme events: regional and seasonal dimension. *Climatic Change* 110:669–696.
- Oro, D., R. Torres, C. Rodríguez, and H. Drummond. 2010. Climatic influence on demographic parameters of a tropical seabird varies with age and sex. *Ecology* 91:1205–1214.
- Oro, D., N. Hernández, L. Jover, and M. Genovart. 2014. From recruitment to senescence: food shapes the age-dependent pattern of breeding performance in a long-lived bird. *Ecology* 95:446–457.
- Pacoureaux, N., M. Authier, K. Delord, and C. Barbraud. 2018. Population response of an apex Antarctic consumer to its prey and climate fluctuations. *Oecologia* 189:1–13.

- Pardo, D., C. Barbraud, M. Authier, and H. Weimerskirch. 2013. Evidence for an age-dependent influence of environmental variations on a long-lived seabird's life-history traits. *Ecology* 94:208–220.
- Penteriani, V., J. Balbontin, and M. Ferrer. 2003. Simultaneous effects of age and territory quality on fecundity in Bonelli's Eagle *Hieraetus fasciatus*. *Ibis* 145:E77–E82.
- Penteriani, V., M. Ferrer, and M. M. Delgado. 2011. Floater strategies and dynamics in birds, and their importance in conservation biology: towards an understanding of nonbreeders in avian populations: Conservation biology needs floaters. *Animal Conservation* 14:233–241.
- Péron, G., P.-A. Crochet, R. Choquet, R. Pradel, J.-D. Lebreton, and O. Gimenez. 2010. Capture–recapture models with heterogeneity to study survival senescence in the wild. *Oikos* 119:524–532.
- Phillips, R. A., B. Phalan, and I. P. Forster. 2004. Diet and long-term changes in population size and productivity of brown skuas *Catharacta antarctica lonnbergi* at Bird Island, South Georgia. *Polar Biology* 27:555–561.
- Pietz, P. J., and D. F. Parmelee. 1994. Survival, site and mate fidelity in South Polar Skuas *Catharacta maccormicki* at Anvers Island, Antarctica. *Ibis* 136:32–38.
- Pradel, R., C. M. Wintrebert, and O. Gimenez. 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multistate capture-recapture model. *Biometrics* 59:43–53.
- Procter, D. L. 1975. The problem of chick loss in the South Polar Skua *Catharacta maccormicki*. *Ibis* 117:452–459.
- Pryor, M. E. 1968. The avifauna of Haswell Island, Antarctica. Pages 57–82 in O. L. Austin Jr., editor. *Antarctic bird studies*. American Geophysical Union, Washington, D.C., USA.
- Rebke, M., T. Coulson, P. H. Becker, and J. W. Vaupel. 2010. Reproductive improvement and senescence in a long-lived bird. *Proceedings of the National Academy of Sciences USA* 107:7841–7846.
- Rodenhouse, N. L., T. W. Sherry, and R. T. Holmes. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology* 78:2025.
- Rolland, V., C. Barbraud, and H. Weimerskirch. 2008. Combined effects of fisheries and climate on a migratory long-lived marine predator: Effects of fisheries and climate on seabirds. *Journal of Applied Ecology* 45:4–13.
- Rolland, V., M. Nevoux, C. Barbraud, and H. Weimerskirch. 2009. Respective impact of climate and fisheries on the growth of an albatross population. *Ecological Applications* 19:1336–1346.
- Ropert-Coudert, Y., et al. 2014. A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events. *Ecography* 38:111–113.
- Schmidt, N. M., R. A. Ims, T. T. Høye, O. Gilg, L. H. Hansen, J. Hansen, M. Lund, E. Fuglei, M. C. Forchhammer, and B. Sittler. 2012. Response of an Arctic predator guild to collapsing lemming cycles. *Proceedings of the Royal Society B* 279:4417–4422.
- Spée, M., M. Beaulieu, A. Dervaux, O. Chastel, Y. Le Maho, and T. Raclot. 2010. Should I stay or should I go? Hormonal control of nest abandonment in a long-lived bird, the Adélie penguin. *Hormones and Behavior* 58:762–768.
- Spellerberg, I. F. 1971a. Aspects of McCormick Skua breeding biology. *Ibis* 113:357–363.
- Spellerberg, I. F. 1971b. Breeding behaviour of the McCormick Skua *Catharacta maccormicki*. *Ardea* 59:189–229.
- Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259–268.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, UK.
- Stearns, S. C., and T. J. Kawecki. 1994. Fitness sensitivity and the canalization of life-history traits. *Evolution* 48:1438.
- Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. *Science* 297:1292–1296.
- Stuecker, M. F., C. M. Bitz, and K. C. Armour. 2017. Conditions leading to the unprecedented low Antarctic sea ice extent during the 2016 austral spring season: record low 2016 Antarctic sea ice extent. *Geophysical Research Letters* 44:9008–9019.
- Sutherland, W. J. 1996. *From individual behaviour to population ecology*. Oxford University Press on Demand, Oxford, UK.
- Tavecchia, G., S. Tenan, R. Pradel, J.-M. Igual, M. Genovart, and D. Oro. 2016. Climate-driven vital rates do not always mean climate-driven population. *Global Change Biology* 22:3960–3966.
- Turrin, C., and B. D. Watts. 2014. Intraspecific intrusion at bald eagle nests. *Ardea* 102:71–78.
- Ver Hoef, J. M. 2012. Who invented the delta method? *American Statistician* 66:124–127.
- Votier, S. C., S. Bearhop, J. E. Crane, J. M. Arcos, and R. W. Furness. 2007. Seabird predation by great skuas *Stercorarius skua*—intra-specific competition for food? *Journal of Avian Biology* 38:234–246.
- Weimerskirch, H., A. Tarroux, O. Chastel, K. Delord, Y. Cherel, and S. Descamps. 2015. Population-specific wintering distributions of adult South Polar Skuas over three oceans. *Marine Ecology Progress Series* 538:229–237.
- Williams, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 1957:398–411.
- Wilson, P. R., D. G. Ainley, N. Nur, S. S. Jacobs, K. J. Barton, G. Ballard, and J. C. Comiso. 2001. Adélie penguin population change in the Pacific sector of Antarctica: relation to sea-ice extent and the Antarctic Circumpolar Current. *Marine Ecology Progress Series* 213:301–309.
- Wood, R. C. 1971. Population dynamics of breeding South Polar Skuas of unknown age. *Auk* 88:805–814.
- Young, E. C. 1963. The breeding behaviour of the South Polar Skua *Catharacta maccormicki*. *Ibis* 105:203–233.
- Young, E. C. 1972. Territory establishment and stability in McCormick's Skua. *Ibis* 114:234–244.
- Young, E. 1994. *Skua and penguin: predator and prey*. Cambridge University Press, Cambridge, UK.
- Young, E. C., and C. D. Millar. 2003. Siblicidal brood reduction in South Polar Skuas. *New Zealand Journal of Zoology* 30:79–93.
- Zabel, R. W., M. D. Scheuerell, M. M. McClure, and J. G. Williams. 2006. The interplay between climate variability and density dependence in the population viability of Chinook salmon. *Conservation Biology* 20:190–200.

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