Extreme climate events and individual heterogeneity shape life-history traits and population dynamics

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Abstract. Extreme climatic conditions and their ecological impacts are currently emerging as critical features of climate change. We studied extreme sea ice condition (ESIC) and found it impacts both life-history traits and population dynamics of an Antarctic seabird well beyond ordinary variability.

The Southern Fulmar (*Fulmarus glacialoides*) is an ice-dependent seabird, and individuals forage near the ice edge. During an extreme unfavorable year (when sea ice area is reduced and distance between ice edge and colony is high), observed foraging trips were greater in distance and duration. As a result, adults brought less food to their chicks, which fledged in the poorest body condition. During such unfavorable years, breeding success was extremely low and population growth rate (λ) was greatly reduced. The opposite pattern occurred during extreme favorable years.

Previous breeding status had a strong influence on life-history traits and population dynamics, and their responses to extreme conditions. Successful breeders had a higher chance of breeding and raising their chick successfully during the following breeding season as compared to other breeding stages, regardless of environmental conditions. Consequently, they coped better with unfavorable ESIC. The effect of change in successful breeder vital rates on λ was greater than for other stages' vital rates, except for pre-breeder recruitment probabilities, which most affected λ.

For environments characterized by ordinary sea ice conditions, interindividual differences were more likely to persist over the life of individuals and randomness in individual pathways was low, suggesting individual heterogeneity in vital rates arising from innate or acquired phenotypic traits. Additionally, unfavorable ESIC tended to exacerbate individual differences in intrinsic quality, expressed through differences in reproductive status.

We discuss the strong effects of ESIC on Southern Fulmar life-history traits in an evolutionary context. ESICs strongly affect fitness components and act as potentially important agents of natural selection of life histories related to intrinsic quality and intermittent breeding. In addition, recruitment is a highly plastic trait that, if heritable, could have a critical role in evolution of life histories. Finally, we find that changes in the frequency of extreme events may strongly impact persistence of Southern Fulmar populations.

Key words: body condition; foraging behaviors; Fulmarus glacialoides; *individual quality; individual stochasticity; life-history trade-offs; sea ice; sensitivities; Southern Fulmar; stochastic population growth; Terre Adelie, East Antarctica.*

INTRODUCTION

Climate extremes are currently emerging as one of the most important facets of climate change (Jentsch et al. 2007), and many studies have reported their impact on ecological processes at scales ranging from individuals to ecosystems (Easterling 2000, Parmesan et al. 2000). Extremity of an event depends on the historic climate record, the biological system, and whether the ecological level of interest focuses on the physiology of individuals, population, or structure of communities or ecosystems,

and several authors urge an appropriate definition of extreme events (Gutschick and BassiriRad 2003, Jentsch et al. 2007, Smith 2011). Here, an extreme climatic event (ECE) is both a rare climate event (sensu the statistical definition from the Intergovernmental Panel on Climate Change; Planton 2013) and alters the life-history traits of a species well outside the bounds of ordinary variability (Smith 2011).

Most studies have shown direct impacts of particular weather events, such as severe droughts, heavy rainfall, and heat waves, on life-history traits (Smith 2011, Jenouvrier 2013). For example, mortality and fertility are affected by extreme temperatures that cause heat stress or hypothermia in adults and offspring, while

droughts, storms, floods, and cyclones can directly kill individuals (Boersma and Rebstock 2014). However, processes through which ECEs affect populations are generally more complex, operating on physiological or behavioral traits through food-web dynamics. For example, ECEs can affect foraging opportunities for predators, further impacting their reproductive success and (or) chances of survival (Lea et al. 2009). Therefore, our goal is to understand the combined direct and indirect effects of ECEs on vital rates (i.e., life-history traits, such as survival, maturation, or breeding, which change the size and composition of a population) through a mechanistic study of individual foraging behaviors and their effects on body conditions of an Antarctic seabird.

Individuals within a population may vary in their ability to respond to these extreme events according to their phenotypes, such as sex, age, or breeding experience. Individual heterogeneity in reproduction is often described as individual quality, which reflects a property of the phenotype that is positively correlated with fitness (Wilson and Nussey 2010, Bergeron et al. 2011). For example, some high-quality individuals may be more efficient foragers, have higher rates of offspring provisioning, and have a higher chance of successfully raising offspring than low-quality individuals (Lewis et al. 2006, Lescroël et al. 2009, 2010). High-quality individuals breeding successfully in a given year may also tend to survive and reproduce with a higher probability in the following year compared to failed breeders and nonbreeders (individuals that skipped reproduction in a given year; Cam and Monnat 2000, Cam et al. 2002, 2012, Aubry et al. 2009, Cam and Aubry 2011). Such high-quality individuals often contribute the majority of recruits in subsequent generations, which in turn has important consequences for population dynamics and evolutionary processes (i.e., they tend to be the most fit; Aubry et al. 2009).

In addition, high-quality individuals are sometimes more robust to deterioration of environmental conditions, maintaining their advantage over low-quality individuals. For example, high-quality Weddell seal females produce more pups than low-quality females, even during extremely harsh conditions (Chambert et al. 2012).

Many studies suggest that individual heterogeneity is likely to be expressed most in extremely poor environmental conditions, when resources are scarce (Barbraud and Weimerskirch 2005). For another Antarctic bird, the Adélie Penguin, Lescroël et al. (2014) showed there was no difference in foraging efficiency when conditions were within standard variability, while the presence of giant icebergs revealed poor and efficient foragers in the population. In contrast, favorable ECEs may be beneficial, as abundant resources or new foraging opportunities arise and the consequent increased reproductive success (regardless of individual quality) may dampen the demographic signal of underlying individual heterogeneity.

This individual heterogeneity can be fixed (Cam and Monnat 2000) or can vary throughout the life of individuals (Bergeron et al. 2011). Fixed heterogeneity refers to permanent individual differences in vital rates that arise from an individual's phenotype that are determined at birth such as genetic makeup and developmental consequences of cohort or maternal effects (Wilson and Nussey 2010, Bergeron et al. 2011). Individual heterogeneity can vary according to factors such as age or experience gained as environmental conditions change. For example, reproductive success can increase as an individual becomes more experienced (Aubry et al. 2009), while survival can be reduced at older ages by accumulated damage induced by the environment. We investigate individual heterogeneity for a seabird in both ordinary conditions and extreme favorable and unfavorable conditions.

In addition, interindividual variation in the outcomes of life-history traits also arises from individual stochasticity (Caswell 2009, 2011, 2014; referred to as dynamic heterogeneity in Tuljapurkar et al. [2009], Orzack et al. [2010], and Steiner et al. [2010]). Individual stochasticity reflects that individual survival and reproductive success can vary throughout an individual's life by random variation only. In other words, individuals with the same life-history traits can take various pathways through the life cycle, resulting in variability in the individual's life-history outcomes, such as living or dying (Caswell 2011, 2014). Thus, even a high-quality, robust individual can encounter an unfortunate fate of dying young by chance only. Quantifying individual stochasticity is important to assess if observed differences in fitness components may likely be evolutionarily neutral (Steiner and Tuljapurkar 2012), and we analyze such individual stochasticity to compare its relative magnitude between ordinary conditions and extreme favorable and unfavorable conditions.

To study how ECEs affect all the life-history traits of a seabird life cycle while accounting for heterogeneity in individual quality, we use a stage-structured demographic model. We include four breeding stages: prebreeders, nonbreeders, failed breeders, and successful breeders (Cam and Monnat 2000, Hunter and Caswell 2009). Whether or not the differences among individuals are acquired by experience or fixed at birth, we expect high-quality individuals to survive better, to have a higher probability of breeding and raising their chick successfully, and hence to be more likely to remain in the successful stage. In addition, they should cope better than failed and nonbreeders with environmental variation and have consequently higher vital rates. Therefore, we expect the vital rates of successful breeders to have the greatest influence on the overall population growth rate.

In addition, we expect (1) individual heterogeneity in quality to be more pronounced during harsh extreme

conditions and lowest during extremely favorable conditions, and (2) the diversity of life pathways to be lower for extreme rather than ordinary conditions. Most birds, regardless of their quality, will reproduce and survive during favorable ECEs, while only the high-quality individuals may be able to reproduce without jeopardizing their subsequent survival and future opportunity to reproduce when conditions are poor. Thus, under harsh ECEs, we expect a reduction in the randomness of individuals' trajectories (i.e., individual stochasticity).

Finally, we project the impact of change in the frequency of ECEs on population dynamics. The frequency of ECEs is increasing in many regions as part of global climate change and will likely continue to increase in the future (Stocker et al. 2013). Although there is a pressing need to understand and predict the ecological impacts of increased frequency of ECEs (Easterling 2000, Parmesan et al. 2000), few studies have integrated the impact of ECEs in a population model to predict the effect of ECE frequency on population dynamics (Jenouvrier 2013).

The most powerful way to infer and predict the consequences of climate variations on vital rates and population dynamics, especially ECE impacts, is to use long-term data sets (Jenouvrier 2013). Our study is based on exceptional long-term individual-based data of an Antarctic seabird: the Southern Fulmar (*Fulmarus glacialoides*). The Antarctic climate is highly variable, and like most Antarctic species, Southern Fulmars are dependent on sea ice dynamics to access marine resources during the breeding season (Ainley et al. 1992, Woehler et al. 2010). Individual heterogeneity may arise from differences in individuals' capacity to cope with this variable environment.

This study includes a longitudinal individual-based demographic data set of ∼50 years and a detailed study on foraging behaviors and body conditions during two years of extreme and contrasting sea ice conditions for a colony in Terre Adélie, East Antarctica. Although the data of the two-year study were limited, they shed light on the possible mechanisms that may drive individual heterogeneity and population dynamics in extreme contrasting environmental conditions over a long-term study. The climatic index derived from this two-year study was estimated over 31 years (1979–2010) using satellite records of sea ice conditions and years of ESIC were identified over the entire satellite study period. The combination of demographic, foraging, and climate data provided a powerful framework to understand and predict the ecological impacts of increased frequency of ECEs on wild animal populations.

METHODS

In this study, we explore the effect of extreme events on foraging distribution, body condition, vital rates, individual differences in reproductive stage, and ultimately the population growth of the Southern Fulmar using a variety of statistical and mathematical models. We begin by describing our focal species and population and by assessing extreme sea ice condition (ESIC). Then we use a detailed 2-yr study of body condition and foraging tracking to analyze foraging grounds and behaviors using a state-space statistical model (during two years of extreme and opposite sea ice condition). Next, we construct and parametrize a life cycle, including differences among individuals in their breeding stage to estimate their vital rates and responses to extreme events using statistical capture–recapture models and a long-term longitudinal data set of ∼50 yr. Subsequently, using properties of Markov chain models, we assess if individuals tend to be persistently successful, unsuccessful, or skip breeding, as well as the amount of individual stochasticity in environments characterized by extreme or ordinary conditions. To complement this, we construct a matrix population model and perform a deterministic analysis of the population in constant environments characterized by extreme or ordinary conditions to understand how extreme events shape population structure. Specifically, we perform a perturbation analysis to explore the functional dependence of the population growth on the vital rates for different stages of individuals (pre-breeder, successful or unsuccessful breeder, or nonbreeder). Finally, we construct a stochastic population model that accounts for variation in sea ice conditions to study the impact of the frequency of ESIC in a study site.

Species and study site

The Southern Fulmar is a seabird species which breeds in the Southern Hemisphere along the mainland coast of Antarctica or on nearby islands. They are strongly associated with the pack ice environment and are thus included in the ice-associated seabird assemblage defined by Ainley et al. (1992). Specifically, they are associated with the southernmost assemblage of the Southern Ocean closely linked to the Antarctic continental shelf and sea ice edge (Woehler et al. 2010). They feed mainly on krill (*Euphausia superba*) and other crustaceans, as well as on small fish (*Pleuragramma antarctica*) and squid (Ridoux and Offredo 1989).

Southern Fulmars arrive to the colony in October and breed during the summer on cliffs in ice-free areas (Appendix A: Fig. A1a). They lay one egg on a ledge or crevice between November and early December. Both parents incubate the egg for ∼45 d and take turns making foraging trips to the ocean to feed their chicks until fledging in March. Adults and chicks leave the colony at the end of the breeding season in March and migrate to subantarctic and subtropical waters.

Our study colony is located on Ile des Pétrels, Pointe Géologie Archipelago (66°40′ S, 140°01′ E), Dumont D'Urville, Terre Adélie, Antarctica. The average number of breeding pairs in this colony was 34 ± 12 (mean ± SD) from 1964 to 2011 (updated from Jenouvrier et al. 2003). Both vital rates and population size are influenced

by environmental variation, especially sea ice concentrations (SIC; Jenouvrier et al. 2003).

Sea ice data

Observed SIC data from 1979 to 2010 were obtained from passive microwave satellite imagery provided by the National Snow and Ice Data Center (NSIDC), processed by the SMMR/SSMI NASA Team sea ice algorithm (Cavalieri et al. 1996; data *available online*).[5] The SIC data are gridded with a cell resolution of 25×25 km and projected according to NSIDC's Southern Hemisphere polar stereographic projection. SIC grids were rasterized and transformed into a geographic coordinate system (WGS84) using the raster package in R (Hijmans 2014). Spatial resolution was set at 0.05° for data visualization and contour calculations.

We calculated the sea ice area as the percentage of sea ice cover (sea ice cover is defined as SIC >15%) within a defined area (60–70° S, 142–155° E) during January for each year between 1979 and 2010 (bounding box in Appendix A: Fig. A2). This area encompasses the fulmar foraging range (Fig. 1) and sea ice conditions that are likely to influence prey availability for fulmars breeding at Dumont D'Urville. We also calculate the distance from the colony to the closest point on the sea ice edge within the specified area (Appendix A: Fig. A2). The widely used threshold in ice concentration of 15% has been used to define ice edge (Massom et al. 2009). Shortest distances between two geographical locations are calculated following the shortest great circle route.

ECEs are rare and according to the IPCC, "an extreme weather event would normally be as rare as or rarer than the 10th or 90th percentile" (Planton 2013). Therefore, we define extreme climatic years as years with sea ice conditions lower or higher than the 10th and 90th percentile, respectively. Our index of sea ice condition was a combination of the area of the sea ice cover and location of the sea ice edge, because both parameters are likely to influence fulmar foraging success through the availability of their prey (*Results*).

Foraging data and analysis

The adult fulmar foraging trips were tracked during the breeding season over two successive years. Thirteen birds were equipped with Argos satellite Platform Transmitter Terminals (PTT 100; Microwave Telemetry, Columbia, Maryland, USA) weighing 20 or 30 g, which corresponded to 2.5–3.5% of the bird body mass (mean 846.5 ± 42 g). PTTs were attached directly to the back feathers using white Tesa tape (Tesa, Hamburg, Germany) and Loctite glue (Loctite, Westlake, Ohio, USA). Three trips were recorded between 1 and 26 January 2000 and 11 trips were recorded between 19 December 2000 and 3 February 2001. Given the large variations in sea ice extent between months during the austral summer, we compared fulmars' foraging trips

performed in January between the two years of tracking (2000 and 2001; Fig. 1).

We filtered the foraging tracks and inferred foraging behavior (traveling or foraging) using state-space models (Jonsen et al. 2005). First, we filtered the Argos locations using a maximum mean velocity of 15 m/s (Freitas et al. 2008) to discard erroneous locations (35% of all raw locations). Next, we fitted a statistical state-space model to each individual track to estimate the sequence of behavioral states from tracking data while accounting for measurement errors in locations. The model includes two behavioral states: (1) traveling or (2) foraging.

We used a Bayesian statistical framework, as described in Jonsen et al. (2005) to estimate behavioral modes from probability distributions of movement parameters (speed and turning angle) and transition matrix. The process model describing animal movement is a two-state switching model, named first difference correlated random walk switching model (DCRWS; Jonsen et al. 2005). We hypothesized two hidden behavioral modes: foraging (large turning angle variance, small step length), and traveling (small turning angle variance, large step length). The model was fitted to each individual bird with a 1-h time step. Analyses were performed using R (R Core Team 2014) and JAGS using the bsam 0.42 package (Jonsen et al. 2005). Relatively flat, uninformative prior probability distributions were used for all model parameters. A total of 80 000 Markov chain Monte Carlo (MCMC) iterations were recovered from two chains (40 000 iterations per chain). The first 30 000 iterations of each chain were discarded as burn-in, while one in every 10th value of the remaining 10 000 iterations was retained to reduce autocorrelation. We thus retained 20 000 MCMC iterations to compute posterior probability distributions for each model parameter. We checked convergence of the error parameter estimates using the potential scale reduction factor, $\hat{R}$. Values close to one were consistent with convergence (Gelman and Rubinpla 1992) and $\hat{R} <$ 1.01 for all of our parameter estimates.

Body condition data and analysis

Adults and chicks were weighed regularly in 2000 and 2001, and the body condition of chicks was measured at fledging in late February. Twenty-two adults were weighed each year, while 15 chicks were weighed in 2000 and six chicks in 2001. Finally, standard morphologic measurements of eight chicks in 2000 and nine chicks in 2001 were recorded at fledging (length of wing, tarsus, and culmen, beak width, mass).

We estimated fledging body condition using the relationship between body mass and a measure of length *L*. Because the four length measures (including beak width) were correlated, we applied a principal component analysis (PCA) to reduce our set of correlated variables into a set of linearly uncorrelated variables called principal components (PC). The first PC account-
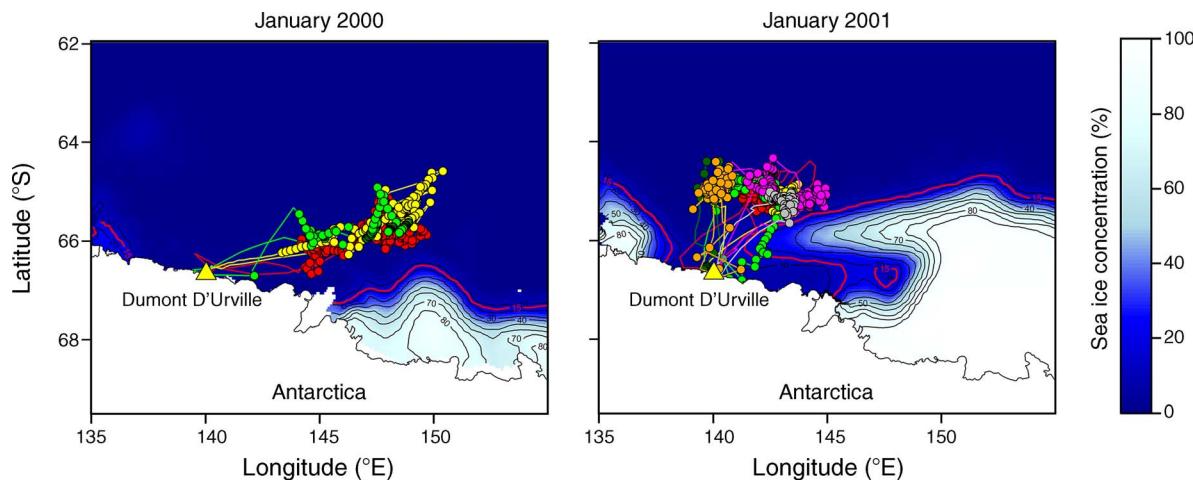
[5] http://nsidc.org/data

FIG. 1. Foraging trips of adult Southern Fulmars (*Fulmarus glacialoides*) over two years of contrasting sea ice conditions in Terre Adélie, Antarctica. The ice edge is defined as the 15% sea ice concentration (SIC) contour (shown in red); open water is dark blue, and 100% SIC is light blue; trips are shown as lines with points. Points correspond to locations where fulmars are more likely to be foraging than traveling according to state-space models (traveling is represented by a line). SIC data were obtained from the National Snow and Ice Data Center, Boulder, Colorado, USA.

ed for ~60% of the variance explained by the four measurements and represented a weighted average of the measurements: $L = 0.51W + 0.50T + 0.51C + 0.48B$, where L is the first PC, W is wing length, T is tarsus length, C is culmen length, and B is beak width. We then calculated the residual body condition index, r_i, as the residuals from a least-squares regression of mass against length L.

To calculate the chick and adult mass gain between each foraging trip, we used the adult presence/absence data at the nest recorded by radio antenna. Radio antenna were placed on the breeding ground near ~10 nests to record the arrival and departure of adults, which were fitted with VHF transmitters.

To estimate the chick mass gain, m, chick mass before the arrival of a parent (m_0) was subtracted from the maximum chick mass when a parent was on the nest (m_1): $m_i = m_{1i} - m_{0i}$ for each chick i. Finally, we expressed m as annual anomaly (a) relative to the mean as $m_{ai} = (m_i - \bar{m})/\bar{m}$ where $\bar{m}$ was the average chick mass gain (91 g) for the two seasons.

To calculate the adult mass gain between each foraging trip, M, we compared adult mass change occurring between a departure M_1 and the next arrival at the nest M_2: $M_j = M_{2j} - M_{1j}$ for each adult j. Again, we calculated the anomaly relative to the mean as $M_{aj} = (M_j - \bar{M})/\bar{M}$ where $\bar{M}$ was the average adult mass gain (98 g) for the two seasons.

Life cycle and demographic model

To analyze the effect of extreme events on the vital rates and population of the Southern Fulmar, we use a periodic life cycle that divides the year into a series of phases (Caswell 2001: chapter 13). The annual life cycle is broken into four stages, which are defined at the end of the breeding season t (one breeding season per year;

Appendix A: Fig. A1b): (1) pre-breeders have yet to breed for the first time and include fledged chicks from season t, (2) successful breeders have successfully raised a chick during season t, (3) failed breeders have not successfully raised a chick during season t because they failed to either hatch an egg or raise a chick, and (4) nonbreeders have bred at least once in their previous breeding attempts, but not in season t.

The annual life cycle starts at the end of the breeding season (fledging) in March of year t (Appendix A: Fig. A1b). This life cycle is separated into four phases to construct a periodic life cycle (Appendix: Fig. A1c): (1) fulmars survive from the end of the breeding season at year t to the next at $t+1$ with probability $\sigma_{s,t}$, where s corresponds to the life-cycle stage; (2) during the breeding season $t+1$, they return to the colony and breed with the breeding probability $\beta_{s,t+1}$, given they survive; (3) during the breeding season $t+1$, they successfully raise a chick with probability $\gamma_{s,t+1}$, given they both survive and breed; (4) the newly produced offspring survive to the end of breeding season $t+1$ and fledge. The first three phases describe the transitions of individuals already present in the population, while phase 4 represents the production of new individuals.

Each phase i is defined by a matrix $\mathbf{M}_i$. The numbering of the nodes on each line of Appendix A: Fig. A1 corresponds to the rows and columns of $\mathbf{M}_i$. Note that while the vital rates may vary with stage, s, and time, t, we include only the stage subscript in the following matrices for clarity. $\mathbf{M}_1$ models the mortality process, $\mathbf{M}_2$ models returning to the breeding site and laying an egg, $\mathbf{M}_3$ models raising successfully a chick, and $\mathbf{M}_4$ models the fledging process.

In the first phase, starting at the end of the breeding season, in March, individuals are classified into the basic four stages. The matrix $\mathbf{M}_1$ controls how many

individuals in each stage survive the entire annual life cycle

$$\mathbf{M}_1 = \begin{pmatrix} \sigma_1 & 0 & 0 & 0 \\ 0 & \sigma_2 & 0 & 0 \\ 0 & 0 & \sigma_3 & 0 \\ 0 & 0 & 0 & \sigma_4 \end{pmatrix}. \quad (1)$$

At the beginning of the second phase, the survivors in all four stages are present in the population. During this phase, individuals may breed at the colony in October (β_s) or may stay at sea ($1 - \beta_s$). Two additional stages are added (rows five and six) to track individuals that had previously bred and did not this year and pre-breeders that did not breed this year, creating $\mathbf{M}_2$

$$\mathbf{M}_2 = \begin{pmatrix} \beta_1 & 0 & 0 & 0 \\ 0 & \beta_2 & 0 & 0 \\ 0 & 0 & \beta_3 & 0 \\ 0 & 0 & 0 & \beta_4 \\ 0 & 1 - \beta_2 & 1 - \beta_3 & 1 - \beta_4 \\ 1 - \beta_1 & 0 & 0 & 0 \end{pmatrix}. \quad (2)$$

At the beginning of the third phase, these six stages are present in the population. During this phase, individuals in stage s may (γ_s) or may not ($1 - \gamma_s$) successfully raise a chick through fledging. At the end of this phase, the individuals who skipped breeding are reincorporated into either the pre-breeder or nonbreeder stages (first and last rows, respectively, of $\mathbf{M}_3$)

$$\mathbf{M}_3 = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 1 \\ \gamma_1 & \gamma_2 & \gamma_3 & \gamma_4 & 0 & 0 \\ 1 - \gamma_1 & 1 - \gamma_2 & 1 - \gamma_3 & 1 - \gamma_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \end{pmatrix}. \quad (3)$$

At the beginning of the fourth phase, individuals are again classified into the four breeding stages, in $\mathbf{M}_4$. During this phase, chicks fledge and transition to pre-breeders with a probability given by the sex ratio ρ (which is fixed to 0.5), and thus the model projects only females. At the end of this phase, the cycle is back to phase 1 (for the next year)

$$\mathbf{M}_4 = \begin{pmatrix} 1 & \rho & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}. \quad (4)$$

Each matrix $\mathbf{M}_i$ projects the population from phase i to phase $i + 1$. The annual dynamics are given by the periodic product of the $\mathbf{M}_i$ (Eqs. 1–4)

$$\mathbf{n}(t + 1) = \mathbf{M}_4 \mathbf{M}_3 \mathbf{M}_2 \mathbf{M}_1 \mathbf{n}(t) = \mathbf{A}\,\mathbf{n}(t). \quad (5)$$

Thus, we obtain an annual projection matrix

$$\mathbf{A} = \begin{pmatrix} \sigma_1\beta_1\gamma_1\rho + (1 - \beta_1)\sigma_1 & \sigma_2\beta_2\gamma_2\rho & \sigma_3\beta_3\gamma_3\rho & \sigma_4\beta_4\gamma_4\rho \\ \sigma_1\beta_1\gamma_1 & \sigma_2\beta_2\gamma_2 & \sigma_3\beta_3\gamma_3 & \sigma_4\beta_4\gamma_4 \\ \sigma_1\beta_1(1 - \gamma_1) & \sigma_2\beta_2(1 - \gamma_2) & \sigma_3\beta_3(1 - \gamma_3) & \sigma_4\beta_4(1 - \gamma_4) \\ 0 & \sigma_2(1 - \beta_2) & \sigma_3(1 - \beta_3) & \sigma_4(1 - \beta_4) \end{pmatrix}. \quad (6)$$

Demographic data and estimation of the vital rates

Long-term demographic monitoring of Southern Fulmars has been conducted since 1963 (October 1963/February 1964, hereafter 1964) at Ile des Pétrels, Terre Adélie. Since then, every austral summer, newly fledged chicks have been marked on the leg with a stainless steel band, and the ring number of all adults present at the colony has been recorded along with their breeding status (breeders or nonbreeders during the first half of the incubation period, success or failure on egg or chicks). The capture–recapture data set consists of $n = 1165$ known-age individuals from 1964 to 2010.

We leveraged this demographic data to estimate vital rates in the matrices $\mathbf{M}_1$, $\mathbf{M}_2$, and $\mathbf{M}_3$. We used multistage capture–recapture methods (Fujiwara and Caswell 2002, Lebreton and Pradel 2002, Lebreton et al. 2009), which provide maximum likelihood estimates and incorporate the detection probability in the estimation of vital rates. We selected a set of models according to parsimonious criteria (Akaike information criterion [AIC] corrected for small sample size [AIC$_c$]) and used model averaging to compute the vital rate estimates and their associated errors (Burnham and Anderson 2002).

Analyses were conducted in the E-surge software (Choquet et al. 2009); see *Data Availability* for the code.

For our life cycle, identifiability of parameters that vary differently according to time and breeding stages requires parameters be constrained to be equal at $t = 1$ and $t = 2$ (i.e., 1964 = 1965), and at $t = N - 2$ and $t = N - 1$ (i.e., 2009 = 2010), with N the total number of occasions (here $N = 47$; Hunter and Caswell 2009). Because Southern Fulmars come back to the colony for the first time at 8 ± 3 yr of age (mean $\pm$ SD; Jenouvrier et al. 2003), the detection probabilities of pre-breeders from 1965 to 1970 were set at zero to account for the progressive recruitment of chicks marked at the start of the study (Jenouvrier et al. 2008*a*). We examined the effect of ECEs by using covariates which define extremely poor years (ECE$_t = -1$), extremely good years (ECE$_t = 1$), and ordinary years (ECE$_t = 0$) on all vital rates. We expect that ESICs during chick rearing (January) at year ECE$_t$ may have a direct effect on breeding success at year t. Seabirds may also skip breeding during breeding season t as a consequence of ECE$_t$, if they are able to rely on proximal cues on the quality of their sea ice habitat and anticipate a high likelihood of poor foraging and reproductive success

that year. In that case, to preserve their own survival, they may skip reproduction (Devney et al. 2009). ECE_t may also have indirect and lagged effects on breeder survival and breeding probabilities from year t to $t + 1$ if reproductive costs during ECE_t influence subsequent survival and breeding. Reproductive costs may be expressed only in extremely poor environmental years, when resources are scarce (Stearns 1992), and thus we test the effect of negative ECE_t by defining a covariate with extremely poor years ($ECE_t = -1$), while extremely good years and ordinary years were pooled together ($ECE_t = 0$).

Measuring individual heterogeneity and stochasticity

To characterize individual stochasticity (variation in life-history outcome within an individual's life; dying or living, breeding or not breeding) and heterogeneity (variation in traits among individuals) in environments characterized by ordinary or extreme conditions, we calculated the amount of individual stochasticity and the persistence of reproductive stages during the life of an individual (Tuljapurkar et al. 2009). To account for survival differences between individuals, we applied the calculation described in Steiner et al. (2010) using an approach developed by Matthews (1970).

We calculated the randomness in breeding stage transitions (i.e., entropy) as a measure of individual stochasticity. We then measured how consistently individuals tend to remain in reproductive stages (i.e., persistence of reproductive stage) as a measure of individual heterogeneity.

If a few fixed reproductive trajectories, caused by fixed individual heterogeneity, exist in any given species, a low entropy (low diversity of reproductive trajectories) and high persistence of reproductive stages is expected (Tuljapurkar et al. 2009). However, Tuljapurkar et al. (2009) point out that there is no necessary association between entropy and persistence. We did these calculations for the three environments of interest separately: extreme (low and high) and ordinary sea ice conditions. Thus, this approach does not account for the fact that an individual may experience a stochastic environmental sequence of extreme low, ordinary, and extreme high sea ice conditions but instead isolates individual stochasticity within a given environment.

We calculated the amount of individual stochasticity as the entropy, H, of the absorbing Markov Chain matrix $\mathbf{R}$ (Matthews 1970, Steiner et al. 2010). $\mathbf{R}$ is calculated from the transition matrix 3×3 of adults already present in the population

$$\mathbf{\Psi} = \begin{pmatrix} \sigma_2\beta_2\gamma_2 & \sigma_2\beta_2(1-\gamma_2) & \sigma_2(1-\beta_2) \\ \sigma_3\beta_3\gamma_3 & \sigma_3\beta_3(1-\gamma_3) & \sigma_3(1-\beta_3) \\ \sigma_4\beta_4\gamma_4 & \sigma_4\beta_4(1-\gamma_4) & \sigma_4(1-\beta_4) \end{pmatrix} \quad (7)$$

and

$$\mathbf{R} = \frac{1}{\iota_1}\mathbf{W}^{-1}\mathbf{\Psi}\mathbf{W}. \quad (8)$$

Here, ι_1 is the dominant eigenvalue of $\mathbf{\Psi}$ and $\mathbf{W}$ is a diagonal $K \times K$ matrix with $K = 3$, and the vector $\mathbf{w}$ in its diagonal. Vectors $\mathbf{w}$ and $\mathbf{v}$ are the normalized dominant right and left eigenvectors, respectively; $\mathbf{v}^\top\mathbf{w} = 1$, and $\mathbf{v}^\top\mathbf{e} = 1$, with $\mathbf{e}$ a vector of ones of size $K = 3$.

Entropy measures the rate at which the diversity of trajectories increases with their length and is calculated as

$$H = -\sum_{i=1}^{K}\sum_{j=1}^{K}\pi_i R_{ij}\log R_{ij} \quad (9)$$

with $\pi = \mathbf{v}^\top\mathbf{W}$. Entropy is scaled relative to its maximum value as $H_{max} = \log K$.

The persistence is given by the subdominant eigenvalue of $\mathbf{R}$, λ_2, and we calculated the correlation between an individual current reproductive stage and its stage two years later as

$$\omega = \exp(-2/\tau) \quad (10)$$

with the characteristic time $\tau = -1/\log|\lambda_2|$.

Deterministic demographic analysis of the effect of ESIC

We then move to study the implications of extreme events on the overall population growth rate (λ). We began by calculating λ_t for each year t from 1979 to 2009; λ_t is the largest real eigenvalue of the population matrix $\mathbf{A}_t$ (Eq. 6).

As a comparison, we performed a deterministic analysis wherein we subjected our modeled fulmar population to constant (1) extreme high (i.e., favorable), (2) extreme low (i.e., unfavorable), and (3) ordinary conditions. We used the mean matrices $\mathbf{A}_{EXH}$, $\mathbf{A}_{EXL}$, and $\mathbf{A}_{ORD}$, which contain the averaged vital rates for the extreme high, extreme low, and ordinary years, respectively. The long-term deterministic λ's are λ_{EXH}, λ_{EXL}, and λ_{ORD}. Stable stage distributions, as well as the perturbation analysis of λ to vital rates, are calculated separately using eigenvalues and eigenvectors of the population matrices $\mathbf{A}_{EXH}$, $\mathbf{A}_{EXL}$, and $\mathbf{A}_{ORD}$ (Caswell 2001).

For the perturbation analysis, we calculated the sensitivities and log-scaled sensitivities (elasticities) following Caswell (2001). Elasticity is a popular analysis to compare the effect of changes in vital rates that are measured on different scales (Caswell 2000). While sensitivities measure the effects of absolute, or unit, changes in a vital rate on deterministic population growth rates, elasticities measure the proportional effect on population growth of a proportional change in a vital rate.

Stochastic demographic analysis of the effect of ESIC

Finally, because individuals may experience a stochastic environmental sequence of extreme and ordinary conditions, we examined the effect of the frequencies of high and low ESICs on λ_S (stochastic population growth rate). To do so, we included environmental stochasticity

TABLE 1. Consequences of sea ice condition on foraging trips, mass gain, and body condition of Southern Fulmars (*Fulmarus glacialoides*).

Variable	Breeding season	
	2000	2001
Sea ice area (km^2)	45 785	125 645
Maximum distance to foraging zone (January; km)	458.6 ± 60	264.5 ± 30
Trip duration (January; d)	6.3 ± 2.2	4.6 ± 1.8
Mean speed (January; km/h)	16.5 ± 1.0	15 ± 6.5
Anomalies of chick mass gain between each trip (g)	−24 ± 42	1 ± 50
Fledging body conditions index (g/mm)	−81 ± 110	72 ± 90
Anomalies of adult mass gain between each trip (g)	4 ± 64	−5 ± 126

Notes: All variables (excepting sea ice area) are shown ±SD. The year 2000 was an extremely unfavorable season (far ice) whereas 2001 was an extremely favorable season (close ice). Anomalies are shown relative to mean chick mass gain (91 g) or mean adult mass gain (98 g).

and the impact of ECEs in our demographic model using three environmental states: extreme high, extreme low, and ordinary. Each environmental state is associated with a set of population matrices based on the occurrence of ECEs: $\mathbf{A}_{EXH} = [\mathbf{A}_1, \cdots \mathbf{A}_{kh}]$, with kh the number of extreme high climate years, $\mathbf{A}_{EXL} = [\mathbf{A}_1, \cdots \mathbf{A}_{kl}]$, with kl the number of extreme low climate years, and $\mathbf{A}_{ORD}$ includes all other years, specifically the non-extreme and extreme demographic years that are not related to ESICs.

At each time step, a matrix was selected randomly within a specific set of matrices according to the frequency of ECEs, low w_l, and high w_h. According to the frequency of the three environmental states [w_l, w_h, 1 − w_l − w_h] and a population vector $\mathbf{n}_0$, we calculated λ_S by projecting the population according to equation

$$\log(\lambda_S) = \lim_{T \to \infty} \frac{1}{T} \log \|\mathbf{A}_{T-1} \cdots \mathbf{A}_0 \mathbf{n}(0)\|. \quad (11)$$

We evaluated λ_S numerically projecting the population over $T = 20\,000$ time steps.

RESULTS

Foraging movements and body condition during two years of extreme and contrasted sea ice conditions

Satellite tracking and state-space modeling revealed that adult fulmars from Terre Adélie foraged near the ice edge while rearing their chicks (Fig. 1). Interestingly, all birds went east of the colony during both years and individuals tracked during the same year had very similar foraging ranges and trip durations (Fig. 1). In contrast, the interannual foraging range varied greatly between 2000 and 2001 (459 km and 264 km, respectively; Table 1) and fulmar foraging trips were 2 d longer in 2000 compared to 2001 (6.3 d vs. 4.6 d; Table 1). Movement parameters of the DCRWS indicated that traveling and foraging speeds were higher in the year of far-ice condition (Appendix B: Table B1). As expected, turning angles were more variable for the behavioral state corresponding to foraging, corresponding to typical areas restricted search (ARS) in profitable food patches. The persistence of movement (probability of remaining in the same behavioral state from one time

step to the next) was high in both years ($\kappa_1 = 0.4$ in 2000 and $\kappa_1 = 0.62$ in 2001). However, the higher persistence of movement in 2001 may be indicative of better foraging conditions since birds remained longer in profitable food patches (displaying ARS) without traveling between patches (lower probability of switching from foraging to traveling or inversely).

Fig. 1 shows that the increase in fulmars' foraging range and trip duration in 2000 was associated with poor sea ice conditions, with a low sea ice cover and a higher distance between the colony and the nearest sea ice edge. During the breeding season in 2000, the sea ice area was reduced and fulmars had to travel 200 km farther east to reach profitable foraging grounds compared to 2001 (Fig. 1, Table 1).

These foraging constraints during 2000 resulted in poor body conditions for chicks (compared to 2001) but not for adults (Table 1). Adult mass gain between foraging trips did not differ between the two years. In addition, there was high interindividual variability in both chick and adult mass gain during both years; however, the variability was greater in 2001. Remote-sensing data of SIC reveals that high interannual variability was observed in summer sea ice conditions around the study area from 1979 to 2010 (Fig. 2).

On the basis of our tracking study, we find that both the distance from the colony to the sea ice edge and the sea ice cover influenced fulmar foraging effort and chick provisioning rates. We thus define an index of sea ice conditions, DC, relevant to fulmars, which is the ratio of the distance between the ice edge and the colony (DIE) over the sea ice area (SIA); DC = DIE/SIA. As an example, the distance to the closest sea ice edge was comparable in January 1987 and 1989 (Fig. 2), but sea ice coverage was higher in 1989, and hence DC smaller.

Using the 1979–2010 time series of SIC, we calculated the summer DC index (January) for each year (Fig. 3). ESIC years are those with a DC index rarer than the 10th or 90th percentile. Close-ice years were those in which the ice edge was close and sea ice cover was high, i.e., DC ≤ 4.44 as in 1979, 1998, and 2001. Far-ice years were those in which the ice edge was far and sea ice cover was low, i.e., DC ≥ 6.98 as in 1986, 1987, and 2000. The
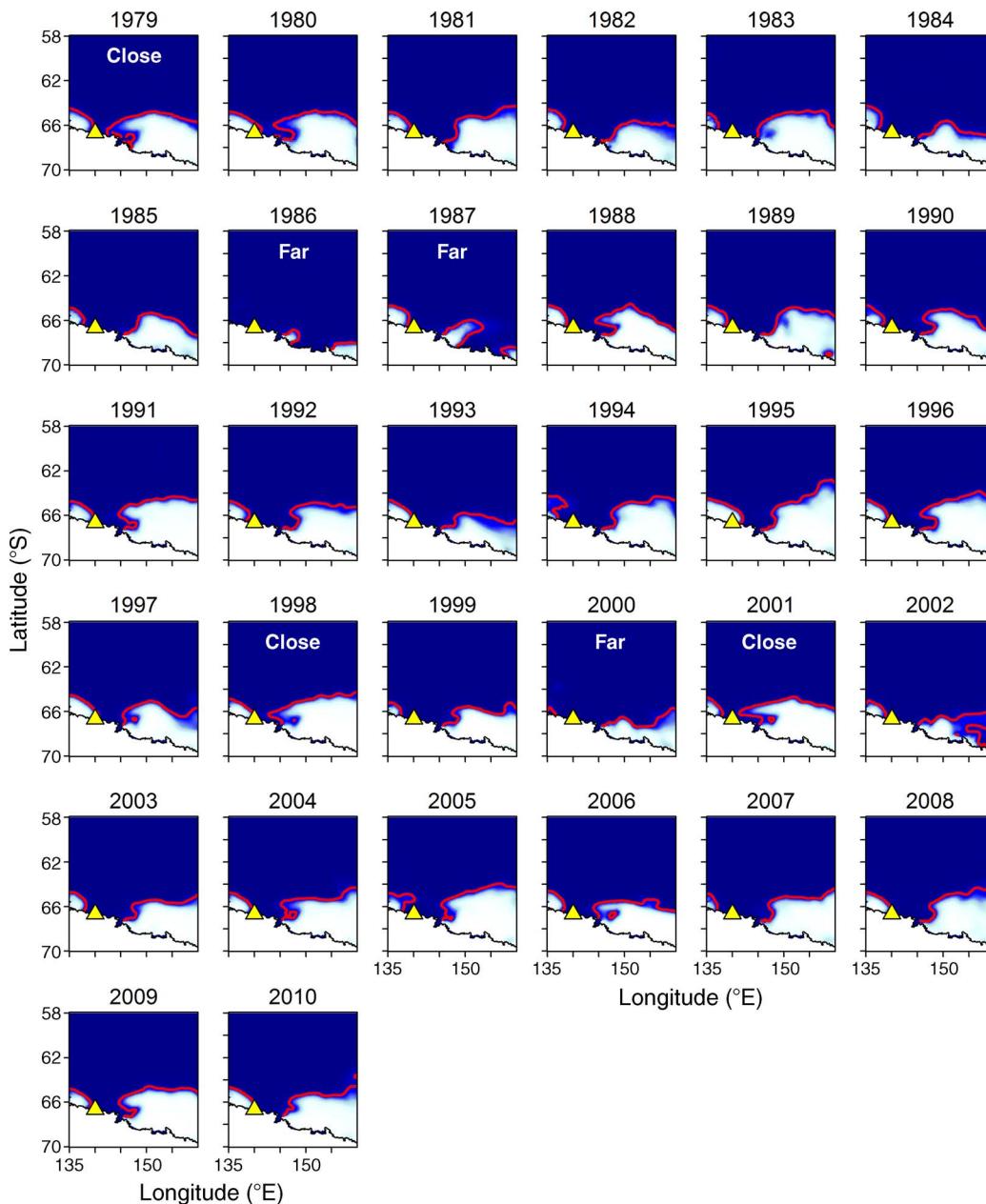
FIG. 2. Maps of sea ice concentration around the Southern Fulmar colony. The colony is shown by the yellow triangle, open water is shown in dark blue, and 100% SIC is shown in light blue; the ice edge is defined as 15% SIC and is denoted by the red contour.

2-yr foraging study during 2000 and 2001 corresponds to two ESICs in the context of the conditions between 1979 and 2010 (Figs. 2, 3, $DC_{2000} = 8.26$ and $DC_{2001} = 3.48$).

Effect of ESIC on vital rates

Our model selection is described in detail in Appendix B: Tables B2 and B3.

Our first model selection of statistical capture–recapture models of the full life cycle shows that successful breeders at the end of breeding season t survived between t and $t + 1$, reproduced, and successfully raised a chick in the following season $t + 1$ with higher probabilities when compared to other stages, regardless of environmental conditions (Appendix B: Table B2; Appendix A: Fig. A3). Our second model selection shows that ESICs likely coincide with extreme success probabilities, are less likely with extreme survival probabilities, and unlikely coincide with breeding probabilities (Appendix B: Table B3).
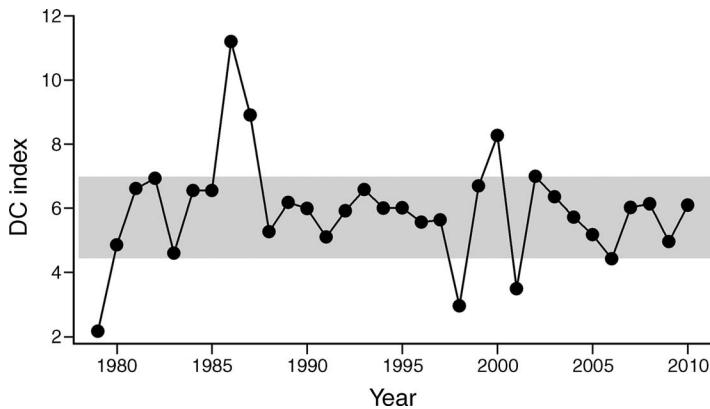
The effect of January ESIC on breeding success of year t was different among stages, and successful breeders were less impacted by ESIC years than other stages (Fig. 4, Appendix B: Table B4). Breeding success decreased by 7% (15%) during far-ice years relative to ordinary years for successful breeders (other stages) and increased by 6% (14%) during close-ice years relative to ordinary years for successful breeders (other stages). The difference between successful breeders and other stages increased during far-ice years, with the breeding success of successful breeders was ~25% higher than that of other stages; this difference was reduced to 11% during close-ice years (Fig. 4; Appendix B: Table B4).

The effect of ESIC on the probability of breeders' survival between year t and $t + 1$ was small (<1%). In addition, the 95% confidence intervals (CI) around each survival estimate were greater than the small survival differences between stages and extreme years (Fig. 4; Appendix B: Table B5).

Although extreme sea ice years did not coincide significantly with extreme values of the breeding probabilities, breeding probabilities were reduced during far-ice years and greater during close-ice years relative to ordinary years for all stages (Fig. 4; Appendix A: Fig. A3). The percentage of change of breeding probabilities between extreme and ordinary years was higher for pre-breeders and lower for successful breeders in magnitude. Indeed, the change in breeding probabilities between extreme close-ice (C) and ordinary (O) years was $P_{C-O}^{\beta_1} = 338\%$ for pre-breeders, $P_{C-O}^{\beta_2} = 8\%$ for successful breeders, $P_{C-O}^{\beta_3} = 20\%$ for failed breeders, and $P_{C-O}^{\beta_4} = 97\%$ for nonbreeders. The change of breeding probabilities between extreme far-ice and ordinary years was $P_{F-O}^{\beta_1} = -79\%$, $P_{F-O}^{\beta_2} = -19\%$, $P_{F-O}^{\beta_3} = -35\%$, and $P_{F-O}^{\beta_4} = -68\%$.

Effect of extreme events on individual heterogeneity and stochasticity

We have shown that successful breeders at the end of breeding season t have a higher probability of breeding
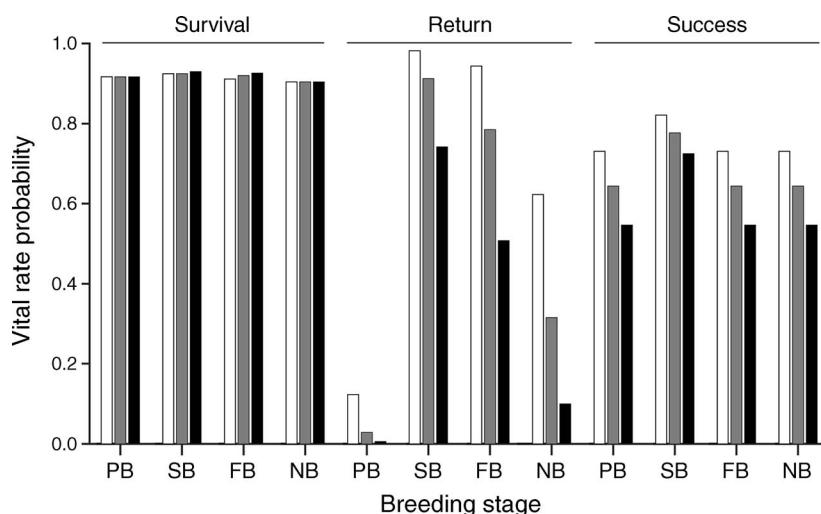

FIG. 4. Vital rates of Southern Fulmars for extreme and ordinary years. Breeding stages are pre-breeders (PB), successful breeders (SB), failed breeders (FB), and nonbreeders (NB). Vital rates include probabilities of survival from year t to $t + 1$, returning and laying an egg (i.e., breeding), and breeding success at $t + 1$. Histogram bars indicate either an extreme (black for far-ice unfavorable years and white for close-ice favorable years) or ordinary (gray) years.

TABLE 2. Results of the individual heterogeneity analysis for extreme and ordinary conditions for the Southern Fulmar.

Conditions	Entropy, H	Persistence, τ	Correlation, ω
Close ice	0.55	0.96	0.12
Ordinary	0.76	1.77	0.32
Far ice	0.50	1.86	0.34

Notes: We assessed the amount of individual stochasticity and the persistence of the intrinsic quality during the life of an individual, expressed as the persistence of reproductive stages. We used H to measure the amount of individual stochasticity, τ to measure the persistence of reproductive stage during the life of an individual, and ω the correlation between an individual's current reproductive stage and its stage two years later for adult birds only.

and raising a chick successfully in the following season, $t + 1$, than do other reproductive stages, regardless of environmental conditions. This result indicates that differences between breeding stages tend to persist between seasons t and $t + 1$. The results of our persistence and individual stochasticity calculations confirm that such heterogeneity persists over an individual's life and validate our predictions (Table 2).

In addition, we expect individual heterogeneity in quality to be more pronounced during extremely harsh conditions and lowest during extremely favorable conditions.

Consistent with this prediction, the persistence of the reproductive stage throughout an individual's life, measured by τ and ω (Table 2) is very low for close-ice relative to far-ice and ordinary conditions. Specifically, the percentage of change of ω is $P^{\omega}_{F-O} \simeq 4\%$ and $P^{H}_{C-O} \simeq -60\%$. This indicates that individuals are more likely to switch between reproductive stages when conditions are favorable.

Finally, as expected, the amount of individual stochasticity measured by the diversity of life pathways, H, is higher during ordinary relative to extreme conditions (Table 2). During extreme conditions, most individuals follow the same life-history pathways (either not breeding in poor conditions or breeding in favorable conditions). The change of H between ordinary and far-ice conditions is $P^{H}_{F-O} \simeq -33\%$ and between ordinary and close-ice conditions is $P^{H}_{C-O} \simeq -26\%$.

## Impact of extreme sea ice environments on deterministic population growth and structure

In the study period, there were six years with an extreme λ (high, 1979, 1991, and 1998; and low, 1987, 1992, and 2008). One-half of the years with an extreme growth rate corresponded to a year with ESICs (squares and circles in Fig. 5).

As a comparison, we studied the population growth and structure in environments characterized by extreme close-ice, far-ice, or ordinary conditions. For constant, extreme close-ice conditions, we project an increase of 9% per year; for constant, ordinary conditions, we project a decrease of 1%, and for constant, far-ice conditions, a decrease of 7%. The asymptotically stable stage distribution (SSD) is a majority of pre-breeders, regardless of environmental conditions (Fig. 6).

Among adults, there is a high proportion of successful breeders and a low proportion of nonbreeders in close-ice conditions, while the opposite pattern occurs in far-ice conditions. In an environment characterized by ordinary conditions, successful breeders are more abundant than failed breeders and nonbreeders.

Finally, we quantify the functional dependence of λ on vital rates for each environment using a perturbation analysis. Figs. 7 and 8 show the results of the perturbation analysis with, respectively, the sensitivities and elasticities of λ to changes in survival, breeding, and success probabilities for the different life cycle stages. The sensitivities show that λ is most sensitive to the pre-breeders' breeding probabilities, for all environments (Fig. 7). In environments characterized by close-ice and ordinary conditions, the sensitivities of λ are highest for survival, breeding, and success probabilities of successful breeders (Fig. 7). In far-ice conditions, the sensitivities of λ are highest for survival of nonbreeders; in contrast, the sensitivities of λ to vital rates of nonbreeders are extremely low in close-ice conditions (Fig. 7). Elasticities analysis (Fig. 8) exhibits different patterns, especially with regard to the perturbation analysis of λ to breeding probabilities. The differences between sensitivities and elasticities relate to scaling issues because elasticity compares the impact of equal percentage of change, whereas sensitivity compares the impact of equal unit (but potentially very different

FIG. 5. Long-term deterministic population growth rate of Southern Fulmars from 1979 to 2009. Dotted lines show the 10th and 90th percentiles. Markers show extreme years defined according to sea ice conditions; far-ice unfavorable years are black squares and open circles show close-ice favorable years.
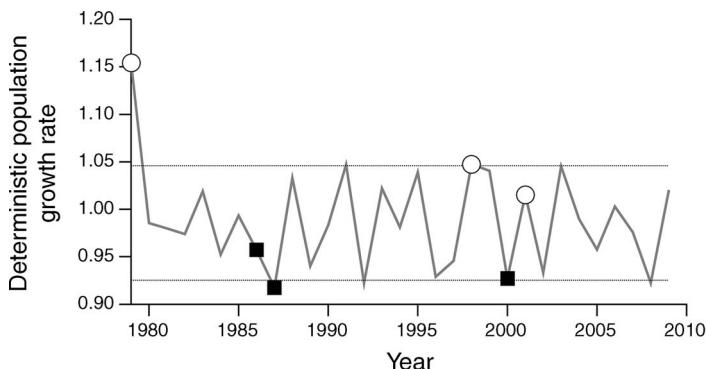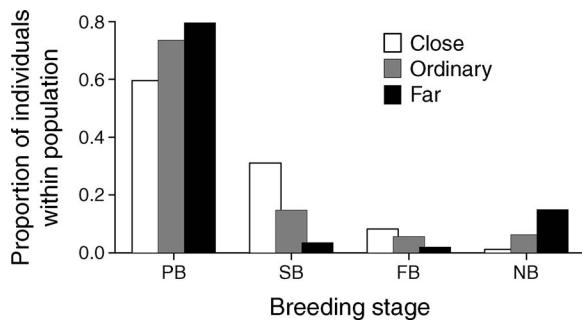
FIG. 6. Asymptotically stable stage distribution for the Southern Fulmar population for environments characterized by extreme or ordinary conditions. Extreme close-ice (favorable) conditions are shown by white bars, extreme far-ice (unfavorable) by black bars, and ordinary conditions by gray bars. See Fig. 4 for definition of breeding stages.
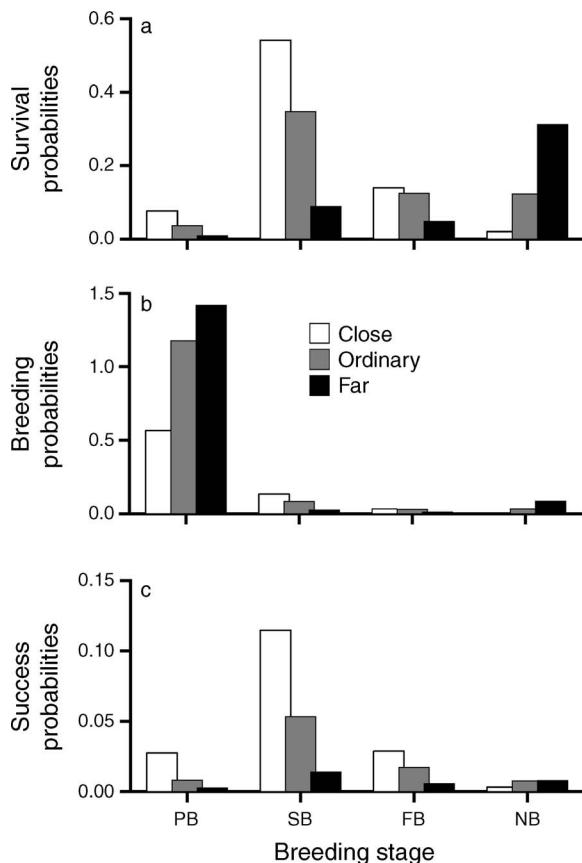

FIG. 7. Perturbation analysis of the deterministic population growth rate (λ) to vital rates for the Southern Fulmar using sensitivities of λ to vital rates. (a) Survival, (b) breeding, and (c) success probabilities are shown for environments characterized by extreme close-ice [favorable; white bars] or far-ice [unfavorable; black bars]) and ordinary conditions (gray bars). Stages are shown for the end of the breeding season t; see Fig. 4 for definitions.
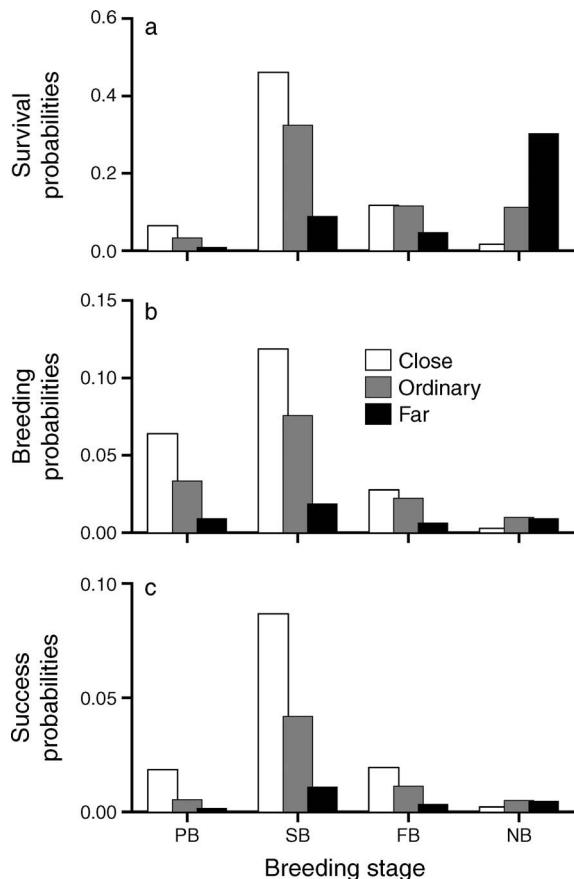

FIG. 8. Perturbation analysis of the deterministic population growth rate (λ) to vital rates for the Southern Fulmar using elasticities of λ to vital rates. See Fig. 7 for further description.

percentage) changes. In our case, the elasticity for recruitment is very small ($e(\beta_1) \in [0.01–0.06]$) and the actual value of recruitment is also small ($\beta_1 \in [0.01–0.13]$). A same-unit change to each vital rate, such as 0.01, is a change of 100% to recruitment during far-ice years ($\beta_1 = 0.01$). On the opposite, since adult survival is very large (0.92), this 0.01-unit change is a very small change in adult survival (1.08%).

Impact of the frequency of extreme events on the λ_S

Using a stochastic extreme-sea-ice-dependent population model, we find that the frequency of ESICs dramatically affects $\log(\lambda_S)$ (Fig. 9); $\log(\lambda_S)$ decreases nearly linearly as the frequency of far-ice years increases (while it increases as the frequency of close-ice years increases). The white contour on Fig. 9 shows the critical combination of extreme close-ice year frequencies below which $\log(\lambda_S) < 0$ and of extreme far-ice year frequencies above which $\log(\lambda_S) < 0$. Interestingly, for equal frequencies of far-and close-ice years below 0.2 ($w_l = w_h < 0.2$), the population is projected to be stable or declining ($\log(\lambda_S) \leq 0$), while for $w_l = w_h \geq 0.2$ the population is projected to be increasing ($\log(\lambda_S) > 0$).
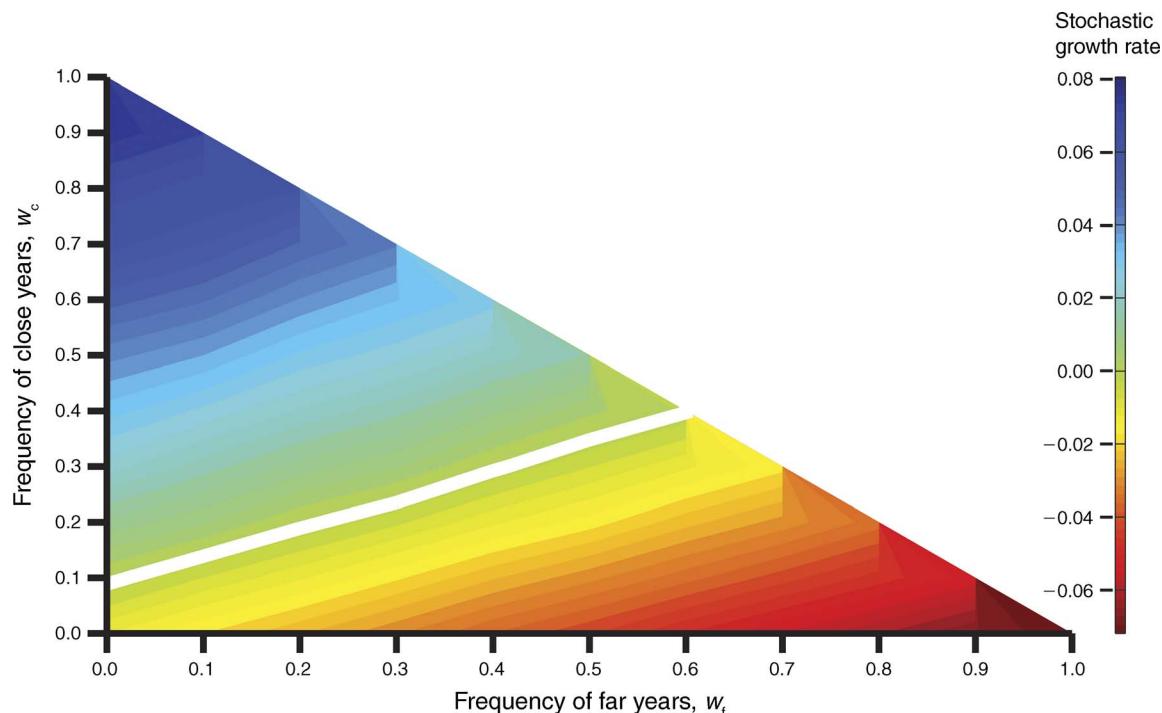
Fig. 9. Stochastic population growth rate $\log(\lambda_S)$ as a function of the frequency of extreme unfavorable far-ice w_f and favorable close-ice w_c years. The frequency of ordinary years is not shown, as it is $w_o = 1 - w_f - w_c$. The white contour stands for a stable population ($\log(\lambda_S) = 0$). Warm colors (red, orange, etc.) indicate negative λ_S, i.e., declining population; while the opposite pattern occurs with cool colors (blue, green, etc.).

This pattern reflects that the slope of the relationship between $\log(\lambda_S)$ and the frequency of ESIC is greater for close-ice than far-ice years.

This pattern occurs because the magnitude of the effect of extreme close-ice years is greater than for extreme far-ice years. Indeed, the deterministic λ (previous section) projects an increase of 9% per year for close-ice conditions, and decreases of 7% during far-ice conditions, respectively.

DISCUSSION

Through our field observations, statistical, and demographic models, we demonstrate that ESICs affect the foraging distribution, body condition, vital rates, and λ of the Southern Fulmar. The effect of these extreme conditions varies among individuals, with some individuals more likely to be successful breeders than others, even during ESICs. By assessing individual stochasticity (randomness in life pathway) and breeding success persistence (Tuljapurkar et al. 2009), we demonstrate that these individual differences are likely to reflect persistent intrinsic individual quality, which differs from what has been found for other species (Tuljapurkar et al. 2009, Orzack et al. 2010, Steiner et al. 2010). Extreme events influence the demographic expression of individual heterogeneity in phenotypes, and could thus be a potentially important agent of natural selection of life histories. Finally, these individ-

ual differences in reproductive stages and change in the frequency of extreme events strongly influence the population dynamics.

Effect of extreme events on life-history traits

We observed the foraging movements at sea and body condition of fulmars over two successive years of contrasting ESICs. Combined with a long-term individual-based study, we show that ESICs drive extreme responses of life-history traits through their effects on foraging and body condition.

Our telemetry study confirms the strong association between Southern Fulmar foraging habitat and the sea ice edge (Woehler et al. 2010, Ryan et al. 2011), where they are known to feed mainly on Antarctic krill (Ridoux and Offredo 1989). All fulmars tracked from Terre Adélie headed east in the direction of Mertz Glacier (Fig. 1), an area of high productivity (Vaillancourt et al. 2003). Sea ice dynamics play a key role in the development of major phytoplankton blooms that occur in spring and summer in Antarctica (Lizotte 2003). As sea ice melts along ice edges, primary productivity increases and boosts the productivity of the entire food web from krill (Atkinson et al. 2008) to top predators (Montes-Hugo et al. 2009).

During the summer of 2000, sea ice cover was greatly reduced and fulmars had to travel further to reach the sea ice edge, which resulted in longer foraging trips and

increasing effort. During this year of extremely poor sea ice conditions (Figs. 2, 3), adults brought less food to their chicks, which then fledged in the poorest body conditions, resulting in extremely low breeding success (Table 1, Fig. 4). The opposite pattern occurred during the 2001 breeding season, where the sea ice edge was close to the colony and sea ice cover more extended (Table 1, Fig. 1). Extensive sea ice cover in summer was thus more favorable to fulmars, which seemed to find more food (krill) to provision their chicks. This result is also consistent with previous studies showing that extensive sea ice cover in winter favors the survival of krill larvae and high recruitment the following summer (Siegel and Loeb 1995, Loeb et al. 1997).

In contrast, adult mass gain between each trip did not differ significantly between the two years of ESICs (Table 1). This finding suggests that adults do not compromise their own body conditions during unfavorable years, but instead reduce their parental effort and food delivered to their offspring. This adaptive strategy of adjusting parental effort has been found in many other seabird species (Weimerskirch et al. 2001) and is typical of long-lived species that adjust their reproductive effort in order to buffer their own survival (Stearns 1992, Erikstad et al. 1998).

Indeed, adult annual survival of Southern Fulmars did not vary significantly from year to year during our 50-year demographic study and was not significantly affected by extreme sea ice years (Fig. 4). Adults are able to adjust their breeding investment rather than compromise their own survival and future breeding opportunities to reproduce during ESICs. This finding is consistent with the bet-hedging theory that selection should favor a strategy of spreading the risk of reproduction rather than jeopardizing adult survival in unpredictably varying environments for long-lived species (Gillespie 1977, Gaillard and Yoccoz 2003, Nevoux et al. 2010).

Intermittent breeding is an important life-history strategy in the context of the bet-hedging theory for long-lived seabirds (Jenouvrier et al. 2005b, Cubaynes et al. 2011). This skipping behavior is common in marine predators experiencing varying environmental conditions (Cam et al. 1998, Jenouvrier et al. 2005a, 2008a, Chambert et al. 2012). For an environment characterized by extremely unfavorable conditions, most of the individuals skip breeding, and non-breeding is the most abundant adult stage in the stable stage population structure of Southern Fulmar. On the other hand, for extremely favorable or ordinary environments, breeders are more abundant in the adult stable stage structure of the population.

Two other sea-ice-obligate long-lived species, the Adélie Penguin and the Weddell seal, show a similar life-history strategy. During extremely harsh conditions related to the presence of giant icebergs, these species show an increase in foraging effort and dispersal rates without change in adult survival (Dugger et al. 2010,

Chambert et al. 2012). In addition, Weddell seals skip breeding when faced with greater ice-covered distance between good foraging areas (Chambert et al. 2015). On the other hand, the extreme iceberg event caused high mortality among Emperor Penguins (Kooyman et al. 2007), probably because their adaptive life-history strategy favors reproducing at every opportunity (Jenouvrier et al. 2005b).

Breeding probabilities for pre-breeders (i.e., recruitment probabilities) play a critical role in the population dynamics of the Southern Fulmar. Indeed, the population growth rate is most sensitive to recruitment (*Different responses to extreme events among individuals*). Recruitment probabilities follow the same pattern of temporal variations as the breeding probabilities of successful, failed, and nonbreeders, suggesting that they are similarly affected by changes in the environment. Consistent with these results, Jenouvrier et al. (2003) have shown that the number of local recruits and breeders are both positively correlated and similarly affected by sea ice conditions during summer. In addition, the response of pre-breeders to extreme conditions are greater than other stages, with a probability close to zero for a first-time breeder during an extreme far-ice year, while this probability is 338% higher during an extreme close-ice year relative to an ordinary year. This indicates a high phenotypic plasticity in recruitment probability. In this species, recruitment age is quite variable (90% CI = 7, 17 years). Stochastic environmental conditions may thus select for different recruitment strategies, given that this trait is quite plastic (Koons et al. 2008); i.e., early recruitment when conditions are advantageous, or delayed recruitment when conditions are unfavorable.

Different responses to extreme events among individuals

We have shown that individuals differ in their reproductive strategy, with successfully breeding individuals more likely to breed and raise a chick during consecutive breeding seasons than other individuals (Fig. 4). Hence, they were more likely to remain in the successful category; a pattern that has been documented for a number of seabirds and mammals (Cam et al. 2002, Lescroël et al. 2009, Aubry et al. 2011, Chambert et al. 2013). Interestingly, statistical uncertainties indicate that survival does not differ among stages (Appendix B: Table B5), suggesting that all individuals adopt a bet-hedging strategy regardless of their phenotype: spreading the risk of reproduction instead of compromising their survival. In addition, successful breeders cope better with unfavorable ESICs than other stages (Fig. 4); their breeding success decreased by only 7% while breeding success of other stages decreased by 15% during extremely harsh conditions. Their breeding probability is also less altered by harsh conditions than pre-breeders', failed breeders', and nonbreeders' breeding probabilities (19% vs. 79%, 35%, and 68%, respectively).

This pattern may reflect heterogeneity among individuals in their ability to acquire resources and/or allocate resources, and therefore the risk of reproduction with which they can cope. Successful individuals may be more experienced in reproduction (Lewis et al. 2006), have better body and physiological conditions (Angelier et al. 2007), and be better foragers (Lescroël et al. 2010), and thus may cope better with breeding costs, especially during poor environmental conditions. Although our study reveals that the processes of ESIC impacts are mediated through acquisition and allocation of resources, data on individual foraging behaviors and their physiology over the long term are needed to study whether or not these successful individuals are indeed better foragers than failed breeders and nonbreeders. Using an exemplary data set on foraging and demography for the Adélie Penguin, Lescroël et al. (2010) showed that "better" breeders (i.e., more likely successful than the average individual) foraged more efficiently under harsh sea ice conditions and when offspring needs were higher. Better breeders brought more food to the colony by achieving shorter foraging trips and diving deeper, thus gaining higher net energy profit to be allocated to reproduction and survival.

Our two-year tracking study revealed low interindividual variability in foraging sites, duration, and behavior within the same year (Fig. 1, Table 1). Such low interindividual differences in foraging grounds of Southern Fulmar could be a result of local enhancement or highly predictable food resources (Weimerskirch 2007). Krill swarms are patchy and birds can locate them by direct visual or olfactory detection and indirect detection (local enhancement) by sighting other predators that are already exploiting a patch (Grünbaum and Veit 2003). However, when foraging in multispecies flocks on the same resource, competition may be high and result in variable foraging success between individuals according to their intrinsic quality.

We showed that adult mass gain and food load delivered to the chick between foraging trips were highly variable among individuals. In this context, body mass, experience, and bird personality could be important factors underlying individual heterogeneity (Barbraud et al. 2013).

Interestingly, during extremely favorable years, breeding probabilities and breeding success differences between stages were reduced (Fig. 4). In addition, the variability of adult mass gain between foraging trips is higher, suggesting that individuals of differing intrinsic quality bred that year (Table 1). These two results suggest that during favorable years most individuals reproduce and successfully raise a chick, regardless of their intrinsic quality, thereby concealing the presence of individual heterogeneity in reproductive traits. As a consequence, heterogeneity among individuals is more likely to be detectable in poor environmental conditions when resources are scarce (Stearns 1992,

Barbraud and Weimerskirch 2005, Tavecchia et al. 2005).

Extreme unfavorable events reveal individual intrinsic quality

We have shown that successful breeders are more likely to breed and successfully raise a chick at the next breeding season than other individuals, indicating these individual differences in reproduction are likely to carry over to the next breeding season. To assess whether or not these differences persist over the life of an individual, reflecting acquired or fixed intrinsic quality, we analyzed persistence of the reproductive stage and individual stochasticty (Tuljapurkar et al. 2009).

In an environment characterized by ordinary conditions, the amount of individual stochasticty is low and the persistence of the reproductive stage is high relative to other species (Tuljapurkar et al. 2009: Figs. 2, 3). This combination reflects that Southern Fulmar remain in the same breeding stage and that breeding success does have a tendency to persist within lifetimes given ordinary environmental conditions. This pattern contrasts to that found for most other species (Tuljapurkar et al. 2009), which frequently switch reproductive stages throughout their lives. For two related seabird species, the Northern Fulmar (*Fulmarus glacialis*) (Orzack et al. 2010) and the Black-legged Kittiwake (*Rissa tridactyla*) (Steiner et al. 2010), the autocorrelation in reproductive stages two years later, ω, is much lower ($\omega_{NF} = 0.05$ and $\omega_K = 0.09$) than for Southern Fulmar ($\omega_{SF} = 0.32$, Table 2). For the Southern Fulmar, persistence of the reproductive stage may reflect high-quality individuals who reproduce better, while nonbreeders may be low-quality individuals. This individual heterogeneity may arise from fixed differences, i.e., permanent differences among individuals arising from genetic and/or ontogenetic developmental conditions, or may develop over time (e.g., experienced breeders and/or foragers).

Our study also shows that climate variability influences the relative importance of individual heterogeneity and stochasticity (Table 2). The amount of individual stochasticity is reduced for extreme rather than ordinary environments because most individuals follow the same life pathways. In an environment characterized by unfavorable sea ice conditions, most individuals skip breeding and individuals remain nonbreeders, while most individuals breed and raise a chick successfully in a favorable environment. The persistence of the reproductive stage during the life of an individual ω is low in an environment characterized by extreme favorable conditions but is high in an environment characterized by extremely harsh conditions. For extremely unfavorable conditions, successful breeders comprise only 3% of the stable stage structure of the population (Fig. 6), but these individuals are probably high-quality individuals, as they are more likely to breed and reproduce the next breeding season despite extremely harsh conditions.

Our results support the existence of individual differences in reproduction, and show that extreme environmental conditions reduce the amount of individual stochasticity within a population of Southern Fulmar. One can thus ask if the lack of evidence for innate or acquired heterogeneity in reproduction reported for other species (Tuljapurkar et al. 2009) is linked to the variability of environmental conditions. Many studies have argued that during ordinary conditions, most trait variations are functionally neutral and hence not subject to significant selection pressure (Gutschick and BassiriRad 2003, Tuljapurkar et al. 2009, Steiner et al. 2010, Steiner and Tuljapurkar 2012) but that strong selection does occur during extreme events (Gutschick and BassiriRad 2003).

Evidence for heterogeneity in reproduction among individuals has also been shown for other Antarctic species during extreme iceberg years (Adelie Penguins; Lescroël et al. 2009; Weddell seals; Chambert et al. 2014). Future work entails comparing species living in various environments (tropical vs. polar) to assess whether individual heterogeneity is more likely to play a significant role during demanding conditions, such as ESICs in polar environments, or hurricanes in tropical environments. Such comparisons should use the same methodological framework as various methodologies may lead to different conclusions about the role that individual heterogeneity plays in life-history trait variability (Cam 2014). The general framework developed by Caswell (2011) will be highly valuable to account for environmental stochasticity, i.e., that individuals experience an array of environmental conditions throughout their life. Indeed, using the Markov chain with rewards theory and a vec-permutation model (Hunter and Caswell 2005), Caswell (2011) derives the moments of the distribution of the lifetime reproductive output of an individual for age- or stage-structured models for constant, periodic, or stochastic environments. Despite the generality and usefulness of this approach, very few empirical studies have applied the framework thus far, limiting the comparison among species, as discussed here.

Effect of extreme events on population growth

Our population viability analysis showed that ESICs during the breeding season explained half of the extreme values of the deterministic population growth rate (λ) over the last three decades. This is a strong response at the population level, as many other factors drive population fluctuations. For example, among climate factors, extreme snow storms during summer could dramatically reduce breeding success through the loss of the egg or the chick to hypothermia, as is observed in other petrel species (Chastel et al. 1995, Descamps et al. 2015). Environmental conditions during winter may also play an important role, as Southern Fulmars exhibit an incredible pan-Antarctic migration (K. Delord et al., *unpublished manuscript*). During winter migration, ful-

mars may be susceptible to extreme hurricanes like other seabird species, such as Cory's Shearwater (Jenouvrier et al. 2008b, Genovart et al. 2013) and Black-capped Petrel (Hass et al. 2012).

Our study shows that extreme events dramatically affect the long-term deterministic growth rate λ and its response to change in vital rates (i.e., perturbation analysis). In an evolutionary context, extreme events represent a potentially important agent of natural selection of life histories. Indeed, results pertaining to selective gradients were similar to results obtained from the sensitivity analysis (Appendix A: Fig. A4) and the long-term λ can be interpreted as a measure of mean population fitness (Lande 1982).

Although many studies have included breeding stages to analyze trade-offs among life-history traits and the role of individual quality on fitness components (Nichols et al. 1994, Cam et al. 1998, Orzack et al. 2010); perturbation analysis of λ, distinguishing the role of breeding stages with successful and failed breeders, has rarely been done. Such perturbation analysis produced three noteworthy results: (1) the sensitivity of λ to pre-breeder breeding probabilities, i.e., recruitment probabilities, is the highest among the vital rates (Fig. 7), (2) the successful breeder vital rates influence the population growth rate the most for environments characterized by extreme favorable or ordinary conditions, (3) for an environment characterized by unfavorable conditions, λ is most sensitive to changes in the adult survival of nonbreeders.

The fact that sensitivity of λ to recruitment probabilities is the highest among the vital rates could appear as an interesting contradiction with the prevailing theory stating that λ is mostly sensitive to adult survival for long-lived species (Saether and Bakke 2000, Gaillard and Yoccoz 2003, Stahl and Oli 2006). However, these studies report elasticities, which give the proportional change in λ caused by a proportional change in a vital rate θ (Caswell 2001). Using elasticities, we found that the elasticity of λ to adult survival probabilities is the highest among the vital rates (Fig. 8), forming a consistent pattern with other studies. Elasticities facilitate comparison across vital rates that are scaled differently, and thus are useful for comparative studies, as some species may have large fecundity rates in comparison to survival probability (Caswell 2000). For Southern Fulmar (which lay a single egg), all vital rates are bounded between zero and one, and thus standardizations of demographic and evolutionary metrics are not necessary for comparing the different responses among vital rates.

In an evolutionary context, perturbation analysis are also useful to assess the selection gradient of trait (van Tienderen 2000), although there is a debate about which standardization of the selection gradient is relevant (Hereford and Hansen 2004). Appendix A: Fig. A4 shows a nonstandardized selection gradient to assess the potential strength of selection following van Tienderen

(2000)'s approach. The evolutionary response of a vital rate can be predicted by the breeder's equation, using the variance-standardized selection gradient and the heritability of a trait (Lande and Arnold 1983). Because the return probabilities showed the highest variance (Appendix A: Fig. A3), the variance-standardized selection gradient is highest for recruitment probabilities. Therefore, recruitment is a highly plastic trait that if heritable, could potentially have a critical role in the evolution of life histories. Further investigation of how environmental variability affects such patterns is required, as the effect on selection on a life-history trait may depends upon the current environmental state and the stochastic sequence of states in which it is embedded (Horvitz et al. 2010).

Our second result demonstrates the critical role of the vital rates of successful breeders on the population dynamics. For environments characterized by extreme favorable or ordinary conditions, the vital rates of successful breeders have the greatest influence on λ (excepting recruitment probabilities). The proportional change in λ resulting from a proportional change in successful vital rates is at least two times larger compared to equal proportional changes in other vital rates.

Finally, for an environment characterized by unfavorable conditions, our last result illustrates the role of extreme events in shaping the functional dependence of λ on the vital rates. Indeed, it reveals the importance of skipping breeding as a strategy, with vital rates of nonbreeders becoming more influential on the population growth.

Effect of change in extreme event frequency on λ_S

We further accounted for environmental stochasticity and extreme environmental conditions, and showed that $\log(\lambda_S)$ is strongly affected by the frequency of extreme events; $\log(\lambda_S)$ increases almost linearly with the frequency of favorable years, but decreases with the frequency of unfavorable years (Fig. 9). Interestingly, $\log(\lambda_S)$ is more sensitive to changes in the frequency of extreme favorable years than unfavorable years, meaning that a smaller increase in frequency of favorable years could potentially counteract the effect of an increase in frequency of unfavorable years; $\log(\lambda_S)$ projects a decrease of 0.6% per year for the frequencies of favorable and unfavorable years observed over the last three decades. Jenouvrier et al. (2003) showed that the observed population trend is increasing, but this trend is driven by immigration while the local population decreases. Our model does not include immigration, and the projected decline for observed extreme event frequencies agrees well with observed local population dynamics.

Sea ice is projected to shrink around Antarctica by the end of the century (Stocker et al. 2013). Thus, the frequency of unfavorable years will likely increase and whether or not immigration will counteract the project-ed decline of the local population remains to be seen. Indeed, strong sea ice decline will probably affect the neighboring source populations as well (Jenouvrier et al. 2014), as sea ice is projected to shrink everywhere in Antarctica (Stocker et al. 2013).

Projecting the future population dynamics of Southern Fulmars requires a link between our stochastic models and projections of frequency of extreme events (Jenouvrier et al. 2009, Hunter et al. 2010, Jenouvrier 2013). The resolution of IPCC class-climate models is too coarse to reliably assess the position of the sea ice edge, which influences the foraging, body condition, vital rates, and population growth rate of Southern Fulmars. Obtaining relevant sea ice conditions for the Southern Fulmars, integrating contrasting effects of sea ice among regions as well as dispersion processes, will be key to predict the fate of Southern Fulmar under future sea ice change and higher frequency of extremely unfavorable years.

CONCLUSION

Quantifying the possible effects of ECEs on wild organisms remains a challenge. This comprehensive study indicates that extreme environmental conditions can impact individual fitness components (i.e., body mass, reproductive success, and survival) through altered behaviors (foraging effort and breeding probability), which overall have profound impacts on population dynamics.

Extreme events further complicate the role that individual heterogeneity plays in shaping life histories and populations. For environments characterized by extremely poor conditions, heterogeneity is more pronounced, indicating an opportunity for phenotypic selection on reproductive success and a tendency for most individuals to skip breeding, which ultimately reduces individual stochasticity. For environments characterized by extremely advantageous conditions, individual stochasticity is also diminished because most individuals reproduce. In that case, individual heterogeneity is reduced due to a relaxed phenotypic selection on reproductive traits, whereby all individuals (of high or low intrinsic quality) are able to successfully reproduce.

These results have profound implications for the evolution of life histories, but also for conservation. With the projected increase in both the frequency and severity of climate extremes, our ability to predict the impacts of such events on wild populations will depend on our understanding of how such complex mechanisms affect individuals (i.e., through altered behavior, demography, and fitness) and on our ability to scale up these effects to populations through demographic and evolutionary responses.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/14-1834.1.sm

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.6pp3d