

Multispecies integrated population model reveals bottom-up dynamics in a seabird predator–prey system

MAUD QUÉROUÉ ^{1,6} CHRISTOPHE BARBRAUD ² FRÉDÉRIC BARRAQUAND ³ DANIEL TUREK ⁴
KARINE DELORD ² NATHAN PACOUREAU ⁵ AND OLIVIER GIMENEZ ¹

¹CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

²Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372, CNRS-La Rochelle Université, Villiers-en-Bois 79360 France

³Institute of Mathematics of Bordeaux, CNRS, University of Bordeaux, 351 Cours de la Libération, Talence 33400 France

⁴Department of Mathematics and Statistics, Williams College, 18 Hoxsey Street, Williamstown, Massachusetts 01267 USA

⁵Department of Biological Sciences, Earth to Ocean Research Group, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6 Canada

Citation: Quéroué, M., C. Barbraud, F. Barraquand, D. Turek, K. Delord, N. Pacoureau, and O. Gimenez. 2021. Multispecies integrated population model reveals bottom-up dynamics in a seabird predator–prey system. *Ecological Monographs* 00(00):e01459. 10.1002/ecm.1459

Abstract. Assessing the effects of climate and interspecific relationships on communities is challenging because of the complex interplay between species population dynamics, their interactions, and the need to integrate information across several biological levels (individuals, populations, communities). Usually used to quantify single-species demography, integrated population models (IPMs) have recently been extended to communities. These models allow fitting multispecies matrix models to data from multiple sources while simultaneously accounting for uncertainty in each data source. We used multispecies IPMs accommodating climatic variables to quantify the relative contribution of climate vs. interspecific interactions on demographic parameters, such as survival and breeding success, in the dynamics of a predator–prey system. We considered a stage-structured predator–prey system combining 22 yr of capture–recapture data and population counts of two seabirds, the Brown Skua (*Catharacta lönbergi*) and its main prey the Blue Petrel (*Halobaena caerulea*), both breeding on the Kerguelen Islands in the Southern Ocean. Our results showed that climate and predator–prey interactions drive the demography of skuas and petrels in different ways. The breeding success of skuas appeared to be largely driven by the number of petrels and to a lesser extent by intraspecific density dependence. In contrast, there was no evidence of predation effects on the demographic parameters of petrels, which were affected by oceanographic factors. We conclude that bottom-up mechanisms are the main drivers of this skua–petrel system.

Key words: Bayesian inference; demography; environmental variation; integrated population model; matrix population model; Nimble; predator–prey interactions.

INTRODUCTION

The effects of climate change on the diversity and the structure of communities have been reported repeatedly (Walther et al. 2002, Parmesan 2006, Hoegh-Guldberg and Bruno 2010, Miller et al. 2018). However, the underlying mechanisms remain poorly understood due to the complex community dynamics of interacting species: interactions occur within species, between species and between species and the environment (Godfray and May 2014). Following disturbance, the abundance and distribution of species are expected to be modified according to the position and extent of the species' niche (Thomas et al. 2004). Because the effects of environmental

variability on mortality, fecundity and dispersal may differ between species (Grosbois et al. 2008, Jenouvrier 2013), changes in structure and diversity appear at the community level. However, studying species-by-species responses to environmental changes may overlook the role played by species interactions on those responses, and contribute to a lesser extent to the broader understanding of species interactions that is required by community ecology.

Models for population dynamics have been used to understand the effect of interspecific interactions and environmental variables on species demography. However, these models are often not demographically structured (Stenseth et al. 2015, Pacoureau et al. 2019a, Stoessel et al. 2019) or only partially (Millon et al. 2014, Saunders et al. 2018, Pacoureau et al. 2019b). Unstructured approaches consider individuals as being equivalent but differences in size, age and ontogenic stages exist within a population and may be of importance in

Manuscript received 26 June 2020; revised 9 February 2021; accepted 3 March 2021. Corresponding Editor: Brian D. Inouye.

⁶E-mail: maud.queroue@gmail.com

the context of interspecific interactions. As argued by Miller and Rudolf (2011), the consideration of the stage structure of populations can lead to a better understanding of community structure and dynamics. Interactions between species such as predation or competition do not necessarily have a homogeneous impact on the different stages of the interacting species. For example, young individuals might be predominantly preyed upon in carnivore–ungulate systems (Gervasi et al. 2015). Therefore, to detect and understand species interactions, we need to consider jointly the demography of several stage-structured populations (Oken and Essington 2015).

Although well developed for single-species dynamics (Tuljapurkar and Caswell 1997, Caswell 2001), demographic stage-structured models have received little attention in community ecology (but see Chu and Adler [2015] on a plant system). The difficulty is that a multi-species demographic analysis requires integrating information across several biological levels (individual – population – community), which, in turn, requires unifying all available data sources into a single framework. Integrated population models (IPMs) have been recently developed to infer population demography by making complete use of all available sources of information (see Schaub and Abadi 2011, Zipkin and Saunders 2018 for reviews). In their simplest form, these models combine population counts and demographic data into a single framework, which allows the estimation of demographic parameters while simultaneously accounting for various sources of uncertainty in each data source (Besbeas et al. 2002). The IPM framework has been extended to multiple species for competition/parasitism (Péron and Koons 2012), and for predator–prey interactions (Barraquand and Gimenez 2019).

Here, our main objective was to quantify the relative contribution of environmental changes and species interactions on demographic parameters of a predator and its prey. To do so, we used a multispecies IPM framework accommodating the effects of local and global climatic conditions on demographic parameters, such as survival and breeding, while explicitly considering species interactions. We applied our approach to a stage-structured predator–prey system combining 22 yr of capture–recapture data and population counts on two seabirds, the Brown Skua (*Catharacta lönnerbergi*) and its main prey the Blue Petrel (*Halobaena caerulea*) ('skua' and 'petrel' hereafter) breeding on the Kerguelen Islands in the Southern Ocean.

Because seabirds often occupy high trophic levels in food webs, bottom-up forcing, which implies population regulation through climate-driven limitation in food availability, has long been featured as the dominant paradigm to understand their dynamics (Lack 1967, Aebischer et al. 1990, Stenseth et al. 2002). Seabird foraging behavior and demography reflect the influences of climate variability, which directly impacts biological processes in marine ecosystems and cascade through food webs up to seabirds (Barbraud and

Weimerskirch 2001, Jenouvrier et al. 2003). However, top-down pressures from predation at breeding colonies are also known to affect the vital rates of seabirds (Hipfner et al. 2012). There is increasing evidence that bottom-up and top-down processes often act in concert and differently affect demographic parameters (Suryan et al. 2006, Horswill et al. 2014, 2016). For example, the effects of predation and resource limitation caused breeding failure of Black-legged Kittiwakes (*Rissa tridactyla*) (Regehr and Montevecchi 1997) and population declines of Arctic Skuas (*Stercorarius parasiticus*) (Perkins et al. 2018). Therefore, quantifying the relative strength of environmental conditions and predator–prey effects is essential for a better understanding of the drivers of population dynamics in seabirds. This is all the more important as climate changes impact the physical properties of the oceans, including the Southern Ocean (Gille 2002, Han et al. 2014) and, through the trophic food web, affect demography and population dynamics of seabirds (Barbraud et al. 2012, Sydeman et al. 2015), the species we study here being no exception (Barbraud and Weimerskirch 2003).

Using a multispecies IPM, we assessed the relative contribution of environment and predator–prey interactions on seabirds' demographic parameters. We estimated survival and adult breeding success for the two interacting species, and assessed the impacts of climatic conditions on these demographic parameters to understand the contribution of predator–prey interactions in shaping population dynamics.

MATERIALS AND METHODS

Study site and species

Skuas and petrels were studied on Mayes Island (49°28' S, 69°57' E), a 2.8 km² uninhabited island of the Kerguelen Islands in the Southern Ocean where the two-species breed during the austral summer (October–February).

The petrel is a small (150–250 g) long-lived seabird belonging to the family of *Procellariiformes*. At Kerguelen Islands, petrels feed on macrozooplankton and micronekton, mainly crustaceans and fishes (Cherel et al. 2002, 2014). Individuals from Mayes Island spend the nonbreeding season (from mid-February to September) between the polar front and the northern limit of the pack-ice (57–62°S) between longitudes 20° W and 90° E (Cherel et al. 2016). Birds return to breeding colonies in early September (Quillfeldt et al. 2020). Mayes Island is covered with dry soils and dense vegetation, providing suitable breeding sites for approximately 142,000 breeding pairs of these burrowing petrels (Barbraud and Delord 2006). In late October, a single egg is laid in a burrow dug in peat soil under tall and dense vegetation. The incubation lasts 45–49 d and the chick-rearing period 43–60 d (Jouventin et al. 1985). The chick fledges in early February. Both sexes participate in

parental care by alternating foraging trips during the incubation and fledging periods.

The skua is a medium sized (1.1–2.2 kg) long-lived seabird belonging to the family of *Charadriiformes*. On Mayes Island between 80 and 120 pairs breed annually (Mougeot et al. 1998). Breeding pairs form in October with a high mate fidelity, and generally establish themselves in the same territory each year (Parmelee and Pietz 1987), which they tenaciously defend throughout the breeding season. Generally, two eggs are laid between October and December. The incubation lasts 28–32 d and the chicks rearing period 40–50 d (Higgins and Davied 1996). Skuas are extremely plastic in their foraging techniques and adapt their diet depending on the local availability of prey (Carneiro et al. 2015). On Mayes Island, during the breeding season, Blue Petrels represent 95% of the skua diet (Pacoureaux et al. 2019c). Skuas from Mayes Island overwinter in the southern hemisphere between 10° E and 150° E (Delord et al. 2018).

During the breeding period on Mayes Island, the predation of petrels by skuas takes place mainly at night, when petrels come out or arrive at their burrows (Mougeot and Bretagnolle 2000a). Skuas mostly prey on petrels on the ground, but they can also catch petrels in flight (Mougeot et al. 1998, Pacoureaux et al. 2019c). Vocalizing petrels, especially those without partners, are more easily detected by skuas during the courtship period (Mougeot and Bretagnolle 2000b). Skuas may also prey on chicks during the fledging period.

Count and capture–recapture data

Data of both skuas and petrels were collected during the breeding seasons from 1996/1997 to 2017/2018. For convenience, breeding seasons are named from 1996 to 2017 hereafter. The time interval used in our model starts before the wintering of species and ends at the end of the breeding period. Two types of data were used: count data corresponding to the number of burrows or territories occupied by seabirds and capture–recapture (CR) data of adult seabirds found on the monitored area. Each year, adult individuals of both species were checked at specific times following the species phenology to determine the breeding status of each bird. The breeding status of marked birds was determined at the end of the breeding period. Count data are considered in a post breeding census. In the following we describe how the data were collected for the two species. For clarity, all parameters for skuas are indicated by *S* and for petrels by *P*.

Around 200 individually marked burrows of petrels were inspected each year from early-to-mid November just after egg-laying, to check for eggs and to identify marked adults, and then in late January, just before fledging of the chicks. Each year since 1985 (see Barbraud and Weimerskirch 2005), all fledglings as well as unknown individuals found in burrows were

marked with a stainless steel band (captured by hand, marked, and replaced in their burrow). Petrels never observed with an egg or a chick during a given breeding season were considered as nonbreeders (NB). Individuals were identified as breeders if they laid a single egg or raised a chick and as successful breeders if their chick fledged (SB). Two categories of failed breeders were used depending on the stage of failure: egg stage (FBE) or chick stage (FBC). Given that the first sampling period occurred just after laying, it is very unlikely that nonbreeders were failed breeders. These breeding statuses allowed the construction of the individual capture histories (Ch_p) and constituted our CR data. The annual number of adult petrels (Y_p), i.e., count data, was estimated as the number of occupied burrows. Each occupied burrow was considered as being frequented by a pair of petrels. We considered that this count included all adult individuals, both breeders and nonbreeders.

For skuas, each year since 1991, the eastern side of Mayes Island was inspected to identify territories of skuas. A territory was considered established when a pair strongly defended an area against other skuas (Mougeot et al. 1998). Around 50 nesting territories were visited four to eight times from mid-October (after egg-laying) to late February (just before fledging of the chicks) each year. Chicks just before fledging, as well as new adult individuals, were marked with a metal ring and a plastic ring to facilitate individual identification using binoculars. Breeding status was determined by checking the nest contents for the presence of eggs or young chicks. Skuas never observed with an egg or a chick were considered as nonbreeders (NB). Individuals were identified as breeders if they laid at least one egg or raised a chick. If the eggs did not hatch or the chicks died, both members of the pair were considered failed breeders (FB). Given that the first sampling period occurred just after laying, it is very unlikely that nonbreeders represented failed breeders. Successful breeders were defined as individuals that fledged one or two chicks, and were denoted as SB1 or SB2, respectively. These breeding statuses allowed the construction of the individual capture histories (Ch_s) and constituted our CR data. The annual number of skuas (Y_s), i.e., count data, was estimated as the number of territories and each territory was considered occupied by a pair of skuas. We considered that this count included all adult individuals, both breeders and nonbreeders.

For both species, individual breeding status could be considered as “uncertain” (C) in case of difficulties to ascertain their breeding status (lack of information, missed checks, individuals never re-observed). Only adult individuals that have bred at least once between the 1996 and the 2017 breeding seasons were kept in the data set for analysis to eliminate potential transient individuals ($n = 318$ for skuas and $n = 1210$ for petrels). Individual capture histories (Ch) started at the first breeding attempt recorded. Based on the high

probability of observing breeders in the study site, we assumed that the first breeding attempt was correctly detected. Unknown individuals found in monitored burrows or territories are considered as immigrants to the study site (N_{im}).

The presence of chicks was used to assign a breeding status to adult individuals captured in the breeding area. In order to maintain the independence of the data, we did not include information on chicks in the model. Therefore, the fecundity was a fixed value. We considered one chick for each pair of seabird, considered as successful breeders ($N_{SB,P}$) for petrels or successful breeders with one chick ($N_{SB1,S}$) for skuas ($f_{SB,P}$ and $f_{SB1,P}$ are equal to 1, respectively). For skuas that successfully fledged two chicks ($N_{SB2,S}$), we considered two chicks per pair of skuas ($f_{SB2,S}$ is equal to 2). Since juveniles only return to the breeding sites as adults to attempt to breed for the first time (from 4 yr old or older), we did not have data on juvenile states.

Integrated population model

We built a two-species IPM that combines count and CR data and allows estimating abundances and demographic rates (Besbeas et al. 2002, Schaub and Abadi 2011). More specifically, we connected two IPMs, one for predatory skuas and one for petrels, their main prey, through explicit predator–prey relationships (Barraquand and Gimenez 2019). We incorporated the effects of predation within species-specific vital rates such as survival and breeding parameters. This IPM is structured by life history states (Fig. 1). We built two likelihoods, one for the CR data and the other for the count data, which we combined into a joint likelihood.

In the following, we detail the state process following a biological timeline and we explain the various likelihoods we used. The structure was the same for the two species but states differed in relation to species biology (Fig. 1). The two main differences were (1) skuas could have up to two chicks vs. only one for petrels, (2) the failed-breeder stage in petrels could be split further according to the timing of failure (failure at the incubation vs. chick-rearing stage). For clarity, parameters are indexed by S (for skuas) or P (for petrels) when differences occur, or by X (for S or P) when the structure is the same for both species. We used Poisson (Po) and binomial (Bin) distributions to account for demographic stochasticity. Notations of all parameters and state variables are detailed in Appendix S1: Table S1.

State process.—Offspring production.—The estimated numbers of skuas and petrels in their first year, i.e., between 0 and 1 yr old ($N_{J1,S,t}$) at year t , are modeled with a Poisson distribution

$$N_{J1,S,t} \sim \text{Po}(0.5 \times f_{SB1,S} \times N_{SB1,S,t-1} + 0.5 \times f_{SB2,S} \times N_{SB2,S,t-1}) \quad (1)$$

$$N_{J1,P,t} \sim \text{Po}(0.5 \times f_{SB,P} \times N_{SB,P,t-1}) \quad (2)$$

with $N_{J1,S}$ the number of chicks produced by all successful skua breeders ($N_{SB1,S}$ and $N_{SB2,S}$) according to their fecundity ($f_{SB1,S}$, one chick and $f_{SB2,S}$, two chicks per female skua, sex ratio: 0.5). For petrels, $N_{J1,P}$ is also Poisson distributed but with only one chick ($f_{SB,P}$) per estimated successful female breeder ($N_{SB,P}$ with a sex ratio of 0.5).

Juvenile survival.—The numbers of juveniles in their second year (N_{J2}), in their third year (N_{J3}), in their fourth year and older (N_{J4+}) are modeled with binomial distributions:

$$N_{J2,X,t} \sim \text{Bin}(\phi_{J1,X}, N_{J1,X,t-1}) \quad (3)$$

$$N_{J3,X,t} \sim \text{Bin}(\phi_{J2,X}, N_{J2,X,t-1}) \quad (4)$$

$$N_{J4+,X,t} \sim \text{Bin}(\phi_{J3,X}, N_{J3,X,t-1}) + \text{Bin}(\phi_{J4,X}, N_{J4NB,X,t-1}) \quad (5)$$

with apparent survival probabilities between 1 and 2 yr (ϕ_{J1}), between 2 and 3 yr (ϕ_{J2}), between 3 and 4 yr (ϕ_{J3}), and for 4 yr old individuals and older that did not attempt to breed during the previous breeding season (ϕ_{J4}), respectively. The N_{J4+} count includes individuals in their fourth year and 4-yr-old individuals and older that did not attempt to breed during the previous breeding season (N_{J4NB}).

As we observed only adult breeding birds, we had no information on the juvenile phase. We assumed that juvenile apparent survival increased with age (Greig et al. 1983, Grande et al. 2009, Fay et al. 2015), as experienced birds are, on average, more effective in foraging (Daunt et al. 2007), in competing with conspecifics or in avoiding predators

$$\text{logit}(\phi_{J_{age},X}) = \lambda_{1,X} + \lambda_{2,X} \times \text{age}_i \quad (6)$$

where ϕ_j is the juvenile apparent survival probability, age_i the age of the juvenile state (from N_{J1} to N_{J4+}), λ_1 the intercept and λ_2 the slope, which is constrained to be positive.

Juvenile first breeding attempt.—The first breeding attempt in skuas and petrels could start from age four. The individuals that attempted to breed for the first time, with a probability Pr , are in the state N_{J4B} and the individuals that did not attempt to breed are in the state N_{J4NB}

$$N_{J4B,X,t} \sim \text{Bin}(\text{Pr}_{X,t}, N_{J4+,X,t}) \quad (7)$$

$$N_{J4NB,X,t} = N_{J4+,X,t} - N_{J4B,X,t} \quad (8)$$

Adult survival.—For the two species, we modeled the number of surviving adults (N_{alive}) at year t among the total number of adult individuals (N_{adtot}) at year $t-1$

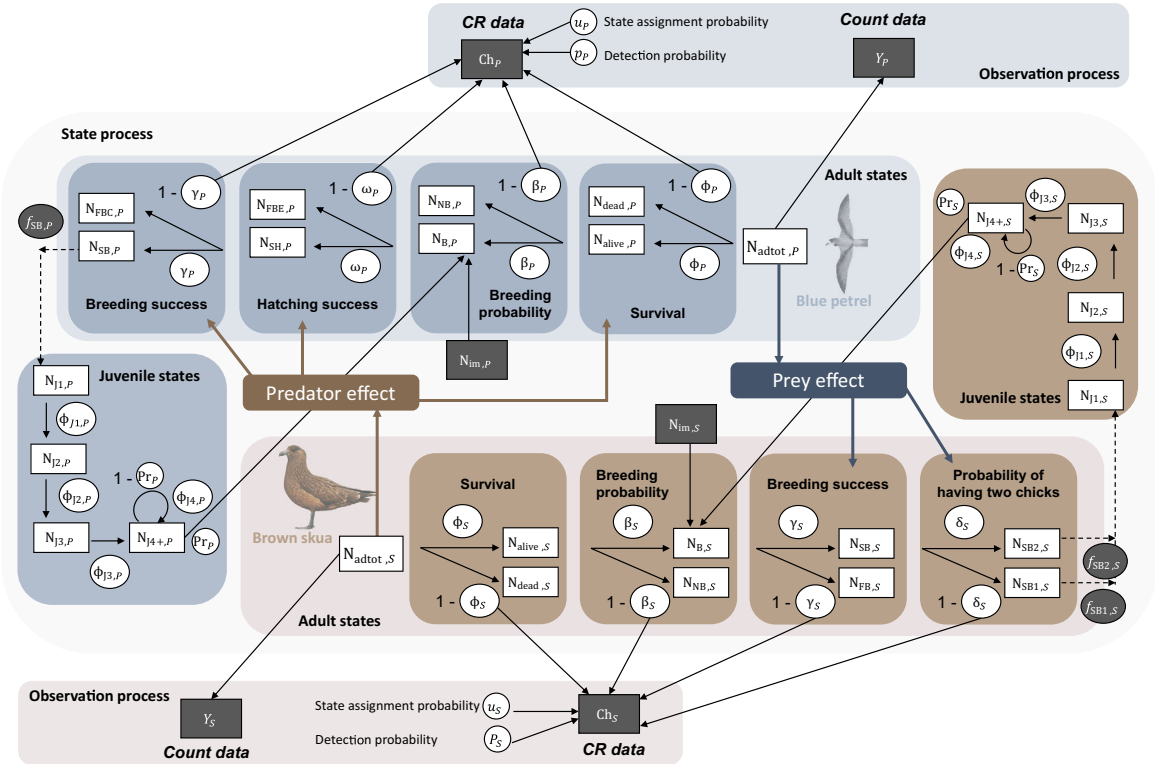


FIG. 1. Structure of the multispecies Integrated Population Model. Squares represent the state variables, circles represent the parameters. Data and fixed values are represented with a dark background, estimated state variables and parameters with a white background. Two types of data are used, capture histories (Ch) from capture–recapture data and count data (Y). Adult apparent survival (ϕ), breeding probability (β), hatching success (ω), breeding success (γ), probability of having two chicks rather than one (δ), apparent survival in each juvenile age class (ϕ_{J1} to ϕ_{J4}), probability of first breeding attempt (Pr), state assignment probability (u) and detection probability (p) are parameters estimated in the model. Fecundity (f) is fixed. The number of adults (N_{adtot}), dead (N_{dead}), alive (N_{alive}), breeders (N_B), nonbreeders (N_{NB}), failed breeders (N_{FB}), failed breeders at the egg stage (N_{FBE}), breeders with an egg hatched (N_{SH}), failed breeders at the chick stage (N_{FBC}), successful breeders (N_{SB}), successful breeders with one chick (N_{SB1}) or with two chicks (N_{SB2}) and the number of juveniles in each juvenile age class (N_{J1} to N_{J4+}) are state variables estimated in the model. The number of immigrants (N_{im}) is a fixed vector. The blue part is for Blue Petrels and the brown part is for Brown Skuas. Interspecific relationships are represented with thick arrows.

with a binomial distribution, with ϕ the adult apparent survival probability

$$N_{\text{alive},X,t} \sim \text{Bin}(\phi_{X,t-1}, N_{\text{adtot},X,t-1}) \quad (9)$$

Breeding probability.—The number of adult individuals that have bred or not bred among those that survived (N_{alive}) is modeled as

$$N_{\text{Balive},X,t} \sim \text{Bin}(\beta_{X,t-1}, N_{\text{alive},X,t}) \quad (10)$$

$$N_{\text{NB},X,t} = N_{\text{alive},X,t} - N_{\text{Balive},X,t} \quad (11)$$

with β the probability of breeding, N_{Balive} the number of adult breeders that survived, and N_{NB} the number of adult nonbreeders. As capture histories started at their first breeding attempt recorded, the immigrants, i.e., newly marked individuals (N_{im}) coming for the first time in the colony, were considered as breeders. Then, the total number of breeders (N_B) corresponds to the sum of

the number of adult breeders that survived (N_{Balive}), the number of immigrants (N_{im}), and the number of juveniles attempting to breed for the first time (N_{J4B})

$$N_{B,X,t} = N_{\text{Balive},X,t} + N_{J4B,X,t} + N_{\text{im},X,t} \quad (12)$$

Breeding success.—Breeding success and failure are modeled differently for skuas and petrels. For skuas, the numbers of failed breeders ($N_{\text{FB},S}$) and successful breeders ($N_{\text{SB},S}$) are modeled using a binomial distribution

$$N_{\text{SB},S,t} \sim \text{Bin}(\gamma_{S,t-1}, N_{B,S,t}) \quad (13)$$

$$N_{\text{FB},S,t} = N_{B,S,t} - N_{\text{SB},S,t} \quad (14)$$

with γ_S the probability of a successful breeding. A successful breeder can then have one or two chicks, respectively, $N_{\text{SB1},S}$ and $N_{\text{SB2},S}$ and this is modeled using a binomial distribution:

$$N_{\text{SB2},S,t} \sim \text{Bin}(\delta_{S,t-1}, N_{\text{SB},S,t}) \quad (15)$$

$$N_{\text{SB1},S,t} = N_{\text{SB},S,t} - N_{\text{SB2},S,t} \quad (16)$$

with δ_s the probability of having two chicks rather than one among the successful breeders.

For petrels, there are two states for failed breeders: one with petrels that failed to hatch their egg (named failed breeder at the egg stage $N_{\text{FBE},P}$) and the second with petrels that failed to fledge their chick (named failed breeder at the chick stage $N_{\text{FBC},P}$). Hence, there is a parameter of successful hatching (ω_p). The numbers of petrels with an egg that successfully hatched ($N_{\text{SH},P}$) and the failed breeders at the egg stage ($N_{\text{FBE},P}$) were modeled using a binomial distribution:

$$N_{\text{SH},P,t} \sim \text{Bin}(\omega_{P,t-1}, N_{B,P,t}) \quad (17)$$

$$N_{\text{FBE},P,t} = N_{B,P,t} - N_{\text{SH},P,t} \quad (18)$$

with ω_p the probability of successful hatching. Successful breeder numbers ($N_{\text{SB},P}$) and numbers of failed breeders at the chick stage ($N_{\text{FBC},P}$) follow a binomial distribution

$$N_{\text{SB},P,t} \sim \text{Bin}(\gamma_{P,t-1}, N_{\text{SH},P,t}) \quad (19)$$

$$N_{\text{FBC},P,t} = N_{\text{SH},P,t} - N_{\text{SB},P,t} \quad (20)$$

with γ_p the probability of successful breeding.

Total number of adults.—For skuas, the total number of adults ($N_{\text{adtot},S}$) corresponds to the sum of adult nonbreeders ($N_{\text{NB},S}$), failed breeders ($N_{\text{FB},S}$), successful breeders with one chick ($N_{\text{SB1},S}$), and successful breeders with two chicks ($N_{\text{SB2},S}$)

$$N_{\text{adtot},S,t} = N_{\text{NB},S,t} + N_{\text{FB},S,t} + N_{\text{SB1},S,t} + N_{\text{SB2},S,t} \quad (21)$$

For petrels, the total number of adults ($N_{\text{adtot},P}$) corresponds to the sum of adults nonbreeders ($N_{\text{NB},P}$), failed breeders at the egg stage ($N_{\text{FBE},P}$), failed breeders at the chick stage ($N_{\text{FBC},P}$), and successful breeders ($N_{\text{SB},P}$)

$$N_{\text{adtot},P,t} = N_{\text{NB},P,t} + N_{\text{FBE},P,t} + N_{\text{FBC},P,t} + N_{\text{SB},P,t} \quad (22)$$

Count data.—As only the adult states were observed on the field, we excluded the juvenile states from the observation equation. The observation equation links the observed adult population count (Y) (i.e., the number of territories/burrows multiplied by two for a pair of seabirds) with the true adult population size (N_{adtot}), with an additional term for observation error

$$Y_{X,t} \sim \text{Norm}(N_{\text{adtot},X,t}, \epsilon_X)$$

$$\epsilon_X \sim \text{Norm}(0, \sigma_{Y,X}^2) \quad (23)$$

where ϵ is the error term and σ_Y^2 its variance. The likelihood for the population count data is denoted as $L_{\text{co},S}(Y_S | \phi_{J1,S}, \phi_{J2,S}, \phi_{J3,S}, \phi_{J4,S}, \text{Pr}_S, \phi_S, \beta_S, \gamma_S, \delta_S, N_{\text{adtot},S}, \sigma_{Y,S}^2)$ for skuas and as $L(Y | \phi, \phi, \phi, \phi, \text{Pr}, \phi, \beta, \omega, \gamma, N, \sigma)$ for petrels.

Capture–recapture data.—For adult CR data, we used multievent capture–recapture models to estimate the demographic parameters (Pradel 2005). These models take into account the imperfect detectability of the individuals as well as the uncertainty in the assignment of states to individuals (Gimenez et al. 2012).

For skuas, our multievent model includes five states, NB, FB, SB1, SB2, dead, and six events, not seen, seen as NB, seen as FB, seen as SB1, seen as SB2, seen as C, i.e., individuals seen with an uncertain breeding status. For petrels, the five states are NB, FBE, FBC, SB, dead, and the six events are not seen, seen as NB, seen as FBE, seen as FBC, seen as SB, seen as C. The following demographic parameters were estimated for the two species: the adult apparent survival probability (ϕ_X), the breeding probability (β_X), and the probability of successful breeding (γ_X). The probability of having two chicks (δ_S) was also estimated for skuas, as well as the probability of hatching (ω_p) for petrels. Two additional parameters were also estimated: the detection probability (p_X) and the state assignment probability of individuals with uncertain state (u_X). All parameters were time-varying through a yearly random effect, except u (Table 1). State transitions were set to be state dependent according to the breeding status in the previous breeding season (Table 1): breeder (\tilde{B}) representing birds that attempted to breed in the previous breeding season (FB, SB1, SB2 for skuas or FBE, FBC, SB for petrels) or nonbreeder (NB) representing birds that already bred previously but did not attempt to breed during the previous breeding season (NB). The detection probability and the state assignment probability also depended on the breeding status (Table 1). The likelihood for the CR data for skuas is denoted as $L_{\text{cr},S}(\text{Chs} | \phi_S, \beta_S, \gamma_S, \delta_S, p_S, u_S)$ and $L_{\text{cr},P}(\text{Chp} | \phi_P, \beta_P, \gamma_P, \delta_P, p_P, u_P)$ for petrels.

Joint likelihood.—The joint likelihood of the skua IPM is the product of the likelihood for the count data ($L_{\text{co},S}$) and CR data ($L_{\text{cr},S}$)

$$\begin{aligned} L_{\text{ipm},S}(Y_S, \text{Chs} | \phi_{J1,S}, \phi_{J2,S}, \phi_{J3,S}, \phi_{J4,S}, \text{Pr}_S, \phi_S, \beta_S, \gamma_S, \\ \delta_S, N_{\text{adtot},S}, p_S, u_S, \sigma_{Y,S}^2) = L_{\text{co},S}(Y_S | \phi_{J1,S}, \phi_{J2,S}, \phi_{J3,S}, \\ \phi_{J4,S}, \text{Pr}_S, \phi_S, \beta_S, \gamma_S, \delta_S, N_{\text{adtot},S}, \sigma_{Y,S}^2) \\ \times L_{\text{cr},S}(\text{Chs} | \phi_S, \beta_S, \gamma_S, \delta_S, p_S, u_S). \end{aligned} \quad (24)$$

TABLE 1. Summary of the demographic parameters and their specificities (year random effect or state dependence) for the two species: the Brown Skua (top) and the Blue Petrel (bottom).

Parameter	Year random effect	State dependence
Skua		
Adult apparent survival ϕ_S	✓	$\tilde{NB}_S \tilde{B}_S$
Breeding probability β_S	✓	$\tilde{NB}_S \tilde{B}_S$
Breeding success γ_S	✓	$\tilde{NB}_S \tilde{B}_S$
Probability of having two chicks δ_S	✓	$\tilde{NB}_S \tilde{B}_S$
Detection probability p_S	✓	$NB_S B_S$
Uncertain state assignment probability u_S	✗	$NB_S FB_S SB1_S SB2_S$
Petrel		
Adult apparent survival ϕ_P	✓	$\tilde{NB}_P \tilde{B}_P$
Breeding probability β_P	✓	$\tilde{NB}_P \tilde{B}_P$
Hatching success ω_P	✓	$\tilde{NB}_P \tilde{B}_P$
Breeding success γ_P	✓	$\tilde{NB}_P \tilde{B}_P$
Detection probability p_P	✓	$NB_P B_P$
Uncertain state assignment probability u_P	✗	$NB_P FBE_P FBC_P SB_P$

Notes: Notations are \tilde{NB} , nonbreeder in the previous breeding season; \tilde{B} , breeder in the previous breeding season; NB , nonbreeder; B , breeder; FB , failed breeder; $SB1$, successful breeder with one fledged chick; $SB2$, successful breeder with two fledged chicks; FBE , failed breeder at the egg stage; FBC , failed breeder at the chick stage; and SB , successful breeder.

For petrels, the product of the likelihood for the count data ($L_{co,P}$) and CR data ($L_{cr,P}$) is denoted as $L_{ipm,P}(Y_P, Ch_P | \phi_{J1,P}, \phi_{J2,P}, \phi_{J3,P}, \phi_{J4,P}, Pr_P, \phi_P \beta_P, \omega_P, \gamma_P, N_{adtot,P}, p_P, u_P, \sigma_{Y,P}^2)$.

Interspecific relationships, intraspecific density dependence, and environmental covariates

Different covariates have been assumed to affect adult demographic parameters depending on the species (Table 2). We focused on demographic parameters of

adult individuals, because only adults were observed in the field. We estimated interspecific predator–prey relationships between skua and petrel (dependence of vital rates on the other species density) and intraspecific relationships (dependence of vital rates on the focal species density) for both species. Moreover, we considered several climatic covariates that were suspected to affect demographic parameters of skuas and petrels, the southern annular mode (SAM) on a large scale, and the sea surface temperature anomalies (SSTa), and chlorophyll *a* concentration (Chl *a*) on a local scale. In the following, we provide more details on covariates and how they may affect the demography of skuas and petrels.

Predator–prey interactions.—Multispecies IPMs allow us to explicitly include interspecific relationships between vital rates of one species and estimated population sizes of the other. Based on the high proportion of petrels in the diet of the skuas during the breeding season (Mougeot et al. 1998, Pacoureaux et al. 2019c), we predicted that petrel adult apparent survival (ϕ_P) should decrease with the number of skuas. As skuas prey on adults and chicks during the fledging period, we predicted that the hatching success (ω_P) and fledging success (γ_P) would be impacted by the number of predators. Conversely, we predicted that a large number of petrels in the breeding colony would provide enough food resources for skua and then be favorable to their breeding success (γ_S) and probability of having two chicks (δ_S).

Intraspecific density dependence.—We investigated the effect of intraspecific density dependence on the demography of the two species, as a higher density of individuals on the breeding ground can lead to an increased competition for food resources or for territories. Skuas are highly territorial and defend their territories vigorously during the whole breeding season. The most violent fights may even lead to their death. Moreover, the limited number of territories could cause emigration of

TABLE 2. Summary of the covariates tested on the demographic parameters of the two species, the Brown Skua (top) and the Blue Petrel (bottom), and the time period (in months) considered for each demographic parameter.

Parameter	Covariates tested	Time period
Skua		
Adult apparent survival ϕ_S	DDISAM	wintering (March–September)
Breeding probability β_S	DDISAM	pre-breeding (July–November)
Breeding success γ_S	PPIDDISAM	breeding (October–February)
Probability of having 2 chicks δ_S	PPIDDISAM	breeding (October–February)
Petrel		
Adult apparent survival ϕ_P	PPIDDISAMISSTaChl <i>a</i>	wintering (February–September)
Breeding probability β_P	DDISAMISSTaChl <i>a</i>	pre-breeding (August–October)
Hatching success ω_P	PPIDDISAMISSTaChl <i>a</i>	breeding (October–December)
Breeding success γ_P	PPIDDISAMISSTaChl <i>a</i>	breeding (December–January)

Notes: Notations are PP, predator–prey interactions; DD, intraspecific density dependence; SAM, southern annular mode; SSTa, sea surface temperature anomalies; Chl *a*, chlorophyll *a* concentration.

skuas without a territory. Thus, we predicted that the apparent survival probability (ϕ_S), which represents both mortality and emigration, would be negatively impacted by the number of skuas. This limited number of territories could also lead to a negative relationship between breeding probability (β_S) and population density. The time spent defending a territory throughout the breeding season, together with its energetic cost, may limit the time spent searching for food, which potentially limits energy investment in reproduction. We thus predicted a negative effect of population density on the successful breeding parameter (γ_S) and the probability of having two chicks rather than one for successful breeders (δ_S). For petrels, we also tested the effects of intraspecific competition for food resources, which could affect their adult apparent survival (ϕ_P) and their breeding parameters: breeding probability (β_P), hatching (ω_P), and fledging success (γ_P).

Environmental covariates.—Climate variability impacts biological processes in marine ecosystems, which cascade through food webs and are integrated by seabirds (Barbraud and Weimerskirch 2001, Jenouvrier et al. 2003). Hence, we considered several covariates that are suspected to affect populations of petrels and skuas through these bottom-up mechanisms. All covariates are used as proxies of food availability at sea at different scales. In the following, we explain how environmental conditions may impact the two species based on their diet and distribution.

Because skuas have broad wintering areas (Delord et al. 2018), we tested a large-scale environmental covariate, the SAM. While skuas are specialized on the Blue Petrel during the breeding season, during winter skuas adopt a mixed diet composed of low trophic level prey items, such as macrozooplankton and crustaceans (Delord et al. 2018). We hypothesized that availability of food resources at sea during the austral winter might have an effect on the body condition of skuas and then affect their survival. Moreover, skuas may experience a carry-over effect: the additional energy invested by individuals to maintain their body condition in poor wintering environments may influence their ability to breed in the next breeding season (Harrison et al. 2011, Bogdanova et al. 2017).

For petrels, the wintering areas have been determined (Cherel et al. 2016) allowing us to test two covariates used at the local scale, SSTa and Chl *a*, in addition to the SAM. As their diet is mainly composed of crustaceans and fish feeding at low trophic levels (Cherel et al. 2002, 2014), food availability at sea may impact the survival of petrels. Moreover, during the breeding season, male and female petrels take turns, one incubating the egg and fasting while the other is foraging at sea, which results in substantial variation in their body mass (Chaurand and Weimerskirch 1994*a, b*, Weimerskirch et al. 1994, Chastel et al. 1995). Therefore, high food availability at sea may allow the foraging partner to

return to land after a short stay at sea, resulting in a good synchronization of the breeding partners. In contrast, poor conditions could increase the time spent at sea by the foraging partner, which would increase desertion of the nest by the fasting partner and then, reduce the breeding success. We thus predicted that conditions at sea during the breeding season would also affect the breeding success of petrels.

Southern annular mode.—The SAM is a large-scale climate index. SAM is the leading mode of climate variability over the Southern Hemisphere. SAM is defined as the difference of atmospheric pressure between the 40° S and 65° S latitudes (Marshall 2003). SAM influences surface wind, sea surface temperature (SST) and surface Chlorophyll concentration. A large majority of the skuas from Mayes Island overwinter north of the polar front (Delord et al. 2018). In the subtropical zone, SAM positive phases induced warm SSTa, low surface chlorophyll concentration and easterly winds driving Ekman transport (the 90° wind-driven net transport on the sea surface), while in the subantarctic zone there is a convergence of waters that increase downwelling and positive SSTa (Lovenduski and Gruber 2005). We thus predicted that the positive phases of SAM, potentially leading to poorer food availability in the areas used by skuas during the nonbreeding period, would have negative impacts on skua survival and limit their ability to breed the next breeding season. South of the polar front, where petrels spend the winter, positive phases of the SAM are associated with westerly winds. This induces cold SSTa, increased equatorward Ekman transport, and drives increased upwelling (Lovenduski and Gruber 2005). Consequently, the biological productivity and potential prey availability for petrels are higher during positive phases of the SAM. We thus predicted that the positive phases of SAM would be favorable for petrel demographic parameters. Data were obtained from the online database of the British Antarctic Survey (*available online*).⁷

Sea surface temperature anomalies.—SSTa reflect local oceanographic conditions that influence the whole marine food web. High SST generally reduces vertical mixing and provides poor growing conditions for zooplankton communities, which, through bottom-up mechanisms, induces reduced trophic resources for seabirds (Barbraud et al. 2012, Sydeman et al. 2015). Consequently, year-to-year variation of SST was previously found to be negatively correlated with petrel body condition (Guinet et al. 1998). Therefore, we predicted that high SSTa would negatively affect overwinter survival and breeding success of petrels. The SSTa data were downloaded from the National Oceanic and Atmospheric Administration (data: NOAA NCEP EMC CMB GLOBAL Reynolds-SmithOIv2 monthly ssta) from 1996 to 2018.

⁷<http://www.nerc-bas.ac.uk/icd/gjma/sam.html>

Chlorophyll a.—Chlorophyll *a* is found in phytoplankton that lies at the bottom of the marine food web and provides resources for higher trophic levels. Because petrel diet is mainly composed of crustaceans and fish feeding at low trophic levels (Cherel et al. 2002, 2014), we predicted that high concentrations of Chl *a* would be favorable to the survival and breeding success of petrels. The Chl *a* data were downloaded from the NASA Ocean Data with a 9 km mapped concentration data of chlorophyll *a* for the years 1997–2001 and from the NASA Earth Observation (NEO AQUA/MODIS data) monthly for the years 2002 to 2018.

Assessing the effect of environmental covariates and population densities.—We fitted a single multispecies IPM including all the biologically relevant effects. Logit-linear regressions were used to estimate the effect of environmental (SAM, SSTa, and Chl *a*) as well as inter- and intraspecific interactions on demographic parameters (adult apparent survival, breeding probability, hatching probability, breeding success; Table 2). We used state variables $N_{\text{adtot},S}$ and $N_{\text{adtot},P}$, respectively the number of adult skuas and petrels, to assess the effects of inter- and intraspecific interactions. For example, we modeled the hatching probability for petrels that bred during the previous breeding season ($\omega_{P,\bar{B}}$) using a logit link

$$\begin{aligned} \text{logit}(\omega_{P,\bar{B},t-1}) = & \mu_{\omega,P,\bar{B}} + \alpha_{\text{SAM},\omega,P,\bar{B}} \times \text{SAM}_{\omega,P,t} \\ & + \alpha_{\text{SSTa},\omega,P,\bar{B}} \times \text{SSTa}_{\omega,P,t} + \alpha_{\text{Chla},\omega,P,\bar{B}} \\ & \times \text{Chla}_{\omega,P,t} + \alpha_{\text{DD},\omega,P,\bar{B}} \times N_{\text{adtot},P,t} \\ & + \alpha_{\text{PP},\omega,P,\bar{B}} \times N_{\text{adtot},S,t} + \varepsilon_{\omega,P,\bar{B},t} \\ \varepsilon_{\omega,P,\bar{B},t} \sim & \text{Norm}(0, \sigma_{\varepsilon,\omega,P,\bar{B}}^2) \end{aligned} \quad (25)$$

with $\mu_{\omega,P,\bar{B}}$ the intercept, $\alpha_{\text{SAM},\omega,P,\bar{B}}$ the slope for the climatic covariate SAM $_{\omega,P}$, $\alpha_{\text{SSTa},\omega,P,\bar{B}}$ the slope for the climatic covariate SSTa $_{\omega,P}$, $\alpha_{\text{Chla},\omega,P,\bar{B}}$ the slope for the climatic covariate Chla $_{\omega,P}$, $\alpha_{\text{DD},\omega,P,\bar{B}}$ the slope indicating the strength of the intraspecific density dependence with $N_{\text{adtot},P}$ the number of adult petrels, $\alpha_{\text{PP},\omega,P,\bar{B}}$ the slope indicating the strength of the predator–prey relationship with $N_{\text{adtot},S}$ the number of adult skuas, $\varepsilon_{\omega,P,\bar{B}}$ is a yearly random effect and $\sigma_{\varepsilon,\omega,P,\bar{B}}^2$ its temporal variance. This temporal random effect allows to capture residual environmental stochasticity that is not explained by temporal covariates. The descriptions of all logit-linear relationships used on demographic parameters are available in Appendix S2 and the within-year ordering of state variables, parameters and covariates is described in Appendix S3: Fig. S1.

For local covariates (SSTa and Chl *a*), we calculated the average values of the covariates in the areas in which petrels were located (Cherel et al. 2016), for a specific time period during which the environment might affect the demographic parameter under investigation (Table 2). Each environmental covariate was

standardized to have zero mean and unit variance. However, the inter- and intraspecific covariates were not standardized prior to the analyses because the population sizes were estimated step by step each year. To compare the relative contribution of the effects of each covariate, we calculated the standardized effect of population size (for inter- and intraspecific relationship) posterior to the analyses by multiplying their slopes (α) by the standard deviation of the estimated population sizes. Then, we compared the relative contribution of each covariate using the regression estimate which we used as a measure of effect size.

We computed the 95% and 80% credible intervals (CRI) for the regression coefficients α . We did not interpret uncertain effects (i.e., 80% CRI including zero) and focused particularly on clear effects whose sign could be reliably assessed (i.e., 95% CRI excluding zero).

Model implementation

To fit the juvenile apparent survival parameters increasing with age, we modeled them as a positive linear function of age by assigning to the slope λ_2 a $U(0, 1)$ prior, and by defining the intercept λ_1 with a normal $N(0, 1)$ prior. The probability of the first breeding attempt Pr_t is time-dependent with a uniform prior: $\text{Pr}_t \sim U(0, 1)$. The state assignment probability of individuals with uncertain state parameter (u) was defined a priori with a $U(0, 1)$ prior. We specified vague priors for the parameters: $\sigma_{Y,S} \sim U(1, 15)$, $\sigma_{Y,P} \sim U(1, 100)$, $\sigma_{\varepsilon} \sim U(0, 10)$, $\alpha \sim N(0, 10^4)$, $\mu \sim N(0, 10^4)$.

Bayesian posterior distributions were approximated via Markov chain Monte Carlo (MCMC) algorithms. Two independent MCMC chains of 190,000 iterations were used with a burn-in period of 90,000. One out of five iterations was kept and final inferences were derived from a sample of $2 \times 20,000$ iterations that resulted from merging the two chains. Gelman-Rubin convergence diagnostics (Brooks and Gelman 1998) were below 1.5 for each parameter and the mixing of the chains was satisfactory. We performed the analyses using Nimble (de Valpine et al. 2017; version 0.9.1) and program R (R Core Team 2020; R version 4.0.3).

RESULTS

Predator–prey relationships

We estimated positive relationships between the two breeding parameters of skuas and the number of adult petrels. The breeding success for at least one chick ($\gamma_{S,\bar{B}}$; slope mean $\alpha_{\text{PP},\gamma,S,\bar{B}} = 0.67$; 95% CRI 0.38, 1.04; Fig. 2a) and the probability of having two chicks ($\delta_{S,\bar{B}}$; slope mean $\alpha_{\text{PP},\delta,S,\bar{B}} = 1.28$; 95% CRI 0.67, 2.08; Fig. 2b) for skuas that were breeders during the previous breeding season increased with petrel numbers. Even though the effects were less clear (95% CRI including zero), we detected a positive relationship between the number of

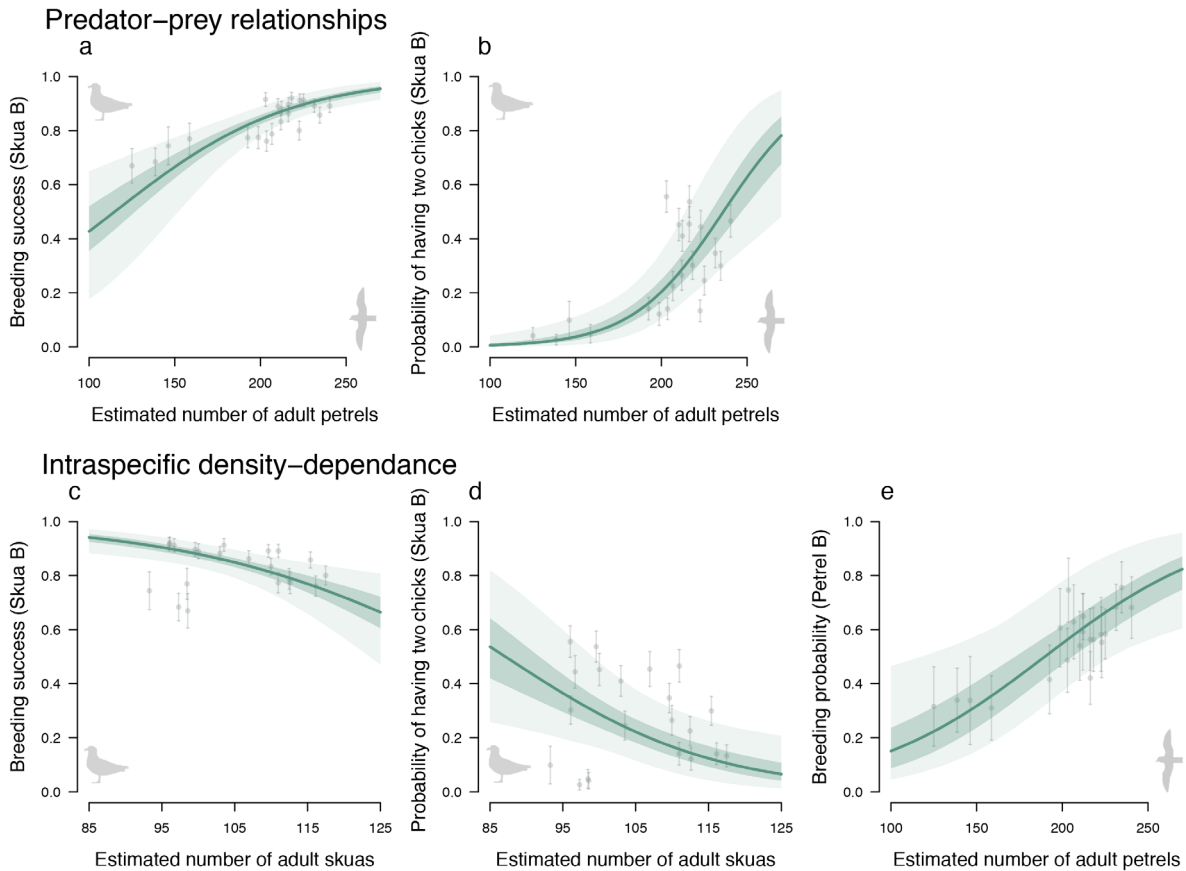


FIG. 2. Effects of predator–prey relationships (top panels) and intraspecific density dependence (bottom panels) on adult demographic parameters for the two seabirds, the Brown Skua (predator) and the Blue Petrel (prey). Solid lines represent the estimated relationship between the covariates and the demographic parameters. Shaded areas are the 50% and 95% credibility intervals. Points represent demographic parameter estimates each year (21 yr) plotted against covariate values. Error bars are standard deviations. Petrel numbers effect on (a) the estimated breeding success $\gamma_{S,\bar{B}}$ and (b) the probability of having two chicks rather than one $\delta_{S,\bar{B}}$ for skuas that bred in the previous breeding season. Intraspecific density dependence effect on (c) the breeding success $\gamma_{S,\bar{B}}$ and on (d) the probability of having two chicks rather than one $\delta_{S,\bar{B}}$ for skuas that were breeders in the previous breeding season and on (e) the breeding probability of petrels that bred in the previous breeding season $\beta_{P,\bar{B}}$.

adult skuas and the hatching success of petrels that were breeders in the previous breeding season ($\omega_{P,\bar{B}}$), with the breeding success ($\gamma_{P,\bar{N}\bar{B}}$) and with the apparent survival ($\phi_{P,\bar{N}\bar{B}}$) of petrels that were nonbreeders during the previous breeding season. We found no other interspecific relationship on the other parameters i.e., without the 80% CRI including zero (Table 3).

Intraspecific density dependence

The number of skuas had a clear effect on two demographic parameters, namely the breeding success and the probability of having two chicks rather than one, for skuas that were breeders in the previous breeding season. We found negative density dependence for the breeding success ($\gamma_{S,\bar{B}}$; slope mean $\alpha_{DD,\gamma,S,\bar{B}} = -0.40$; 95% CRI $-0.66, -0.15$; Fig. 2c) and for the probability of having two chicks ($\delta_{S,\bar{B}}$; slope mean $\alpha_{DD,\delta,S,\bar{B}} = -0.54$;

95% CRI $-1.04, -0.13$; Fig. 2d). As these two breeding parameters were also affected by the other species density, we could observe that the predator–prey effects were stronger than intraspecific effects ($|\text{mean } \alpha_{PP,\gamma,S,\bar{B}}| = 0.67$; $|\text{mean } \alpha_{DD,\gamma,S,\bar{B}}| = 0.40$, respectively) for the breeding success and ($|\text{mean } \alpha_{PP,\delta,S,\bar{B}}| = 1.28$; $|\text{mean } \alpha_{DD,\delta,S,\bar{B}}| = 0.54$, respectively) for the probability of having two chicks (Table 3).

We estimated a positive effect of increased numbers of adult petrels on the breeding probability for petrels that were breeders in the previous breeding season ($\beta_{P,\bar{B}}$; slope mean $\alpha_{DD,\beta,P,\bar{B}} = 0.65$; 95% CRI 0.19, 1.06; Fig. 2e). Even though the effects were less clear (95% CRI including zero), the number of petrels tended to negatively affect the apparent survival ($\phi_{P,\bar{N}\bar{B}}$) and the breeding success ($\gamma_{P,\bar{N}\bar{B}}$) of petrels that did not breed in the previous breeding season (Table 3).

TABLE 3. Regression coefficients for the relationships between covariates (DD: intraspecific density dependence; PP: predator-prey interactions; SAM: southern annular mode; SSTa, sea surface temperature anomalies; Chl *a*, chlorophyll *a* concentration) and demographic parameters (ϕ , adult apparent survival; β , breeding probability; γ , breeding success; δ , probability of having two chicks rather than one; ω , hatching success) for Brown Skuas (top) and Blue Petrels (bottom); B, breeders or NB, nonbreeders in the previous breeding season.

Parameters	DD				PP				SAM				SSTa				Chl <i>a</i>			
	Slope	SD	10%	90%	Slope	SD	10%	90%	Slope	SD	10%	90%	Slope	SD	10%	90%	Slope	SD	10%	90%
Skua																				
$\phi_{S,B}$	-0.09	0.11	-0.22	0.06																
$\phi_{S,NB}$	-0.12	0.16	-0.29	0.10																
$\beta_{S,B}$	0.22	0.22	-0.09	0.51																
$\beta_{S,NB}$	0.09	0.19	-0.18	0.32																
$\gamma_{S,B}$	-0.40	0.13	-0.57	-0.24	0.67	0.17	0.47	0.89	-0.10	0.18	-0.33	0.13								
$\gamma_{S,NB}$	-0.26	0.28	-0.59	0.12	0.28	0.40	-0.20	0.77	-0.24	0.60	-0.96	0.48								
$\delta_{S,B}$	-0.54	0.23	-0.86	-0.25	1.28	0.36	0.86	1.74	-0.29	0.37	-0.75	0.15								
$\delta_{S,NB}$	-0.41	0.45	-0.96	0.17	0.69	0.96	-0.48	1.71	-0.53	1.65	-2.30	1.33								
Petrel																				
$\phi_{P,B}$	-0.12	0.31	-0.51	0.26	0.27	0.25	-0.05	0.58	-0.05	0.39	-0.54	0.42	-0.16	0.23	-0.45	0.12	-0.57	0.46	-1.14	0.01
$\phi_{P,NB}$	-0.99	0.73	-1.87	-0.12	0.73	0.33	0.27	1.10	1.37	2.28	-0.88	3.88	0.12	1.00	-0.91	1.37	-1.42	1.46	-2.83	0.15
$\beta_{P,B}$	0.65	0.23	0.35	0.95					-0.23	0.32	-0.65	0.17	0.11	0.24	-0.18	0.39	0.36	0.44	-0.21	0.88
$\beta_{P,NB}$	0.34	0.33	-0.10	0.74					0.11	0.37	-0.33	0.55	0.31	0.25	0.03	0.64	0.78	0.46	0.24	1.36
$\omega_{P,B}$	0.14	0.23	-0.14	0.43	0.29	0.12	0.15	0.43	0.29	0.17	0.09	0.50	0.13	0.15	-0.06	0.32	-0.23	0.28	-0.56	0.11
$\omega_{P,NB}$	-0.39	0.44	-0.88	0.06	0.29	0.28	-0.05	0.62	0.64	0.39	0.18	1.13	0.01	0.37	-0.44	0.45	-0.26	0.57	-0.95	0.44
$\gamma_{P,B}$	-0.13	0.55	-0.76	0.54	-0.05	0.27	-0.37	0.27	0.53	0.33	0.13	0.95	-0.34	0.33	-0.74	0.02	-0.19	0.52	-0.79	0.45
$\gamma_{P,NB}$	-1.01	0.56	-1.71	-0.39	0.61	0.30	0.22	0.99	0.42	0.48	-0.18	0.97	-0.51	0.47	-1.10	0.05	-0.85	0.77	-1.84	0.03

Note: 80% credible intervals that do not include zero are in boldface type.

Environmental covariates

We found ecologically relevant relationships between environmental covariates and demographic parameters of the two species (Table 3). For petrels, we found positive relationships between the two local environmental covariates (SSTa and Chl *a*) and the breeding probability for individuals that were nonbreeders in the previous breeding season ($\beta_{P,NB}$). The effect of these environmental covariates on the breeding probability was stronger for Chl *a* than SSTa ($|\text{mean}\alpha_{\text{Chl}a, \beta, P, NB}| = 0.78$; $|\text{mean}\alpha_{\text{SST}a, \beta, P, NB}| = 0.31$, respectively). We estimated a positive relationship between the SAM and the hatching success ($\omega_{P,B}$) as well as breeding success ($\gamma_{P,B}$) of petrels that were breeders in the previous breeding season and with the hatching success ($\omega_{P,NB}$) of petrels that were nonbreeders in the previous breeding season. For skuas, we also found a positive relationship between the SAM and the breeding probability ($\beta_{S,NB}$) of skuas that were nonbreeders in the previous breeding season.

In addition to the results above, we also estimated the demographic parameters and the number of individuals in each state for both species from 1996 to 2017 (see Appendix S4: Figs. S1–S6).

DISCUSSION

In this paper, we provide the first application of a multispecies IPM in a predator–prey context. Joint analysis of empirical data for two seabird species allowed us to estimate demographic parameters and population size for both species simultaneously. The key advantage of using a multispecies IPM was that it enabled us to use the population sizes estimated by the model for one species to analyze its effect on the demographic parameters of the other species while propagating all sources of uncertainty. Hence, it allowed us to understand the contribution of interspecific interactions on the demographic parameters while further taking into account the effects of climatic conditions. Our results showed that the demography of the predatory skua was mainly driven by the number of petrel prey individuals during the breeding season, whereas petrels were mostly impacted by the environment. This suggests that this predator–prey system is mainly driven by bottom-up processes.

Effects of predator–prey relationships

Prey population size is a determining factor in the breeding success of skuas according to our results. Food availability is known to be positively related with breeding parameters in seabirds (Cairns 1988, Piatt et al. 2007, Oro et al. 2014). As the diet of skuas during the breeding period is dominated by petrels (Mougeot et al. 1998, Pacoureaux et al. 2019c), a large abundance of petrels provides suitable conditions for skuas to feed

themselves and their chicks, resulting in a high breeding success.

Interestingly, we did not find the reverse effect of the predator onto prey dynamics. Our model provided no evidence for a negative effect of the number of skuas on the demographic parameters of the petrel (effects were mostly positive whenever present). As skuas prey on both adults and juveniles during the breeding season, we expected a negative effect of the number of skuas on the petrel breeding parameters. This lack of negative effect could be explained by the large abundance of petrels compared to the skuas on Mayes Island. Oro et al. (2006) reported that, in another seabird predator–prey system, the highest breeding success of the prey occurred when the prey/predator ratio was very high. On Mayes Island, the breeding population of petrels is estimated at approximately 142,000 breeding pairs (Barbraud and Delord 2006), and this does not include chicks (around 71,000 each year) and nonbreeders (approximately 30% of the petrels). Hence, there are about 476,000 petrels during a breeding season vs. about 200 skuas, resulting in a very high prey/predator ratio. Moreover, Mougeot et al. (1998) showed that skuas breeding at Mayes Island preyed on about 40,000 petrels each breeding season. This corresponds to about 8% of the petrel population of the island. It is therefore possible that skua predation is only a minor contributor to petrel demographics, and this effect may be too weak to be detected by our model. Conversely, although the relationships estimated were less clear, our results suggest that the hatching success and breeding success of the prey tended to increase slightly with the density of skuas. However, it is unlikely that the presence of predators increased the reproductive success or survival of petrels. To explain these relationships, we might rely on the other strong effects estimated by our model. Indeed, we found that the number of petrels positively affected the breeding success of skuas and that skuas were sensitive to intraspecific density dependence. Therefore, years when prey experience a high survival and breeding success correspond to years with particularly abundant food resources for skuas and this until the end of the breeding season as petrels stay longer on the breeding area when they successfully breed. Since skuas are less affected by abundance of conspecifics than by abundance of prey, they could potentially breed in higher numbers in good years for petrel reproduction, explaining this puzzling relationship.

Effects of intraspecific density dependence

For skuas, we found negative density-dependent effects on breeding success and probability of having two chicks rather than one, in accordance with our predictions. Egg and chick predation by conspecifics has been reported in the Great Skua (*Catharacta skua*) (Hamer et al. 1991, Ratcliffe and Furness 1999). Hence, a higher abundance of skuas increases the risk of predation on eggs and chicks, resulting in higher breeding failure. To avoid

predation by conspecifics, the skuas start defending their territories from conspecifics just a few days after arrival on a breeding site until the end of the season. This activity is energetically costly and may also limit the time spent searching for food, potentially limiting energy investment in reproduction. The heterogeneous habitat hypothesis already demonstrated in territorial birds (Dhondt et al. 1992, Krüger and Lindström 2001, Ferrer and Donazar 2015) could also explain the relationships we found. Indeed, when the population increases, some individuals may be forced to occupy poorer quality habitats, resulting in lower reproductive success. We did not find an effect of density dependence on the breeding probability of skuas. As skuas are territorial with high site fidelity, we initially hypothesized that in years with a high abundance of skuas, the breeding probability would decrease, as all the skuas would not succeed in acquiring a territory. It is possible that we did not observe this effect because the logistic function used for density dependence does not accurately model the territory acquisition dynamics by floaters (e.g., van de Pol et al. 2010, Barraquand et al. 2014).

We estimated that the breeding success of skuas was affected by both predator–prey relationships and intraspecific density dependence. Predator–prey relationships had a higher contribution to the variability in breeding success of skuas than the density-dependent effect. Hamer et al. (1991) reported that, following a reduction of sandeel (*Ammodytes marinus*) abundance, Great skuas increased their foraging effort, thereby reducing the adult territorial attendance. In turn, breeding failure increased due to predation from adults of neighboring territories. We then may assume that petrel abundance allowed a suitable territorial attendance for skuas, moderating the negative density-dependent effects, such as chick predation by conspecifics.

For petrels, we found a negative relationship between the survival and breeding success of petrels that did not breed in the previous breeding season and the number of petrels on the colony. Combined effects of density dependence and climate have already been observed in petrels, with a low winter survival when density is high (Barbraud and Weimerskirch 2003), suggesting a mechanism of competition between conspecifics for food resources. As nonbreeders are known to be in poorer condition than breeders (Chastel et al. 1995), they are potentially more sensitive to the competition for food resources explaining why this effect was only found on petrels that were nonbreeders in the previous breeding season. Interestingly, we found a positive intraspecific density dependence on the breeding probability of petrels that bred in the previous breeding season. This suggests that years with a high abundance of petrels reflected a good return rate to the breeding site because environmental conditions were favorable for breeding. This is in agreement with studies showing that petrels might skip breeding and take sabbatical years when

environmental conditions are poor (Warham 1990, Chastel et al. 1995).

Effects of environmental conditions

We detected positive relationships between the hatching and breeding success of petrels and the SAM. South of the polar front, where petrels feed during the breeding season, positive phases of the SAM increase the biological productivity and potential prey availability for petrels (Lovenduski and Gruber 2005), which may have a positive impact on their breeding success. Breeding probability of petrels tended to be positively impacted by two of the environmental covariates tested, namely SSTa and Chl *a*. This effect of environmental conditions on the breeding probability is in accordance with previous research showing that the body condition of petrels might impact their decision to attempt breeding (Warham 1990, Chastel et al. 1995). High Chl *a* increases resources availability for organisms at higher trophic levels (macrozooplankton, fishes), which are consumed by petrels (Cherel et al. 2002). Consequently, high Chl *a* may increase abundance of petrel prey, with a positive effect on the breeding performances and body condition of petrels. We detected a positive effect of SSTa on breeding probability of petrels. This result was more surprising as a previous study showed that warm SST events negatively affected the breeding performances and body condition of petrels at Kerguelen Islands (Guinet et al. 1998). Indeed, high SST generally reduces vertical mixing and provides poor growing conditions for zooplankton communities that in turn reduce trophic resources for seabirds (Barbraud et al. 2012, Sydeman et al. 2015). However, it has been showed recently that during the pre-laying period petrels use water masses situated at more northerly latitudes than during the winter period or the breeding period (Quillfeldt et al. 2020), where relationships between SST and primary productivity may differ. Indeed, the covariance between SST and Chl *a* depends on location and shows particularly complex patterns in the Southern Ocean (Dunstan et al. 2018). Positive effects of SSTa have already been identified in other subantarctic seabirds (Pinaud and Weimerskirch 2002, Nevoux et al. 2007, Horswill et al. 2014). Furthermore, we estimated that Chl *a*, at the bottom of the trophic food chain, had a larger effect on the breeding probability than SSTa, which reflects oceanographic conditions. This indicated that the effect size of environmental covariates increased when the covariates approached the trophic level occupied by the prey of the petrels, suggesting a bottom-up mechanism. This result is consistent with many studies showing that climatic conditions affect seabirds indirectly through prey availability, resulting in alterations of their population dynamics (Frederiksen et al. 2006, Barbraud et al. 2012, Jenouvrier 2013, Lauria et al. 2013).

We did not detect any relationship between the breeding success of the skuas and the environmental

covariates. This lack of effect could be explained by an absence of a direct link between skuas and the environmental covariates tested, as breeding skuas remain on their territory to defend it or to forage. However, we found an effect of SAM on the breeding probability for skuas that were nonbreeders during the previous season. It was proposed that only seabirds attaining a threshold condition decide to breed (Weimerskirch 1992). Therefore, environmental conditions before the breeding period may impact the conditions of skuas and consequently, their breeding decision. Nonbreeders are generally in poorer conditions than breeders (Chastel et al. 1995, Cam et al. 1998) and thus more sensitive to environmental conditions explaining why this effect is only detected on previous nonbreeders. Nevertheless, we found a positive relationship between breeding probability and SAM whereas we expected a negative relationship. Indeed, skuas mainly overwinter north of the polar front (Delord et al. 2018) where positive phases of SAM induce warm SST, low surface Chl *a* concentration (Lovenduski and Gruber 2005), and thus potentially poor feeding conditions. However, only breeding skuas were studied in Delord et al. (2018) and nonbreeding individuals may use different wintering areas where the relationships between SAM and oceanographic variables differ. Several studies reviewed in Jenouvrier (2013) highlighted multifaceted effects of climatic conditions on the demography of seabirds involving direct, time-lagged and non-linear effect, which we did not consider here. Therefore, despite our contribution to understanding environmental effects in our predator–prey system, disentangling the complex mechanistic pathways between environmental covariates and seabirds' demographic parameters remains challenging.

Bottom-up predator–prey dynamics

Overall, our study has highlighted the important role of bottom-up processes in the dynamics of this marine predator–prey system, i.e., the population dynamics of these two seabirds was mostly driven by food availability. Petrel dynamics were more strongly affected by environmental covariates (since we did not directly measure their food resources) and the number of petrels impacted the dynamics of skuas. The bottom-up control of demographic rates in oceanic predators is a common assumption (Jenouvrier 2013). This is because the functioning of oceanic systems is controlled and structured by physical processes impacting nutrient fluxes (Behrenfeld et al. 2006) and consequently the whole trophic food web. We found no evidence of top-down processes, i.e., predation effects, in this system, although these two mechanisms have been found to jointly affect ecosystems (Hunter and Price 1992, Sinclair et al. 2003) including some other seabird systems (Horswill et al. 2014, 2016, Perkins et al. 2018). Effects of skua predation on petrel vital rates were expected, based on skua diet during the breeding season. However, given the very large number of petrels present

on the island compared to the number of predators, the impact of predation may have been too small to be detected by our model.

CONCLUSION

Our multispecies IPM framework allowed us to estimate demographic parameters and abundances for skuas and petrels. Taking into account both species interactions and environmental covariates in the same analysis improved our understanding of their joint population dynamics. We concluded that bottom-up mechanisms are the main drivers of population dynamics in this skua-petrel system. Generalizing such assessments of interspecific relationships and environmental effects in a unified demographic framework may be essential to predict how contrasted climatic scenarios will affect communities. A promising avenue of research in multispecies IPMs lies in fitting models to data on a larger number of species, which will likely require further methodological developments.

ACKNOWLEDGMENTS

This study was made possible thanks to all the field workers involved in the monitoring programs on Brown Skuas and Blue Petrels since 1985 at Mayes Island, Kerguelen Islands. These monitoring programs were supported financially and logistically by the French Polar Institute IPEV (program 109, resp. Henri Weimerskirch), the Zone Atelier Antarctique (CNRS-INEE), Terres Australes et Antarctiques Françaises. All work was carried out in accordance with the guidelines of the IPEV ethics committee. We thank Chloé R. Nater for constructive feedback and helpful suggestions on the manuscript. We acknowledge Dominique Joubert for the management of the demographic database. We thank Dave Koons and Matthew Farr for useful comments that helped improved a previous version of the manuscript. This research was funded by the French National Research Agency (grant ANR-16-CE02-0007).

LITERATURE CITED

- Aebischer, N. J., J. C. Coulson, and J. M. Colebrook. 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature* 347:753–755.
- Barbraud, C., and K. Delord. 2006. Population census of blue petrels *Halobaena caerulea* at Mayes Island, Iles Kerguelen. *Antarctic Science* 18:199–204.
- Barbraud, C., V. Rolland, S. Jenouvrier, M. Nevoux, K. Delord, and H. Weimerskirch. 2012. Effects of climate change and fisheries bycatch on Southern Ocean seabirds: a review. *Marine Ecology Progress Series* 454:285–307.
- Barbraud, C., and H. Weimerskirch. 2001. Emperor penguins and climate change. *Nature* 411:183–186.
- Barbraud, C., and H. Weimerskirch. 2003. Climate and density shape population dynamics of a marine top predator. *Proceedings of the Royal Society B* 270:2111–2116.
- Barbraud, C., and H. Weimerskirch. 2005. Environmental conditions and breeding experience affect costs of reproduction in blue petrels. *Ecology* 86:682–692.
- Barraquand, F., and O. Gimenez. 2019. Integrating multiple data sources to fit matrix population models for interacting species. *Ecological Modelling* 411:108713.

- Barraquand, F., T. T. Høye, J.-A. Henden, N. 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: long-tailed skuas and arctic lemmings. *Journal of Animal Ecology* 83:375–387.
- Behrenfeld, M. J., R. T. O'Malley, D. A. Siegel, C. R. McClain, J. L. Sarmiento, G. C. Feldman, A. J. Milligan, P. G. Falkowski, R. M. Letelier, and E. S. Boss. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* 444:752–755.
- Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole. 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* 58:540–547.
- Bogdanova, M. I., et al. 2017. Multi-colony tracking reveals spatio-temporal variation in carry-over effects between breeding success and winter movements in a pelagic seabird. *Marine Ecology Progress Series* 578:167–181.
- Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7:434–455.
- Cairns, D. K. 1988. Seabirds as indicators of marine food supplies. *Biological Oceanography* 5:261–271.
- Cam, E., J. E. Hines, J.-Y. Monnat, J. D. Nichols, and E. Danchin. 1998. Are adult nonbreeders prudent parents? The Kittiwake model. *Ecology* 79:2917.
- Carneiro, A. P. B., A. Manica, W. Z. Trivelpiece, and R. A. Phillips. 2015. Flexibility in foraging strategies of Brown Skuas in response to local and seasonal dietary constraints. *Journal of Ornithology* 156:625–633.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Chastel, O., H. Weimerskirch, and P. Jouventin. 1995. Influence of body condition on reproductive decision and reproductive success in the blue petrel. *Auk* 112:964–972.
- Chaurand, T., and H. Weimerskirch. 1994a. The regular alternation of short and long foraging trips in the blue petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *Journal of Animal Ecology* 63:275–282.
- Chaurand, T., and H. Weimerskirch. 1994b. Incubation routine, body mass regulation and egg neglect in the Blue Petrel *Halobaena caerulea*. *Ibis* 136:285–290.
- Cherel, Y., P. Bocher, C. Trouvé, and H. Weimerskirch. 2002. Diet and feeding ecology of blue petrels *Halobaena caerulea* at Iles Kerguelen, Southern Indian Ocean. *Marine Ecology Progress Series* 228:283–299.
- Cherel, Y., M. Connan, A. Jaeger, and P. Richard. 2014. Seabird year-round and historical feeding ecology: blood and feather $\delta^{13}C$ and $\delta^{15}N$ values document foraging plasticity of small sympatric petrels. *Marine Ecology Progress Series* 505:267–280.
- Cherel, Y., P. Quillfeldt, K. Delord, and H. Weimerskirch. 2016. Combination of at-sea activity, geolocation and feather stable isotopes documents where and when seabirds molt. *Frontiers in Ecology and Evolution* 4:3.
- Chu, C., and P. B. Adler. 2015. Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. *Ecological Monographs* 85:373–392.
- Daunt, F., V. Afanasyev, A. Adam, J. P. Croxall, and S. Wanless. 2007. From cradle to early grave: Juvenile mortality in European shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. *Biology Letters* 3:371–374.
- de Valpine, P., D. Turek, C. J. Paciorek, C. Anderson-Bergman, D. T. Lang, and R. Bodik. 2017. Programming with models: writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics* 26:403–413.
- Delord, K., Y. Cherel, C. Barbraud, O. Chastel, and H. Weimerskirch. 2018. High variability in migration and wintering strategies of brown skuas (*Catharacta antarctica lonnbergi*) in the Indian Ocean. *Polar Biology* 41:59–70.
- Dhondt, A. A., B. Kempenaers, and F. Adriaensens. 1992. Density-dependent clutch size caused by habitat heterogeneity. *Journal of Animal Ecology* 61:643–648.
- Dunstan, P. K., S. D. Foster, E. King, J. Risbey, T. J. O'Kane, D. Monselesan, A. J. Hobday, J. R. Hartog, and P. A. Thompson. 2018. Global patterns of change and variation in sea surface temperature and chlorophyll a. *Scientific Reports* 8:1–9.
- Fay, R., H. Weimerskirch, K. Delord, and C. Barbraud. 2015. Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. *Journal of Animal Ecology* 84:1423–1433.
- Ferrer, M., and J. A. Donazar. 2015. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles. *Ecology* 77:69–74.
- Frederiksen, M., M. Edwards, A. J. Richardson, N. C. Halliday, and S. Wanless. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology* 75:1259–1268.
- Gervasi, V., E. B. Nilsen, and J. D. C. Linnell. 2015. Body mass relationships affect the age structure of predation across carnivore-ungulate systems: A review and synthesis. *Mammal Review* 45:253–266.
- Gille, S. T. 2002. Warming of the Southern Ocean since the 1950s. *Science* 295:1275–1277.
- Gimenez, O., J. D. Lebreton, J. M. Gaillard, R. Choquet, and R. Pradel. 2012. Estimating demographic parameters using hidden process dynamic models. *Theoretical Population Biology* 82:307–316.
- Godfray, H. C. J., and R. M. May. 2014. Open questions: Are the dynamics of ecological communities predictable? *BMC Biology* 12:22.
- Grande, J. M., D. Serrano, G. Tavecchia, M. Carrete, O. Ceballos, R. Díaz-Delgado, J. L. Tella, and J. A. Donazar. 2009. Survival in a long-lived territorial migrant: effects of life-history traits and ecological conditions in wintering and breeding areas. *Oikos* 118:580–590.
- Greig, S. A., J. C. Coulson, and P. Monaghan. 1983. Age-related differences in foraging success in the herring gull (*Larus argentatus*). *Animal Behavior* 31:1237–1243.
- Grosbois, V., O. Gimenez, J.-M. Gaillard, R. Pradel, C. Barbraud, J. Clobert, A. P. Møller, and H. Weimerskirch. 2008. Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews* 83:357–399.
- Guinet, C., O. Chastel, M. Koudil, J. P. Durbec, and P. Jouventin. 1998. Effects of warm sea-surface temperature anomalies on the blue petrel at the Kerguelen Islands. *Proceedings of the Royal Society B* 265:1001–1006.
- Hamer, K. C., R. W. Furness, and R. W. G. Caldow. 1991. The effects of changes in food availability on the breeding ecology of great skuas *Catharacta skua* in Shetland. *Journal of Zoology* 223:175–188.
- Han, W., J. Vialard, M. J. McPhaden, T. Lee, Y. Masumoto, M. Feng, and W. P. M. de Ruijter. 2014. Indian ocean decadal variability: a review. *Bulletin of the American Meteorological Society* 95:1679–1703.
- Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80:4–18.

- Higgins, P. J., and S. J. Davied. 1996. Handbook of Australia, New Zealand & Antarctic Birds. Volume 3, Snipe to pigeons. Oxford University Press, Melbourne, Victoria, Australia.
- Hipfner, M. J., L. K. Blight, R. W. Lowe, S. I. Wilhelm, G. J. Robertson, R. T. Barrett, T. Anker-Nilssen, and T. P. Good. 2012. Unintended consequences: How the recovery of sea eagle *Haliaeetus* spp. populations in the northern hemisphere is affecting seabirds. *Marine Ornithology* 40:39–52.
- Hoegh-Guldberg, O., and J. F. Bruno. 2010. The impact of climate change on the world's marine ecosystems. *Science* 328:1523–1528.
- Horswill, C., J. Matthiopoulos, J. A. Green, M. P. Meredith, J. Forcada, H. Peat, M. Preston, P. N. Trathan, and N. Ratcliffe. 2014. Survival in macaroni penguins and the relative importance of different drivers: Individual traits, predation pressure and environmental variability. *Journal of Animal Ecology* 83:1057–1067.
- Horswill, C., N. Ratcliffe, J. A. Green, R. A. Phillips, P. N. Trathan, and J. Matthiopoulos. 2016. Unravelling the relative roles of top-down and bottom-up forces driving population change in an oceanic predator. *Ecology* 97:1919–1928.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732.
- Jenouvrier, S. 2013. Impacts of climate change on avian populations. *Global Change Biology* 19:2036–2057.
- Jenouvrier, S., C. Barbraud, and H. Weimerskirch. 2003. Effects of climate variability on the temporal population dynamics of southern fulmars. *Journal of Animal Ecology* 72:576–587.
- Jouventin, P., J. L. Mougouin, J.-C. Stahl, and H. Weimerskirch. 1985. Comparative biology of the burrowing petrels of the Crozet Islands. *Notornis* 32:157–220.
- Krüger, O., and J. Lindström. 2001. Habitat heterogeneity affects population growth in goshawk *Accipiter gentilis*. *Journal of Animal Ecology* 70:173–181.
- Lack, D. 1967. Interrelationships in breeding adaptations as shown by marine birds. Pages 3–42 in D. W. Snow, editor. *Proceedings of the XIV International Ornithological Congress*. Volume 14. Blackwell Scientific Publications, Oxford, UK.
- Lauria, V., M. J. Attrill, A. Brown, M. Edwards, and S. C. Votier. 2013. Regional variation in the impact of climate change: Evidence that bottom-up regulation from plankton to seabirds is weak in parts of the Northeast Atlantic. *Marine Ecology Progress Series* 488:11–22.
- Lovenduski, N. S., and N. Gruber. 2005. Impact of the Southern Annular Mode on Southern Ocean circulation and biology. *Geophysical Research Letters* 32:L11603.
- Marshall, G. J. 2003. Trends in the Southern Annular Mode from observations and reanalyses. *Journal of Climate* 16:4134–4143.
- Miller, D. A. W., et al. 2018. Quantifying climate sensitivity and climate-driven change in North American amphibian communities. *Nature Communications* 9:3926.
- Miller, T. E. X., and V. H. W. Rudolf. 2011. Thinking inside the box: community-level consequences of stage-structured populations. *Trends in Ecology and Evolution* 26:457–466.
- Millon, A., S. J. Petty, B. Little, O. Gimenez, T. Cornulier, and X. Lambin. 2014. Dampening prey cycle overrides the impact of climate change on predator population dynamics: a long-term demographic study on tawny owls. *Global Change Biology* 20:1770–1781.
- Mougeot, F., and V. Bretagnolle. 2000a. Predation risk and moonlight avoidance in nocturnal seabirds. *Journal of Avian Biology* 31:376–386.
- Mougeot, F., and V. Bretagnolle. 2000b. Predation as a cost of sexual communication in nocturnal seabirds: an experimental approach using acoustic signals. *Animal Behaviour* 60:647–656.
- Mougeot, F., F. Genevois, and V. Bretagnolle. 1998. Predation on burrowing petrels by the brown skua (*Catharacta skua lönnbergi*) at Mayes Island, Kerguelen. *Journal of Zoology* 244:429–438.
- 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.
- Oken, K. L., and T. E. Essington. 2015. How detectable is predation in stage-structured populations? Insights from a simulation-testing analysis. *Journal of Animal Ecology* 84:60–70.
- 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.
- Oro, D., A. Martínez-Abraín, M. Paracuellos, J. C. Nevado, and M. Genovart. 2006. Influence of density dependence on predator–prey seabird interactions at large spatio-temporal scales. *Proceedings of the Royal Society B* 273:379–383.
- Pacoureaux, N., M. Authier, K. Delord, and C. Barbraud. 2019a. Population response of an apex Antarctic consumer to its prey and climate fluctuations. *Oecologia* 189:279–291.
- Pacoureaux, N., K. Delord, S. Jenouvrier, and C. Barbraud. 2019b. Demographic and population responses of an apex predator to climate and its prey: a long-term study of South Polar Skuas. *Ecological Monographs* 89:e01388.
- Pacoureaux, N., E. Gaget, K. Delord, and C. Barbraud. 2019c. Prey remains of brown skua is evidence of the long-term decline in burrow occupancy of blue petrels and thin-billed prions at Mayes Island, Kerguelen. *Polar Biology* 42:1873–1879.
- Parmelee, D. F., and P. J. Pietz. 1987. Philopatry, mate and nest-site fidelity in the Brown Skuas of Anvers Island, Antarctica. *Condor* 89:916–919.
- Parnesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637–669.
- Perkins, A., N. Ratcliffe, D. Suddaby, B. Ribbands, C. Smith, P. Ellis, E. Meek, and M. Bolton. 2018. Combined bottom-up and top-down pressures drive catastrophic population declines of Arctic skuas in Scotland. *Journal of Animal Ecology* 87:1573–1586.
- Péron, G., and D. N. Koons. 2012. Integrated modeling of communities: parasitism, competition, and demographic synchrony in sympatric ducks. *Ecology* 93:2456–2464.
- Piatt, J. F., A. M. A. Harding, M. Shultz, S. G. Speckman, T. I. van Pelt, G. S. Drew, and A. B. Kettle. 2007. Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series* 352:221–234.
- Pinaud, D., and H. Weimerskirch. 2002. Ultimate and proximate factors affecting the breeding performance of a marine top-predator. *Oikos* 99:141–150.
- Pradel, R. 2005. Multievent: an extension of multistate capture-recapture models to uncertain states. *Biometrics* 61:442–447.
- Quéroué, M. 2021. *maudqueroue/MultispeciesIPM_SkuaPetrel: First release mIPM SkuaPetrel (Version v1.0.0)*. Zenodo, data set. <https://doi.org/10.5281/zenodo.4588375>
- Quillfeldt, P., H. Weimerskirch, K. Delord, and Y. Cherel. 2020. Niche switching and leapfrog foraging: movement ecology of sympatric petrels during the early breeding season. *Movement Ecology* 8:23.

- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
- Ratcliffe, N., and R. W. Furness. 1999. The effect of parental age and experimentally manipulated brood size on the foraging effort and breeding performance of great skuas (*Catharacta skua*). *Journal of Zoology* 249:195–201.
- Regehr, H. M., and W. A. Montevecchi. 1997. Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: Indirect effects of fisheries activities and implications for indicator species. *Marine Ecology Progress Series* 155:249–260.
- Saunders, S. P., F. J. Cuthbert, and E. F. Zipkin. 2018. Evaluating population viability and efficacy of conservation management using integrated population models. *Journal of Applied Ecology* 55:1380–1392.
- Schaub, M., and F. Abadi. 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology* 152:227–237.
- Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator–prey system. *Nature* 425:288–290.
- Stenseth, N. C., et al. 2015. Testing for effects of climate change on competitive relationships and coexistence between two bird species. *Proceedings of the Royal Society B* 282:20141958.
- 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.
- Stoessel, M., B. Elmhagen, M. Vinka, P. Hellström, and A. Angerbjörn. 2019. The fluctuating world of a tundra predator guild: bottom-up constraints overrule top-down species interactions in winter. *Ecography* 42:488–499.
- Suryan, R. M., F. Sato, G. R. Balogh, K. David Hyrenbach, P. R. Sievert, and K. Ozaki. 2006. Foraging destinations and marine habitat use of short-tailed albatrosses: A multi-scale approach using first-passage time analysis. *Deep-Sea Research Part II: Topical Studies in Oceanography* 53:370–386.
- Sydeeman, W. J., E. Poloczanska, T. E. Reed, and S. A. Thompson. 2015. Climate change and marine vertebrates. *Science* 350:772–777.
- Thomas, C. D., et al. 2004. Extinction risk from climate change. *Nature* 427:145–148.
- Tuljapurkar, S., and H. Caswell. 1997. Structured-population models in marine, terrestrial, and freshwater systems. Chapman & Hall, New York, New York, USA.
- van de Pol, M., Y. Vindenes, B.-E. Sæther, S. Engen, B. J. Ens, K. Oosterbeek, and J. M. Tinbergen. 2010. Effects of climate change and variability on population dynamics in a long-lived shorebird. *Ecology* 91:1192–1204.
- Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Warham, J. 1990. The petrels: their ecology and breeding systems. Academic Press, London, UK.
- Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the wandering albatross. *Oikos* 64:464–473.
- Weimerskirch, H., O. Chastel, L. Ackermann, T. Chaurand, F. Cuenot-Chaillet, X. Hindermeyer, and J. Judas. 1994. Alternate long and short foraging trips in pelagic seabird parents. *Animal Behavior* 47:472–476.
- Zipkin, E. F., and S. P. Saunders. 2018. Synthesizing multiple data types for biological conservation using integrated population models. *Biological Conservation* 217:240–250.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1459/full>

OPEN RESEARCH

Code and data (Quéroué 2021) are available on Zenodo at: <https://doi.org/10.5281/zenodo.4588375>