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

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Abstract

Assessing the effects of climate and interspecific relationships on communities is challenging because of the complex dynamic of species in interactions and the need to integrate information across several biological levels (individuals – populations – communities). To quantify species interactions, integrated population models (IPMs) have recently been extended to communities and allow fitting multispecies matrix models to data from multiple sources. However, abiotic factors are still rarely considered. Here, we used multispecies IPMs accommodating climate conditions 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 years of capture—recapture data and population counts of two seabirds, namely the Brown skua (*Catharacta lönnbergi*) and its main prey the Blue petrel (*Halobaena caerulea*) both breeding on the Kerguelen Islands in the Southern Indian Ocean. Our results showed that the demography of the petrel and the skua were not driven in the same way by climate and prey-predator interactions. While the breeding success of skuas appears to be largely driven by the number of petrels, we did not find any link between climate fluctuations and the demography of skuas. In contrast, petrel breeding success was not explained by the number of skuas but mainly by the environmental conditions. We discuss the mechanisms by which climate variability and predator-prey relationships may affect the demographic parameters of these seabirds. We highlighted that bottom-up mechanisms drive this skua-petrel system. Taking into account both species interactions and environmental covariates in the same analysis improved our understanding of species dynamics in the face of environmental changes.

Keywords: Bayesian inference, Demography, Environmental variations, Integrated Population Model, Matrix population model, Nimble, Predator-Prey interactions

Introduction

The effects of climate changes 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 (Godfray and May 2014) due to the complex dynamics of interacting species (within species, between species and between species and the environment). 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 miss the role played by species interactions on those responses, and does not contribute to the larger understanding of species interactions that is required by community ecology.

Population dynamics models have been used to understand the effect of interspecific interactions and environment on species demography. However, these models are in general not demographically structured (Stenseth et al. 2015, Pacoureau et al. 2019a, Stoessel et al. 2019) or only partially (Millon et al. 2014, Pacoureau et al. 2019b). Unstructured approaches consider individuals as being equivalent while differences in size, age and ontogenic stages exist within a population and may be of importance to decipher interspecific interactions. As argued by Miller

& Rudolf (2011), the consideration of the structure of species in stages 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 plant system). The difficulty is that multispecies demography 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 and Saunders et al. 2018 for reviews). In their simplest form, these models combine population counts and demographic data into a single analysis, which allows the estimation of demographic parameters while simultaneously accounting for various sources of uncertainty in each data source (e.g., measurement error or parameter estimation) (Besbeas et al. 2002). The IPM framework has been extended to multiple species (Péron and Koons 2012) for competition/parasitism, and more recently 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. Therefore, 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 on a stage-structured predator–prey system combining 22 years of capture-recapture data and population counts on two seabirds, the Brown skua (*Catharacta lönnbergi*) and its main prey the Blue petrel (*Halobaena caerulea*) ('skua' and 'petrel' hereafter) breeding on the Kerguelen Islands in the southern Indian Ocean. The Southern and Indian Oceans have experienced a substantial increase in temperature (Gille 2002, Han et al. 2014), making the Kerguelen Islands a critical location for studying the effects of climate change on ecosystems. Seabirds are top predators that play an important role in ecosystem functioning and are considered indicators of environmental changes in marine ecosystems (Hazen et al. 2019). Their foraging behavior and demography reflect the influences of climate variability that directly impacts biological processes in marine ecosystems, which cascade through food webs and are integrated by seabirds (Barbraud and Weimerskirch 2001, Jenouvrier et al. 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

Site and Species

Skua and Petrel were studied on Mayes Island (49°28'S, 69°57'E), a 5-km uninhabited island of the Kerguelen archipelago in the Southern Indian Ocean. We considered 22 breeding seasons from 1996/1997 to 2017/2018.

The petrel is a small (150–250g) long-lived Procellariiformes seabird. At Kerguelen, the petrel is a macrozooplankton and micronekton feeder, its diet being mainly composed of 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 ice pack (57-62°S) between longitudes 20°W and 90°E (Cherel et al. 2016). Birds return to colonies in early September (Quillfeldt et al. 2020). On Mayes Island the breeding population is estimated at approximately 142,000 breeding pairs (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 phase takes between 45 and 49 days and the chick rearing period between 43 and 60 days (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 Charadriiformes seabird. 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 phase takes between

28 and 32 days and the chicks rearing period between 40 and 50 days (Higgins and Davied 1996). With their different foraging techniques, skuas adapt their diet depending on the availability of prey (Carneiro et al. 2015). On Mayes Island, during the breeding season, Blue petrels represent 95% of the skua diet (Pacoureau 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 the petrels come out or arrive at their burrows (Mougeot & Bretagnolle, 2000a). Skuas mostly predate petrels on the ground, but they can also predate petrels in flight (Mougeot et al. 1998, Pacoureau 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 predate chicks during the fledging period.

Counts and capture-recapture data

Individuals of each 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.

Around 200 individually marked burrows of petrels were inspected each year from early-to-mid November just after laying to check for eggs and to record marked adults, and then in late January just before fledging. Each year since 1985 (see Barbraud and Weimerskirch 2005), all fledglings found in burrows were marked with a stainless steel band, as well as new individuals found in monitored burrows (captured by hand, marked, and replaced in their burrow). We used capture-recapture data from 1996 and considered new individuals found in monitored burrows as

immigrants to the study site. Petrels never observed with an egg or a chick during a given breeding season were considered as nonbreeders (NB_p). Individuals were identified as breeders (B_p) if they laid a single egg or raised a chick and as successful breeders if their chick fledged (SB_p). Two categories of failed breeders were used depending on the stage of failure: egg stage (FBE_p) or chick stage (FBC_p). Given that the first sampling period occurred just after laying, it is very unlikely that nonbreeders were failed breeders. The annual number of petrels was estimated as the number of occupied burrows.

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 laying) to late-March (just before fledging) each year. Chicks were marked just before fledging, as well as new adult individuals 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_s). Individuals were identified as breeders (B_s) if they laid at least one egg or raised a chick. If the eggs did not hatch or the chicks died, the breeding pair was considered as failed breeder (FB_s). Given that the first sampling period occurred just after laying, it is very unlikely that nonbreeders represented failed breeders. Successful breeders were able to fledge one or two chicks which are denoted as $SB1_s$ or $SB2_s$, respectively. The annual number of skuas was estimated as the number of territories.

For both species, individuals could be considered as "uncertain" (C) in case of difficulties to assign their breeding status (lack of information, missed checks, individuals never re-observed). Only

individuals that have bred at least once between the 1996 and the 2017 breeding seasons were kept in the data set for analysis (n = 320 for skuas and n = 1210 for petrels). Individual capture histories started at their 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.

Integrated Population Model

We built a two-species IPM that combines counts and capture-recapture data and allows estimating abundances and demographic rates (Besbeas et al. 2002, Schaub and Abadi 2011). More specifically, we connected two IPMs, one for the skuas, the predators, and one for the petrels, the preys, through explicit predator-prey relationships (Barraquand and Gimenez 2019). Counts and capture-recapture data for both species were combined into a joint likelihood that also included the effects of intra-species and inter-species density-dependence and climatic covariates on demographic parameters.

The two IPMs have the same structure but states differ in relation to species biology. The two main differences are: (1) skuas can have up to two chicks versus only one for petrels, (2) additional information is available for petrels which can determine the precise stage of breeding in case of failure (egg or chick stage). We explain the structure of the IPMs based on the skua model and differences are noted when they occur. See Appendix S1 for a full description of the petrel model. For clarity, all parameters for skuas are indicated by s and for petrels by p.

Count data

State process:

We use Poisson (Po) and binomial (Bin) distributions to account for demographic stochasticity. Skuas from one year old to four years old are considered as juveniles. The number of skuas in their first year ($J_{1_{s_t}}$) at year *t* is modelled with a Poisson distribution:

$$J_{1_{s_t}} \sim Po(0.5 \times f_{SB1_s} \times SB1_{s_{t-1}} + 0.5 \times f_{SB2_s} \times SB2_{s_{t-1}}) \quad (1)$$

with J_{1_s} the number of chicks by successful breeder ($SB1_s$ and $SB2_s$) female (sex ratio: 0.5) according to their fecundity (f_{SB1_s}: 1 chick and f_{SB2_s}: 2 chicks per skua). For petrels, J_{1_p} is also Poisson distributed but with only one chick per successful breeder (Appendix S1). The number of juveniles of two (J_{2_s}), three (J_{3_s}), and four years old (J_{4_s}) are modelled with binomial distributions:

$$J_{2_{s_t}} \sim Bin(\phi_{J_{1_s}}, J_{1_{s_{t-1}}}) \quad (2)$$

$$J_{3_{s_t}} \sim Bin(\phi_{J_{2_s}}, J_{2_{s_{t-1}}}) \quad (3)$$

$$J_{4_{s_t}} \sim Bin(\phi_{J_{3_s}}, J_{3_{s_{t-1}}}) \quad (4)$$

with the apparent survival between one and two years ($\phi_{J_{1_s}}$), between two and three years ($\phi_{J_{2_s}}$) and between three and four years ($\phi_{J_{3_s}}$) respectively. As the first breeding attempt in skuas could start from age four, the J_{4+_s} state was considered as the immature state with four years old skuas (J_{4_s}) and older that have never reproduced ($J^{NB}_{4+_s}$):

$$J^{B}_{4+_{s_t}} \sim Bin\left(Pr_{s_t}, \phi_{J_{4_s}} \times J_{4+_{s_{t-1}}}\right) \quad (5)$$

$$J^{NB}_{4+_{s_t}} = \phi_{J_{4_s}} \times J_{4+_{s_{t-1}}} - J^{B}_{4+_{s_t}} \quad (6)$$

$$J_{4+_{s_t}} = J_{4_{s_t}} + J^{NB}_{4+_{s_t}} \qquad (7)$$

with $\phi_{J_{4_s}}$ the apparent survival for immatures skuas, Pr_s the probability of first breeding attempt for skuas in the state J_{4+_s} that have not recruited yet and $J^{B}_{4+_s}$ the number of skuas that attempt to breed for the first time.

Because 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:

$$logit\left(\phi_{j_{i_s}}\right) = \lambda_{1_s} + \lambda_{2_s} \times i \qquad (8)$$

where $\phi_{j_{i_s}}$ is the juvenile apparent survival, i the age of the juvenile state (from J_{1_s} to J_{4_s}), λ_{1_s} the intercept and λ_{2_s} the slope which is constrained to be positive.

We use binomial distributions to account for stochasticity in the different adult states. We modelled the number of surviving adult skuas (N_{alive_s}) with a binomial distribution:

$$N_{alive_{s_t}} \sim Bin\left(\phi_{ad_{s_{t-1}}}, N_{ad_{s_{t-1}}}\right) \qquad (9)$$

with ϕ_{ad_s} the adult apparent survival. The number of skuas that have not bred among those that survived (NB_s) is modelled as:

$$B_{ad_{s_t}} \sim Bin\left(\beta_{s_{t-1}}, N_{alive_{s_t}}\right) \qquad (10)$$

$$NB_{s_t} = N_{alive_{s_t}} - B_{ad_{s_t}} \qquad (11)$$

with β_s the probability of breeding and B_{ad_s} the number of adult breeders. The total number of breeders (B_s) correspond to the sum of the number of adult breeders (B_{ad_s}), the number of immigrants (*i.e.,* newly marked) skuas (N_{im_s}) and the number of juveniles attempting to breed for the first time($J^B_{4+_{s_t}}$):

$$B_{s_t} = B_{ad_{s_t}} + J^B_{4+_{s_t}} + N_{im_{s_t}} \qquad (12)$$

The number of failed breeders (FB_s) and successful breeders (SB_s) are modelled following a binomial distribution:

$$SB_{s_t} \sim Bin\left(\gamma_{s_{t-1}}, B_{s_t}\right) \qquad (13)$$

$$FB_{s_t} = B_{s_t} - SB_{s_t} \qquad (14)$$

with γ_s the probability of a successful breeding. A successful breeder can then have one or two chicks, respectively $SB1_s$ and $SB2_s$ and this is modelled following a binomial distribution:

$$SB2_{s_t} \sim Bin\,(\delta_{s_{t-1}}, SB_{s_t}) \qquad (15)$$

$$SB1_{s_t} = SB_{s_t} - SB2_{s_t} \qquad (16)$$

with δ_s the probability of successful breeding with two chicks among the successful breeders.

For the petrel, there are two states for failed breeders: one with petrels that failed to hatch their egg (called failed breeder at the egg stage FBE_p) and the second with petrels that failed to fledge their chick (named failed breeder at the chick stage FBC_p). Hence, there is a parameter of successful hatching (ω_p). There is only one state for successful breeders (SB_p) defined with a parameter of successful breeding (y_p) (Appendix S1).

Observation process:

The observation equation links the observed adult population count ($N_{s_{counts}}$) (*i.e.,* the number of territories multiplied by two for a pair of skuas) with the true adult population size (N_{ad_s}), with an additional term for observation error.

$$N_{s_{counts_t}} = (0\ 0\ 0\ 0\ 1\ 1\ 1\ 1) \begin{pmatrix} J1_s \\ J2_s \\ J3_s \\ J4_s \\ NB_s \\ FB_s \\ SB1_s \\ SB2_s \end{pmatrix}_t + \varepsilon_{s_t}$$

$$\varepsilon_{s_t} \sim N(0, \sigma^2_{N_{s_{counts}}}) \qquad (17)$$

where ε_{s_t} is the error term and $\sigma^2_{N_{s_{counts}}}$ its variance. As only the adult states were observed on the field, we used a (0 0 0 0 1 1 1 1) vector, excluding the juvenile states from the observation equation. The likelihood for the population count data is denoted as $L_{co_s}(N_{s_{counts}} | \phi_{J_{1_s}}, \phi_{J_{2_s}}, \phi_{J_{3_s}}, \phi_{J_{4_s}}, Pr_s, \phi_{ad_s}, \beta_s, \gamma_s, \delta_s, N_{ad_s})$.

Capture-recapture data

For adult capture-recapture 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).

Our multievent model includes five states: Nonbreeder (NB_s), Failed breeder (FB_s), Successful breeder with one chick ($SB1_s$), Successful breeder with two chicks ($SB2_s$) and the uncertain individuals (C_s). The following demographic parameters were estimated: the adult apparent survival probability (ϕ_{ad_s}), the breeding probability (β_s), the probability of successful breeding (γ_s) and the probability of successful breeding with two chicks (δ_s). Two additional parameters were also estimated: the detection probability (p_s) and the state assignment probability of individuals with uncertain state (u_s). In the petrel model there are two states for failed breeders (at egg stage FBE_p or at chick stage FBC_p) but one state for successful breeder (SB_s), and the hatching success parameter (ω_p) is also estimated (for details see Appendix S1). All parameters are time-varying through a yearly random effect, except u_s (Table 1). State transitions are set to be state dependent according to the breeding status in the previous breeding season: Breeder ($\widetilde{B_s}$) representing birds that try to breed the previous breeding season (FB_s , $SB1_s$, $SB2_s$) or Nonbreeder ($\widetilde{NB_s}$) representing birds that already bred previously but did not try to breed during the previous breeding season (NB_s), immigrants (N_{im_s}) and immature birds (J_{4_s}) that attempt to breed for the first time in the colony (Table 1). The detection probability and the state assignment probability also depend on the breeding status (Table 1). The likelihood for the capture-recapture data is denoted as $L_{cr_s}(ch_s|\phi_{ad_s}, \beta_s, \gamma_s, \delta_s, p_s, u_s)$.

Joint likelihood

The joint likelihood of this IPM is the product of the likelihood for the count data (L_{co_s}) and capture-recapture data (L_{cr_s}):

$$L_{ipm_s}(N_{s_{counts}}, ch_s | \phi_{J_{1_s}}, \phi_{J_{2_s}}, \phi_{J_{3_s}}, \phi_{J_{4_s}}, Pr_s, \phi_{ad_s}, \beta_s, \gamma_s, \delta_s, N_{adtot_s}, p_s, u_s)$$

$$= L_{co_s}(N_{s_{counts}} | \phi_{J_{1_s}}, \phi_{J_{2_s}}, \phi_{J_{3_s}}, \phi_{J_{4_s}}, Pr_s, \phi_{ad_s}, \beta_s, \gamma_s, \delta_s, N_{ad_s}) \times L_{cr_s}(ch_s | \phi_{ad_s}, \beta_s, \gamma_s, \delta_s, p_s, u_s)$$

(18)

Interspecific relationship, intraspecific density-dependence, and environmental covariates

We used different covariates to quantify their contribution to the adult demographic parameters estimated for the two species (Table 2). We tested predator-prey relationships between the skua, the predator, and its prey, the petrel, and intraspecific relationships with density dependence for both species. 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 (Chla) on a local scale.

Predator-prey interactions

We combined the two IPMs for skuas and petrels in the same model, which allowed us to consider interspecific relationships. Based on the high proportion of petrels in the diet of the skuas during the breeding season (Pacoureau et al. 2019c), we predicted that petrel adult apparent survival (ϕ_{ad_p}), hatching success (ω_p) and fledging success (γ_p), should decrease with the number of adult skuas. Inversely, skua breeding success (γ_s) and breeding success with two chicks (δ_s) should increase with the number of petrels.

295 **Intraspecific density-dependence**

296 As skuas are highly territorial and defend vigorously their territories, we expected a negative
297 density-dependence relationship between breeding probability (β_s) and population density.
298 Furthermore, the energetic cost and the time spent in defending a territory throughout the breeding
299 season could jeopardized the breeding success and increase the adult mortality. We thus predicted
300 a negative density-dependence relationship on the successful breeding parameter (γ_s), the
301 probability to have two chicks for successful breeders (δ_s) and the adult apparent survival
302 parameter (ϕ_{ad_s}). For petrels, we also tested the effects of intraspecific competition for food
303 resources, which could affect their adult apparent survival (ϕ_{ad_p}) and their breeding parameters:
304 breeding probability (β_p), hatching (ω_p) and fledging success (γ_p).

305 **Southern Annular Mode**

306 The Southern Annular Mode (SAM) is a large-scale climate index. SAM is the leading mode of
307 climate variability over the Southern Hemisphere. SAM is defined as the difference of atmospheric
308 pressure between the 40°S and 65°S latitudes (Marshall 2003). SAM influences surface wind, sea
309 surface temperature (SST) and surface chlorophyll concentration. Data were obtained from the
310 online database of the British Antarctic Survey (http://www.nerc-bas.ac.uk/ icd/gjma/sam.html).

311 South of the Polar Front, where petrels winter, positive phases of the SAM are associated with
312 westerly winds. It induce cold SST anomalies and Ekman transport (the 90° wind-driven net
313 transport on the sea surface) and drive increased upwelling (Lovenduski and Gruber 2005).
314 Consequently, the biological productivity and potential prey availability for petrels are accentuated

during positive phases of the SAM. We thus predicted that the positive phases of SAM would be favorable to petrel survival and breeding success.

Since skuas have broad wintering areas (Delord et al. 2018), we have chosen to test a large-scale environmental covariate, the SAM. Contrary to their diet during the breeding season specialized on the Blue petrel, during winter they adopt a mixed diet composed of low trophic level preys, macrozooplankton and crustaceans (Delord et al. 2018). Availability of food resources at sea during their wintering might have an effect on the condition of skuas. 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 SST anomalies, low surface chlorophyll concentration and easterly winds driving Ekman transport, while in the Subantarctic zone there is a convergence of waters that increase downwelling and positive SST anomalies (Lovenduski and Gruber 2005). We thus predicted that the positive phases of SAM, leading to poorer food availability in the areas used by skuas during the nonbreeding period, would have negative impacts on skua survival and on their ability to reproduce in the next breeding season.

Sea Surface Temperature anomalies

We used the SSTa as a proxy of food availability because it is known to indirectly affect seabird demography through its effects on marine food webs (Barbraud et al. 2012). Because the year-to-year variation of SST was negatively correlated with the body condition of petrels (Guinet et al. 1998), we predicted that high SSTa would negatively affect its survival and breeding success. The SSTa data were downloaded from NOAA ("data: NOAA NCEP EMC CMB GLOBAL Reyn_SmithOIv2 monthly ssta") from 1996 to 2018.

Chlorophyll a

Because the 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 Chla would be favorable to survival and breeding success via bottom-up mechanisms. The Chlorophyll a concentration (Chla) data were downloaded from the NASA Ocean Data with a 9km mapped concentration data of chlorophyll a for the years 1997 to 2001 and from the Nasa Earth Observation (NEO AQUA/MODIS data) monthly for the years 2002 to 2018.

For local covariates (SSTa and Chla), we recovered the average values of the covariates in the areas in which petrels were located (Cherel et al. 2016) in 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.

Assessing the effect of covariates and state variables

We fitted a single model including all the biologically relevant effects. Logit-linear regressions were used to estimate the effect of environmental (SAM, SSTa and Chla) and inter- and intra-specific interactions on demographic parameters (adult apparent survival, breeding probability, hatching probability, breeding success) (Table 2). We used state variables N_{ad_s} and N_{ad_p}, i.e. the number of adult skuas and petrels respectively, to assess the effects of inter- and intra-specific interactions. For example, we modelled the hatching probability for petrels that breed the previous year (ω_p^B) using a logit link:

$$logit(\omega_{p_t}^B) = \mu_{\omega_p^B} + \alpha_{SAM\omega_p^B} \times SAM_{\omega_{p_t}} + \alpha_{SST\omega_p^B} \times SST_{\omega_{p_t}} + \alpha_{Chla\omega_p^B} \times Chla_{\omega_{p_t}} + \alpha_{DD\omega_p^B} \times Nad_{p_t} + \alpha_{PP\omega_p^B} \times Nad_{s_t} + \varepsilon_{\omega_{p_t}^B}$$

$$\varepsilon_{\omega_{p_t}^B} \sim N(0, \sigma^2{}_{\varepsilon_{\omega_p^B}}) \quad (19)$$

with $\mu_{\omega_p^B}$ the intercept, $\alpha_{SAM\omega_p^B}$ the slope for the climatic covariate $SAM_{\omega_{p_t}}$, $\alpha_{SST\omega_p^B}$ the slope for the climatic covariate $SST_{\omega_{p_t}}$, $\alpha_{Chla\omega_p^B}$ the slope for the climatic covariate $Chla_{\omega_{p_t}}$, $\alpha_{DD\omega_p^B}$ the slope indicating the strength of the intra-specific density dependence with Nad_{p_t} the number of adult petrels between year *t* and *t+1*, $\alpha_{PP\omega_p^B}$ the slope indicating the strength of the predator-prey relationship with Nad_{s_t} the number of adult skuas between year *t* and *t+1*, $\varepsilon_{\omega_{p_t}^B}$ is a yearly random effect and $\sigma^2{}_{\varepsilon_{\omega_p^B}}$ its temporal variance. The descriptions of all equations and parameter notations are available in Appendix S2.

We computed the 95% credible intervals for the regression coefficients α. Effects were considered statistically significant when credible intervals did not include 0 as described in Kéry and Schaub (2011). We compared the relative contribution of each covariate using the regression estimate which we used as a measure of effect size.

Model implementation

To fit the juvenile apparent survival parameters increasing with age, we modelled 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) is time-dependent with a non-informative prior: $Pr_t \sim \mathrm{U}(0,1)$. We modelled covariate effects on the adult demographic parameters as linear functions of time on the logit scale by assigning normal priors $N(0,10^4)$ to the regression coefficients (α). For the variance of the random year effects (σ_ε^2),

we used a $U(0,10)$ non-informative prior. The state assignment probability of individuals with uncertain state parameter (u_s) was defined *a priori* with a $U(0,10)$ non-informative prior.

Bayesian posterior distributions were approximated *via* Markov chain Monte Carlo (MCMC) algorithms. Two independent MCMC chains of 220,000 iterations were used with a burn-in period of 120,000. One out of five iterations was kept and final inferences were derived from a sample of 2 × 20,000 iterations that resulted from merging the two chains. Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998) was 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) and program R (R Core Team 2020) (R version 4.0.0). Code and data are available on GitHub at https://github.com/maudqueroue/MultispeciesIPM_SkuaPetrel.

Results

For skuas, we found no significant effect of the SAM covariate on adult demographic parameters (Table 3). We estimated that the number of skuas (for intra-specific relationship) and the number of petrels (for inter-specific relationship) had a significant effect on two demographic parameters, namely the breeding success and the breeding success with two chicks for skuas that were breeders the previous breeding season. We found negative density-dependence for the breeding success ($\gamma_s B$) [mean $\alpha_{DD\ {}^{B}_{S}} = -0.56$; Credible intervals CRI $(-0.77, -0.34)$] (Fig. 1a) and for the breeding success with two chicks ($\delta_s B$) [mean $\alpha_{DD\ {}^{B}_{S}} = -0.78$; CRI $(-1.10, -0.38)$] (Fig. 1c). We found positive predator-prey relationships for breeding success ($\gamma_s B$) and breeding success with two chicks ($\delta_s B$) with an increase in these parameters with increasing number of petrels [mean $\alpha_{PP\gamma_S^B} = 0.76$; CRI $(0.41, 1.14)$ and mean $\alpha_{PP\delta_S^B} = 1.14$; CRI $(0.57, 1.76)$] (Fig. 1b,

d). The predator-prey effects had stronger slopes than the intra-specific density-dependence effects for the breeding success of skuas ($|\text{mean } \alpha_{PP\gamma_s^B}| = 0.76$; $|\text{mean } \alpha_{DD\gamma_s^B}| = 0.56$, respectively) or the breeding success with two chicks ($|\text{mean } \alpha_{PP\delta_s^B}| = 1.14$; $|\text{mean } \alpha_{DD\delta_s^B}| = 0.78$, respectively).

For petrels, we found significant relationships between the three environmental covariates (SAM, SSTa and Chla) and hatching success for individuals that were nonbreeders the previous breeding season ($\omega_p NB$). We found negative relationships with the SAM covariate [mean $\alpha_{SAM\omega_p^{NB}} = -1.03$; CRI $(-1.93, -0.27)$] (Fig. 1e) and with the SSTa covariate [mean $\alpha_{SST\omega_p^{NB}} = -1.16$; CRI $(-1.99, -0.47)$] (Fig. 1f). A positive relationship was estimated with the Chla covariate [mean $\alpha_{Chla\omega_p^{NB}} = 1.19$; CRI $(0.47, 2.11)$] (Fig. 1g). The contributions of these environmental covariates to hatching success increase in the order SAM → SSTa → Chla. There was no significant effect of skua densities on petrel adult demographic parameters. We estimated a positive effect of increased petrel adult number on the breeding probability for petrels that were breeders the previous breeding season ($\beta_p B$) [mean $\alpha_{DD\beta_p^B} = 0.71$; CRI $(0.44, 0.90)$] (Fig. 1h).

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 S3: Figs. S1– S6).

Discussion

In this paper, we provide the first application of an IPM integrating predator-prey relationships to empirical data. Our results showed that the demography of the prey, the petrel, and the predator, the skua, was not driven in the same way by the different environmental variations. We found that

417 the petrel dynamic was mainly impacted by the environment whereas the skua dynamic was
418 primarily driven by the number of prey individuals, highlighting a bottom-up system.

419 **Effects of predator-prey relationships**

420 The number of prey is a determining factor in the breeding success of skuas. Food availability is
421 known to be positively related with breeding parameters in seabirds (Cairns 1988, Piatt et al. 2007,
422 Oro et al. 2014). As diet of skuas during the breeding period in Mayes Island is dominated by
423 petrels (Mougeot et al. 1998, Pacoureau et al. 2019c), a large abundance of petrels provides easier
424 conditions for skuas to feed themselves and their chicks resulting in a high breeding success.

425 Interestingly, we did not find the opposite relationship in the prey dynamic. Our model indicates
426 that the number of skuas had no effect on the demographic parameters of the petrel. However, it
427 has already been shown that in predator-prey terrestrial bird systems, the presence of a predator
428 might have consequences on the reproduction of the prey by increasing brood failures (Mueller et
429 al. 2016) or by reducing clutch sizes (Morosinotto et al. 2010). This lack of effect could be
430 explained by the large abundance of petrels compared to the skuas on Mayes Island. Oro et al.
431 (2006) reported that in another seabird predator-prey system, the highest breeding success of the
432 prey occurred when the prey/predator ratio was very high. On Mayes Island, the breeding
433 population of petrels is estimated at approximately 142,000 breeding pairs (Barbraud and Delord
434 2006), but this does not include the chicks (around 71,000 each year) and nonbreeders
435 (approximately 30% of the petrels). Hence, there are about 476,000 petrels during a breeding
436 season versus about 200 skuas showing a very high prey/predator ratio. Moreover, Mougeot et al.
437 (1998) showed that skuas of Mayes Island predated 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 did not affect petrel demographics or that the effect was not sufficient to be detected in our model. In addition, as shown in our results and discussed later, it is likely that petrel dynamics were mostly driven by climatic conditions.

Effects of intra-specific density-dependence

We found negative density-dependent effects on breeding success and probability to fledge two chicks in the skua population. 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 other skuas 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 are forced to occupy poorer quality habitats, resulting in lower reproductive success.

Predator-prey relationships had a higher contribution to the breeding success of skuas than the density-dependent effect. Hamer et al. (1991) reported that, following a reduction of sandeel abundance, Great skua increased their foraging effort reducing the adult territorial attendance. In turn, breeding failure has increased due to predation from adults of neighboring territories. We

458 then may assume that petrel abundance allowed a suitable skua territorial attendance reducing the
459 negative density-dependent effects such as chick predation by conspecifics.

460 We did not find an effect of density-dependence on the breeding probability of skuas. As skuas
461 are territorial with a high degree of site fidelity, we assumed that in years with a high abundance
462 of skuas, the breeding probability would decrease as all the skuas would not have territories. It is
463 possible that we did not observe this effect because the logistic function used for density-
464 dependence does not accurately model the territory acquisition dynamics by floaters (e.g. van de
465 Pol et al. 2010, Barraquand et al. 2014).

466 Interestingly, we found a positive density-dependence relationship on the breeding probability of
467 petrels that bred the previous year. Combined effects of density-dependence and climate have
468 already been observed in the Blue petrel, with a lower winter survival when density is high
469 (Barbraud and Weimerskirch 2003), suggesting a mechanism of competition between conspecifics
470 for the resource. The inverse relationship we found rather suggests that years with a high
471 abundance of petrels reflect a good return rate to the breeding site because environmental
472 conditions were favorable for breeding. Indeed, petrels are known to skip breeding and take
473 sabbatical years when environmental conditions are poor (Warham, 1990; Chastel, Weimerskirch,
474 & Jouventin, 1995).

475 **Effects of environmental conditions**

476 Our results showed that the hatching success for the petrels that did not breed the year before was
477 impacted by the environmental covariates we tested, namely SAM, SST and Chla. Hatching
478 success is the only parameter that was impacted by the environment according to our model. This

479 result is in agreement with former studies showing that the hatching period is paramount during
480 the breeding period for Procellariiformes. The partners alternate on the nest, one incubating and
481 fasting and the other making foraging trips at sea, causing important variations in their body mass
482 (Chaurand and Weimerskirch 1994a, 1994b, Weimerskirch et al. 1994, Chastel et al. 1995). Blue
483 petrels can temporarily desert their burrow if they fall below a certain threshold mass (Chaurand
484 and Weimerskirch 1994b), even if the shift of the partner has not occurred. This desertion increases
485 the risk of hatching failure (Boersma and Wheelwright 1979, Chaurand and Weimerskirch 1994b).
486 It was shown that half of the failures during the breeding season occurred during the first
487 incubation shift, and were related to males in poor body condition (Chastel et al. 1995). Our model
488 might detect an effect on petrels that did not breed the previous year because nonbreeder petrels
489 are known to be in poorer condition than breeders (Chastel et al. 1995), potentially making them
490 more sensitive to environmental conditions.

491 High SST generally reduces vertical mixing and provides poor growing conditions for zooplankton
492 communities and then through bottom-up mechanisms induce reduced trophic resources for
493 seabirds (Barbraud et al. 2012, Sydeman et al. 2015). In contrast, high chlorophyll a concentration,
494 at the bottom of the trophic food chain, provides resources for higher trophic organisms including
495 seabirds. Hence high SSTs could decrease the foraging efficiency of petrels during incubation and
496 cause desertion of eggs whereas the high level concentration of chlorophyll a could have a positive
497 effect as shown in our results. Negative relationships have also be found between the SST during
498 the chick rearing period and the fledging success of petrels (Guinet et al. 1998). The negative
499 relationship detected in our analyses between the SAM and the hatching success contradicts our
500 expectations. Indeed, our assumption was that the positive phase of SAM would increase the

biological productivity and the prey availability in the petrel's feeding area south of the polar front. A negative relationship was also found between SAM and juvenile survival in snow petrels *Pagodroma nivea* (Sauser et al. 2018). These authors suggested that the extension of fast ice during positive phases of SAM (Holland et al. 2017) decreases prey accessibility in the Antarctic zone at the polar front, where the blue petrel feeds during the breeding season.

The effects of environmental covariates, used as a proxy of prey abundance, increase when the covariates approach the trophic level occupied by the prey of the petrels (SAM → SST → Chlorophyll a). According to these results, the dynamic of petrels seems to be driven indirectly by climate through bottom-up mechanisms. These mechanisms are consistent with many studies showing that climatic conditions affect seabirds through indirect processes by influencing prey availability and resulting in changes in their dynamics (Frederiksen et al. 2006, Barbraud et al. 2012, Jenouvrier 2013, Lauria et al. 2013).

We did not detect a significant relationship between the demographic parameters of the skua and the environmental covariates. The lack of effect on breeding parameters 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, skuas are always at sea during their wintering and their survival might be affected by environmental conditions. To our knowledge, only few studies have attempted to link environmental covariates to skua survival and an environmental effect was only detected on juvenile survival (Pacoureau et al. 2019b). We possibly did not detect an effect of SAM because skuas showed high inter-individuals variations in wintering area (Delord et al. 2018) making difficult to estimate the effects of SAM on oceanographic conditions in such diversified areas. Nevertheless, even if skuas appear unaffected

by environmental conditions, we may assume an indirect effect of the environment through bottom-up mechanisms in this skua-petrel system. Indeed, poor conditions at sea altered the breeding success of petrels resulting in lower abundance of adults and chicks of the main prey of skua. Since the breeding success of skuas depended on the abundance of petrels, as shown in our results, it might be indirectly affected by the environmental conditions.

Bottom up processes affect breeding parameters

Overall, we highlighted a bottom-up effect in the dynamics of this marine predator-prey system, *i.e.,* the dynamics of these two seabirds was mostly driven by food availability. Petrel dynamics were more strongly affected by environmental covariates near to their trophic level and the number of petrels impacted the dynamics of skuas. We found no evidence of top-down impact, *i.e.,* predation effects, in this system, although these two mechanisms have been found to jointly affect ecosystems (Hairston et al. 1960, Hunter and Price 1992, Sinclair et al. 2003). Only breeding parameters were affected by climate or intra- and interspecific relationships whereas the survival did not seem to be impacted. In long-lived iteroparous species, environmental disturbance such as a decreased in food availability is known to affect mainly the breeding processes whereas the survival tends to remain constant (Pons and Migot 1995, Benton and Grant 1996, Oro et al. 1999).

Conclusion

Our multispecies IPM provided estimates of survival, breeding success and population size for two seabird species. It had the advantage of using the population sizes estimated by the model for one species to analyze its effect on the demographic 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 taking into account the effects of climatic conditions. The estimated interspecific interactions revealed an effect of prey density on predator breeding parameters, while predator density had no effect on prey parameters, showing bottom-up predator-prey dynamics. Environmental effects were found on prey parameters but not on predator parameters, although they may have indirect effects by propagating to top predator dynamics through its prey. It highlights the crucial need of taking simultaneously into account both species interactions and environmental covariates to understand species dynamics in the face of environmental changes.

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Tables

Table 1: Summary of the demographic parameters and their specificities (year random effect or state dependence) for the two species: the skua and the petrel. Notations are $\widetilde{NB}$: Nonbreeder the previous year, $\widetilde{B}$: Breeder the previous year, NB: Nonbreeder, 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.

Species	Parameter	Year random effect	State dependence
Skua	Adult apparent survival ϕ_{ad_s}	✓	$\widetilde{NB_s} \mid \widetilde{B_s}$
	Breeding probability β_s	✓	$\widetilde{NB_s} \mid \widetilde{B_s}$
	Breeding success γ_s	✓	$\widetilde{NB_s} \mid \widetilde{B_s}$
	Breeding success 2 chicks δ_s	✓	$\widetilde{NB_s} \mid \widetilde{B_s}$
	Detection probability p_s	✓	$\widetilde{NB_s} \mid \widetilde{B_s}$
	Uncertain state assignment probability u_s	✗	$NB_s \mid FB_s \mid SB1_s \mid SB2_s$
Petrel	Adult apparent survival ϕ_{ad_p}	✓	$\widetilde{NB_p} \mid \widetilde{B_p}$
	Breeding probability β_p	✓	$\widetilde{NB_p} \mid \widetilde{B_p}$
	Hatching success ω_p	✓	$\widetilde{NB_p} \mid \widetilde{B_p}$
	Breeding success γ_p	✓	$\widetilde{NB_p} \mid \widetilde{B_p}$
	Detection probability p_p	✓	$\widetilde{NB_p} \mid \widetilde{B_p}$
	Uncertain state assignment probability u_p	✗	$NB_p \mid FBE_p \mid FBC_p \mid SB_p$

Table 2: Summary of the covariates tested on the demographic parameters of the two species – the skua and the petrel – and the time period (in months) considered for each demographic parameter. Notation are PP: Predator-Prey interactions, DD: intraspecific density dependence, SAM: Southern Annual Mode, SSTa: Sea Surface Temperature Anomalies, Chla: Chlorophyll a concentration.

Seabird	Parameter	Covariates tested	Time period
Skua	Adult apparent survival ϕ_{ad_s}	DD|SAM	Wintering (March-September)
	Breeding probability β_s	DD|SAM	Pre-Breeding (July-November)
	Breeding success γ_s	PP|DD|SAM	Breeding (October-February)
	Breeding success 2 chicks δ_s	PP|DD|SAM	Breeding (October-February)
Petrel	Adult apparent survival ϕ_{ad_p}	PP|DD|SAM|SSTa|Chla	Wintering (February-September)
	Breeding probability β_p	DD|SAM|SSTa|Chla	Pre-Breeding (August-October)
	Hatching success ω_p	PP|DD|SAM|SSTa|Chla	Breeding (October – December)
	Breeding success γ_p	PP|DD|SAM|SSTa|Chla	Breeding (December-January)

Table 3: Regression coefficients estimates for the relationships between covariates (DD: density-dependence, PP: predator-prey interaction, SAM: southern annular mode, SSTa: sea surface temperature anomalies, Chla: chlorophyll a concentration) and demographic parameters (ϕad: adult apparent survival, β: breeding probability, γ: breeding success, δ: breeding success with two chicks, ω: hatching success) for skuas (top) and petrels (bottom), B: breeder or NB: non breeder the previous years. 95% credible intervals that do not include 0 are in bold.

SKUA	**DD**				**PP**				**SAM**			
Parameters	slope	sd	2.5 %	97.5 %	slope	sd	2.5 %	97.5 %	slope	sd	2.5 %	97.5 %
$\boldsymbol{\phi ad_s B}$	-0.09	0.10	-0.24	0.12					0.31	0.31	-0.29	0.97
$\boldsymbol{\phi ad_s NB}$	-0.07	0.17	-0.30	0.34					-1.19	0.78	-2.89	0.27
$\boldsymbol{\beta_s B}$	-0.05	0.15	-0.25	0.35					-0.06	0.33	-0.72	0.61
$\boldsymbol{\beta_s NB}$	-0.10	0.22	-0.47	0.32					-0.18	0.55	-1.23	0.94
$\boldsymbol{\gamma_s B}$	**-0.56**	**0.11**	**-0.77**	**-0.34**	**0.76**	**0.18**	**0.41**	**1.14**	-0.05	0.23	-0.50	0.40
$\boldsymbol{\gamma_s NB}$	-0.33	0.35	-0.95	0.46	0.67	0.53	-0.42	1.73	-0.24	0.68	-1.70	1.00
$\boldsymbol{\delta_s B}$	**-0.78**	**0.19**	**-1.10**	**-0.38**	**1.14**	**0.31**	**0.57**	**1.76**	0.60	0.33	-0.04	1.26
$\boldsymbol{\delta_s NB}$	-0.17	0.64	-1.08	1.03	-0.25	1.64	-3.53	2.38	4.09	3.99	-3.00	13.0

PETREL	**DD**				**PP**				**SAM**				**SSTa**				**Chla**			
Parameters	slope	sd	2.5 %	97.5 %	slope	sd	2.5 %	97.5 %	slope	sd	2.5 %	97.5 %	slope	sd	2.5 %	97.5 %	slope	sd	2.5 %	97.5 %
$\boldsymbol{\phi ad_p B}$	-0.30	0.28	-0.91	0.21	0.21	0.27	-0.21	0.75	-0.08	0.45	-0.95	0.86	-0.10	0.25	-0.65	0.36	-0.35	0.51	-1.40	0.62
$\boldsymbol{\phi ad_p NB}$	-1.32	0.90	-2.62	0.70	0.70	0.35	-0.10	1.12	0.51	1.92	-2.65	5.00	0.13	0.96	-1.63	2.35	-0.36	1.47	-2.70	3.37
$\boldsymbol{\beta_p B}$	**0.71**	**0.12**	**0.44**	**0.90**					0.11	0.25	-0.37	0.63	-0.23	0.22	-0.69	0.17	0.44	0.42	-0.36	1.30
$\boldsymbol{\beta_p NB}$	0.21	0.31	-0.44	0.73					0.10	0.27	-0.40	0.66	-0.08	0.20	-0.47	0.32	0.71	0.44	-0.24	1.56
$\boldsymbol{\omega_p B}$	0.40	0.30	-0.29	1.01	0.01	0.20	-0.40	0.39	-0.43	0.39	-1.24	0.30	-0.43	0.32	-1.10	0.16	0.47	0.37	-0.22	1.23
$\boldsymbol{\omega_p NB}$	0.21	0.36	-0.40	1.14	-0.29	0.22	-0.72	0.16	**-1.03**	**0.42**	**-1.93**	**-0.27**	**-1.16**	**0.39**	**-1.99**	**-0.47**	**1.19**	**0.43**	**0.43**	**2.11**
$\boldsymbol{\gamma_p B}$	-0.33	0.48	-1.43	0.49	0.03	0.28	-0.42	0.63	0.15	0.48	-0.73	1.25	-0.04	0.32	-0.67	0.65	-0.18	0.46	-1.17	0.67
$\boldsymbol{\gamma_p NB}$	-0.07	0.49	-1.04	0.83	0.08	0.34	-0.56	0.83	-0.10	0.64	-1.30	1.00	-0.16	0.58	-1.31	0.84	0.70	0.80	-0.50	2.85

Figures

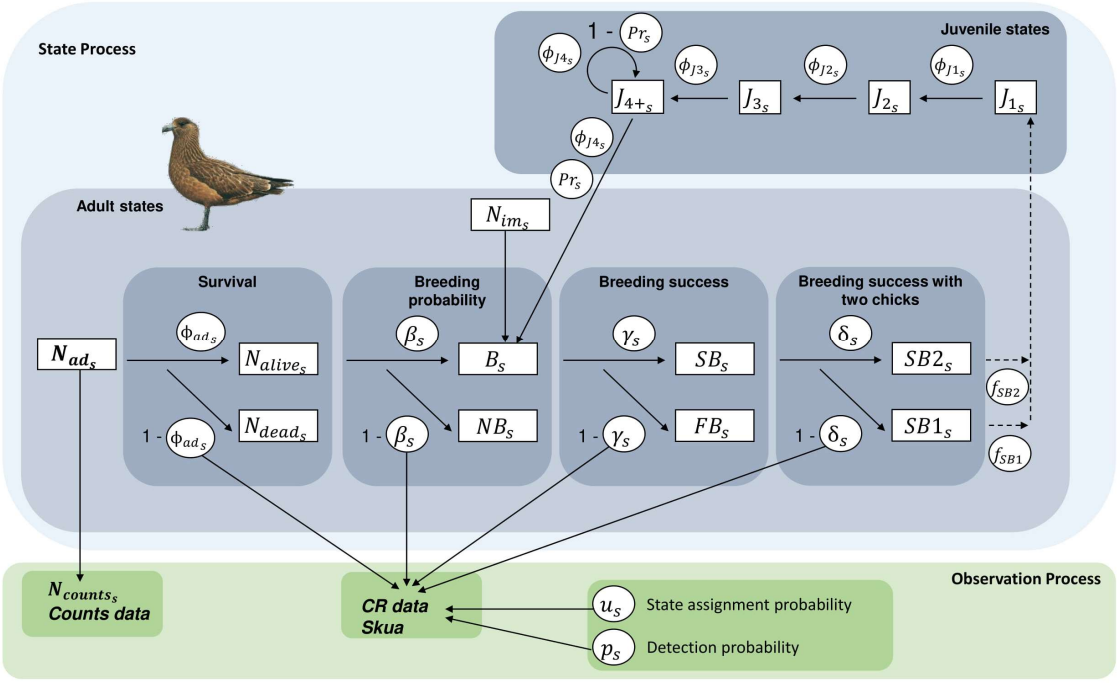

Figure 1: Structure of the skua IPM. Squares represent the state variables, circles represent the parameters. Two types of data are used, capture-recapture (CR) data and counts data (N_{counts_s}). Adult apparent survival (ϕ_{ad_s}), breeding probability (β_s), breeding success with at least one chick (γ_s), breeding success with two chicks (δ_s) for successful breeders, juvenile apparent survival for one to four years old and older ($\phi_{J1_s} to\ \phi_{J4_s}$), probability of first reproduction (Pr_s), state assignment probability (u_s) and detection probability (p_s) are parameters estimated in the model. Fecundity of breeder with one ($f_{SB\ s}$) or two chicks ($f_{SB\ s}$) are fixed. The number of adults (N_{ad_s}), dead (N_{dead_s}), alive (N_{alive_s}), breeder (B_s), nonbreeder (NB_s), failed breeder (FB_s), successful breeder (SB_s), successful breeder with one chick ($SB1_s$) or with two chicks ($SB2_s$) and the number of juveniles of one year old to four years old and older ($J_{1_s} to\ J_{4_s}$) are state variables estimated by the model. The number of immigrants (N_{im_s}) is a fixed vector.

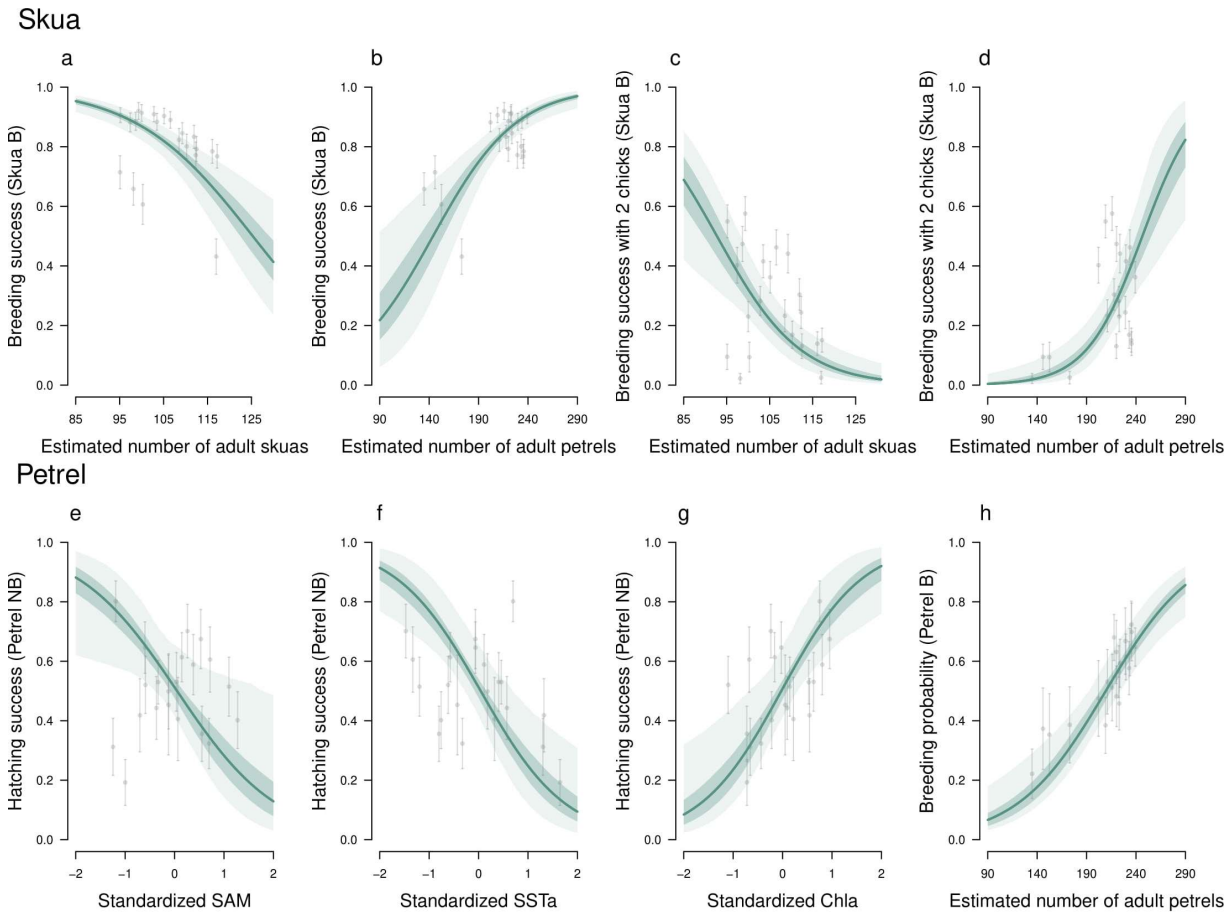

Figure 2: State variables and covariates effects on adult demographic parameters for the skua (top panels) and the petrel (bottom panels). Solid lines represent the estimated relationship between the covariates and the demographic parameters. Shaded areas are the 50% and 95% credibility intervals. Points represent demographic parameter estimates each year (21 years) plotted with respect to the covariate. Error bars are standard deviation. (a) Density-dependence effect and (b) prey effect on the estimated breeding success probability for skuas that bred the previous breeding season. (c) Density-dependence effect and (d) prey effect on the estimated breeding success probability for two chicks for skuas that bred the previous breeding season. Effects of (e) Southern Annular Mode, (f) Sea surface temperature anomalies and (g) Chlorophyll a concentration on the

835 estimated hatching success probability for petrels that were nonbreeders during the previous
836 breeding season. (h) Density-dependence effect on the breeding probability for petrels that bred
837 the previous breeding season.