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1 ***Running head: Multispecies integrated population model***

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

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20 **Abstract**

21 Assessing the effects of climate and interspecific relationships on communities is challenging
22 because of the complex interplay between species population dynamics, their interactions, and
23 the need to integrate information across several biological levels (individuals – populations –
24 communities). Usually used to quantify species interactions, integrated population models
25 (IPMs) have recently been extended to communities. These models allow fitting multispecies
26 matrix models to data from multiple sources while simultaneously accounting for various sources
27 of uncertainty in each data source. We used multispecies IPMs accommodating climate
28 conditions to quantify the relative contribution of climate vs. interspecific interactions on
29 demographic parameters, such as survival and breeding success, in the dynamics of a predator-
30 prey system. We considered a stage-structured predator–prey system combining 22 years of
31 capture–recapture data and population counts of two seabirds, the Brown Skua (*Catharacta*
32 *lönnerbergi*) and its main prey the Blue Petrel (*Halobaena caerulea*) both breeding on the
33 Kerguelen Islands in the Southern Ocean. Our results showed that climate and predator-prey
34 interactions drive the demography of skuas and petrels in different ways. The breeding success
35 of skuas appeared to be largely driven by the number of petrels and to a lesser extent by
36 intraspecific density-dependence. In contrast, there was no evidence of predation effects on the
37 demographic parameters of petrels, which were affected by oceanographic factors (chlorophyll a
38 and sea surface temperature anomalies). We conclude that bottom-up mechanisms are the main
39 drivers of this skua-petrel system. We discuss the mechanisms by which climate variability and
40 predator-prey relationships may affect the demographic parameters of these seabirds. Taking into

41 account both species interactions and environmental covariates in the same analysis improved
42 our understanding of species dynamics.

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

45 **Introduction**

46 The effects of climate change on the diversity and the structure of communities have been
47 reported repeatedly (Walther et al. 2002, Parmesan 2006, Hoegh-Guldberg and Bruno 2010,
48 Miller et al. 2018). However, the underlying mechanisms remain poorly understood due to the
49 complex dynamics of interacting species: within species, between species and between species
50 and the environment (Godfray and May 2014). Following disturbance, the abundance and
51 distribution of species are expected to be modified according to the position and extent of the
52 species' niche (Thomas et al. 2004). Because the effects of environmental variability on
53 mortality, fecundity and dispersal may differ between species (Grosbois et al. 2008, Jenouvrier
54 2013), changes in structure and diversity appear at the community level. However, studying
55 species-by-species responses to environmental changes may overlook the role played by species
56 interactions on those responses, and contribute to a lesser extent to the larger understanding of
57 species interactions that is required by community ecology.

58 Models for population dynamics have been used to understand the effect of interspecific
59 interactions and environment on species demography. However, these models are generally not
60 demographically structured (Stenseth et al. 2015, Pacoureau et al. 2019a, Stoessel et al. 2019) or
61 only partially (Millon et al. 2014, Saunders et al. 2018, Pacoureau et al. 2019b). Unstructured

62 approaches consider individuals as being equivalent but differences in size, age and ontogenic
63 stages exist within a population and may be of importance in the context of interspecific
64 interactions. As argued by Miller and Rudolf (2011), the consideration of the stage structure of
65 populations can lead to a better understanding of community structure and dynamics.
66 Interactions between species such as predation or competition do not necessarily have a
67 homogeneous impact on the different stages of the interacting species. For example, young
68 individuals might be predominantly preyed upon in carnivore–ungulate systems (Gervasi et al.
69 2015). Therefore, to detect and understand species interactions, we need to consider jointly the
70 demography of several stage-structured populations (Oken and Essington 2015).

71 Although well developed for single-species dynamics (Tuljapurkar and Caswell 1997, Caswell
72 2001), demographic stage-structured models have received little attention in community ecology
73 (but see Chu and Adler (2015) on a plant system). The difficulty is that multispecies
74 demographic analysis requires integrating information across several biological levels
75 (individual – population – community) which, in turn, requires unifying all available data
76 sources into a single framework. Integrated population models (IPMs) have been recently
77 developed to infer population demography by making complete use of all available sources of
78 information (see Schaub and Abadi 2011, and Zipkin and Saunders 2018 for reviews). In their
79 simplest form, these models combine population counts and demographic data into a single
80 framework, which allows the estimation of demographic parameters while simultaneously
81 accounting for various sources of uncertainty in each data source (e.g. measurement error or
82 parameter estimation) (Besbeas et al. 2002). The IPM framework has been extended to multiple

83 species (Péron and Koons 2012) for competition/parasitism, and more recently for predator-prey
84 interactions (Barraquand and Gimenez 2019).

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

93 Because seabirds often occupy high level positions in food-webs, bottom-up forcing which
94 implies population regulation through climate driven limitation in food availability, has long
95 been featured as the dominant paradigm to understand their dynamics (Lack 1967, Aebischer et
96 al. 1990, Stenseth et al. 2002). Seabird foraging behavior and demography reflect the influences
97 of climate variability which directly impacts biological processes in marine ecosystems and
98 cascade through food webs up to seabirds (Barbraud and Weimerskirch 2001, Jenouvrier et al.
99 2003). However, top-down pressures from predation at breeding colonies are also known to
100 affect the vital rates of seabirds (Hipfner et al. 2012). There is increasing evidence that bottom-
101 up and top-down processes often act in concert and differently affect demographic parameters
102 (Suryan et al. 2006, Horswill et al. 2014, 2016). For example, the effects of predation and
103 resource limitation caused breeding failure of Black-legged Kittiwakes (*Rissa tridactyla*)
104 (Regehr and Montevecchi 1997) and population declines of Arctic Skuas (*Stercorarius*

105 *parasiticus*) (Perkins et al. 2018). Therefore, quantifying the relative strength of environmental
106 conditions and predator-prey effects is essential for a better understanding of the drivers of
107 population dynamics in seabirds. This is all the more important as climate changes impact the
108 physical properties of the oceans, including the Southern Ocean (Gille 2002, Han et al. 2014)
109 and, through the trophic food web, affect demography and population dynamics of seabirds
110 (Barbraud et al. 2012, Sydeman et al. 2015), including some of the species studied here
111 (Barbraud and Weimerskirch 2003).

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

117 **Materials and Methods**

118 **Study site and Species**

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

122 The petrel is a small (150–250g) long-lived seabird belonging to the family of *Procellariiformes*.
123 At Kerguelen Islands, petrels feed on macrozooplankton and micronekton, mainly crustaceans
124 and fishes (Cherel et al. 2002, 2014). Individuals from Mayes Island spend the nonbreeding

125 season (from mid-February to September) between the polar front and the northern limit of the
126 pack-ice (57-62°S) between longitudes 20°W and 90°E (Cherel et al. 2016). Birds return to
127 breeding colonies in early September (Quillfeldt et al. 2020). Mayes Island is covered with dry
128 soils and dense vegetation, providing suitable breeding sites for approximately 142,000 breeding
129 pairs of these burrowing petrels (Barbraud and Delord 2006). In late October, a single egg is laid
130 in a burrow dug in peat soil under tall and dense vegetation. The incubation lasts 45-49 days and
131 the chick rearing period 43-60 days (Jouventin et al. 1985). The chick fledges in early February.
132 Both sexes participate in parental care by alternating foraging trips during the incubation and
133 fledging periods.

134 The skua is a medium sized (1.1 – 2.2 kg) long-lived seabird belonging to the family of
135 *Charadriiformes*. On Mayes Island between 80 and 120 pairs breed annually (Mougeot et al.
136 1998). Breeding pairs form in October with a high mate fidelity, and generally establish
137 themselves in the same territory each year (Parmelee and Pietz 1987), which they tenaciously
138 defend throughout the breeding season. Generally, two eggs are laid between October and
139 December. The incubation lasts 28-32 days and the chicks rearing period 40-50 days (Higgins
140 and Davied 1996). Skuas are extremely plastic in their foraging techniques and adapt their diet
141 depending on the local availability of prey (Carneiro et al. 2015). On Mayes Island, during the
142 breeding season, Blue Petrels represent 95% of the skua diet (Pacoureaux et al. 2019c). Skuas
143 from Mayes Island overwinter in the southern hemisphere between 10°E and 150°E (Delord et
144 al. 2018).

145 During the breeding period on Mayes Island, the predation of petrels by skuas takes place mainly
146 at night, when petrels come out or arrive at their burrows (Mougeot and Bretagnolle 2000a).

147 Skuas mostly prey on petrels on the ground, but they can also catch petrels in flight (Mougeot et
148 al. 1998, Pacoureaux et al. 2019c). Vocalizing petrels, especially those without partners, are more
149 easily detected by skuas during the courtship period (Mougeot and Bretagnolle 2000b). Skuas
150 may also prey on chicks during the fledging period.

151 **Count and capture-recapture data**

152 Data of both skuas and petrels were collected during the breeding seasons from 1996/1997 to
153 2017/2018. For convenience, breeding seasons are named from 1996 to 2017 hereafter. The time
154 interval used in our model starts before the wintering of species and ends at the end of the
155 breeding period. Two types of data were used: count data corresponding to the number of
156 burrows or territories occupied by seabirds and capture-recapture (CR) data of adult seabirds
157 found on the monitored area. Each year, adult individuals of both species were checked at
158 specific times following the species phenology to determine the breeding status of each bird. The
159 breeding status of marked birds was determined at the end of the breeding period. Count data are
160 considered in a post-breeding census. In the following we describe how the data were collected
161 for the two species. For clarity, all parameters for skuas are indicated by S and by P for petrels.

162 Around 200 individually marked burrows of petrels were inspected each year from early-to-mid
163 November just after the egg-laying to check for eggs and to identify marked adults, and then in
164 late January just before fledging of the chicks. Each year since 1985 (see Barbraud and
165 Weimerskirch 2005), all fledglings as well as new individuals found in burrows were marked
166 with a stainless steel band (captured by hand, marked, and replaced in their burrow). Petrels
167 never observed with an egg or a chick during a given breeding season were considered as

168 nonbreeders (*NB*). Individuals were identified as breeders if they laid a single egg or raised a
169 chick and as successful breeders if their chick fledged (*SB*). Two categories of failed breeders
170 were used depending on the stage of failure: egg stage (*FBE*) or chick stage (*FBC*). Given that
171 the first sampling period occurred just after laying, it is very unlikely that nonbreeders were
172 failed breeders. These breeding statuses allowed the construction of the individual capture
173 histories (Ch_p) and constituted our CR data. The annual number of adult petrels (Y_p), *i.e.* count
174 data, was estimated as the number of occupied burrows. Each occupied burrow was considered
175 as being frequented by a pair of petrels. We considered that this count included all adult
176 individuals, both breeders and non-breeders.

177 For skuas, each year since 1991, the eastern side of Mayes Island was inspected to identify
178 territories of skuas. A territory was considered established when a pair strongly defended an area
179 against other skuas (Mougeot et al. 1998). Around 50 nesting territories were visited four to eight
180 times from mid-October (after egg-laying) to late-February (just before fledging of the chicks)
181 each year. Chicks just before fledging, as well as new adult individuals, were marked with a
182 metal ring and a plastic ring to facilitate individual identification using binoculars. Breeding
183 status was determined by checking the nest contents for the presence of eggs or young chicks.
184 Skuas never observed with an egg or a chick were considered as nonbreeders (*NB*). Individuals
185 were identified as breeders if they laid at least one egg or raised a chick. If the eggs did not hatch
186 or the chicks died, both members of the pair were considered as failed breeders (*FB*). Given that
187 the first sampling period occurred just after laying, it is very unlikely that nonbreeders
188 represented failed breeders. Successful breeders were defined as individuals that fledged one or
189 two chicks, and were denoted as *SB1* or *SB2*, respectively. These breeding statuses allowed the

190 construction of the individual capture histories (Ch_S) and constituted our CR data. The annual
191 number of skuas (Y_S), *i.e.* count data, was estimated as the number of territories and each
192 territory was considered occupied by a pair of skuas. We considered that this count included all
193 adult individuals, both breeders and non-breeders.

194 For both species, individual breeding status could be considered as “uncertain” (C) in case of
195 difficulties to assign their breeding status (lack of information, missed checks, individuals never
196 re-observed). Only adult individuals that have bred at least once between the 1996 and the 2017
197 breeding seasons were kept in the data set for analysis to eliminate potential transient individuals
198 ($n = 318$ for skuas and $n = 1210$ for petrels). Individual capture histories (Ch) started at their first
199 breeding attempt recorded. Based on the high probability of observing breeders in the study site,
200 we assumed that the first breeding attempt was correctly detected. New individuals found in
201 monitored burrows or territories are considered as immigrants to the study site (N_{im}).

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

210 **Integrated Population Model**

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

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

228 **State process**

229 *Offspring production*

230 The estimated number of skuas and petrels in their first year *i.e.* between 0 and 1 year old

231 ($N_{J1,S,t}$) at year t , is modelled with a Poisson distribution:

232
$$N_{J1,S,t} \sim Po(0.5 \times f_{SB1,S} \times N_{SB1,S,t-1} + 0.5 \times f_{SB2,S} \times N_{SB2,S,t-1}) \quad (1)$$

233
$$N_{J1,P,t} \sim Po(0.5 \times f_{SB,P} \times N_{SB,P,t-1}) \quad (2)$$

234 with $N_{J1,S}$ the number of chicks produced by all successful skua breeders ($N_{SB1,S}$ and $N_{SB2,S}$)

235 according to their fecundity ($f_{SB1,S}$: 1 chick and $f_{SB2,S}$: 2 chicks per female skua, sex ratio: 0.5).

236 For petrels, $N_{J1,P}$ is also Poisson distributed but with only one chick ($f_{SB,P}$) per estimated

237 successful female breeder ($N_{SB,P}$ with a sex ratio of 0.5).

238 *Juvenile survival*

239 The number of juveniles between one and two years (N_{J2}), two and three years (N_{J3}), and three

240 and four years (N_{J4}), are modelled with binomial distributions:

241
$$N_{J2,X,t} \sim Bin(\phi_{J1,X}, N_{J1,X,t-1}) \quad (3)$$

242
$$N_{J3,X,t} \sim Bin(\phi_{J2,X}, N_{J2,X,t-1}) \quad (4)$$

243
$$N_{J4,X,t} \sim Bin(\phi_{J3,X}, N_{J3,X,t-1}) \quad (5)$$

244 with the apparent survival between one and two years (ϕ_{J1}), between two and three years (ϕ_{J2})

245 and between three and four years (ϕ_{J3}) respectively. As we observed only adult breeding birds,

246 we had no information on the juvenile phase. We assumed that juvenile apparent survival

247 increased with age (Greig et al. 1983, Grande et al. 2009, Fay et al. 2015), as experienced birds
 248 are on average more effective in foraging (Daunt et al. 2007), in competing with conspecifics or
 249 in avoiding predators:

$$250 \text{ logit}(\phi_{Jage_i,X}) = \lambda_{1,X} + \lambda_{2,X} \times age_i \quad (6)$$

251 where ϕ_J is the juvenile apparent survival, age_i the age of the juvenile state (from N_{J_1} to N_{J_4}),
 252 λ_1 the intercept and λ_2 the slope which is constrained to be positive.

253 *Juvenile first breeding attempt*

254 The first breeding attempt in skuas and petrels could start from age four. Four years old
 255 individuals and older that did not attempt to breed are in the state ($N_{J_{4+}}$). The individuals that
 256 attempted to breed for the first time with a first breeding attempt probability Pr are in the state
 257 $N_{J_{4B}}$ and the individuals that did not attempt to breed are in the state $N_{J_{4NB}}$:

$$258 N_{J_{4B},X,t} \sim Bin (Pr_{X,t}, \phi_{J_{4,X}} \times N_{J_{4+,X,t-1}}) \quad (7)$$

$$259 N_{J_{4NB},X,t} = \phi_{J_{4,X}} \times N_{J_{4+,X,t-1}} - N_{J_{4B},X,t} \quad (8)$$

260 with ϕ_{J_4} the apparent survival for the $N_{J_{4+}}$ state. The $N_{J_{4+}}$ state includes individuals that did not
 261 attempt to breed ($N_{J_{4NB}}$) and individuals aged between three and four years (N_{J_4}):

$$262 N_{J_{4+,X,t}} = N_{J_4,X,t} + N_{J_{4NB},X,t} \quad (9)$$

263 *Adult survival*

264 For the two species, we modelled the number of surviving adults (N_{alive}) at year t among the
265 total number of adult individuals (N_{adtot}) at year $t-1$ with a binomial distribution, with ϕ the
266 adult apparent survival:

$$267 \quad N_{alive,X,t} \sim Bin(\phi_{X,t-1}, N_{adtot,X,t-1}) \quad (10)$$

268 *Breeding probability*

269 The number of adult individuals that have bred or not bred among those that survived (N_{alive}) is
270 modelled as:

$$271 \quad N_{Balive,X,t} \sim Bin(\beta_{X,t-1}, N_{alive,X,t}) \quad (11)$$

$$272 \quad N_{NB,X,t} = N_{alive,X,t} - N_{Balive,X,t} \quad (12)$$

273 with β the probability of breeding, N_{Balive} the number of adult breeders that survived and N_{NB}
274 the number of adult nonbreeders. As capture histories started at their first breeding attempt
275 recorded, the immigrants, *i.e.* newly marked individuals (N_{im}) coming for the first time in the
276 colony, were considered as breeders. Then, the total number of breeders (N_B) corresponds to the
277 sum of the number of adult breeders that survived (N_{Balive}), the number of immigrants (N_{im})
278 and the number of juveniles attempting to breed for the first time (N_{J4B}):

$$279 \quad N_{B,X,t} = N_{Balive,X,t} + N_{J4B,X,t} + N_{im,X,t} \quad (13)$$

280 *Breeding success*

281 Breeding success and failure are modelled differently for skuas and petrels. For skuas, the
282 numbers of failed breeders ($N_{FB,S}$) and successful breeders ($N_{SB,S}$) are modelled following a
283 binomial distribution:

$$284 \quad N_{SB,S,t} \sim Bin(\gamma_{S,t-1}, N_{B,S,t}) \quad (14)$$

$$285 \quad N_{FB,S,t} = N_{B,S,t} - N_{SB,S,t} \quad (15)$$

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

$$288 \quad N_{SB2,S,t} \sim Bin(\delta_{S,t-1}, N_{SB,S,t}) \quad (16)$$

$$289 \quad N_{SB1,S,t} = N_{SB,S,t} - N_{SB2,S,t} \quad (17)$$

290 with δ_S the probability of producing two chicks rather than one among the successful breeders.

291 For petrels, there are two states for failed breeders: one with petrels that failed to hatch their egg
292 (named failed breeder at the egg stage $N_{FBE,P}$) and the second with petrels that failed to fledge
293 their chick (named failed breeder at the chick stage $N_{FBC,P}$). Hence, there is a parameter of
294 successful hatching (ω_P). The numbers of petrels with an egg that successfully hatched ($N_{SH,P}$)
295 and the failed breeders at the egg stage ($N_{FBE,P}$) were modelled following a binomial
296 distribution:

$$297 \quad N_{SH,P,t} \sim Bin(\omega_{P,t-1}, N_{B,P,t}) \quad (18)$$

$$298 \quad N_{FBE,P,t} = N_{B,P,t} - N_{SH,P,t} \quad (19)$$

299 with ω_p the probability of successful hatching. Successful breeders ($N_{SB,p}$) and failed breeders
 300 at the chick stage ($N_{FBC,p}$) were modelled following a binomial distribution:

$$301 \quad N_{SB,p,t} \sim \text{Bin}(\gamma_{p,t-1}, N_{SH,p,t}) \quad (20)$$

$$302 \quad N_{FBC,p,t} = N_{SH,p,t} - N_{SB,p,t} \quad (21)$$

303 with y_p the probability of successful breeding.

304 *Total number of adults*

305 For skuas, the total number of adults ($N_{adtot,S}$) corresponds to the sum of adults nonbreeders
 306 ($N_{NB,S}$), failed breeders ($N_{FB,S}$), successful breeders with one chick ($N_{SB1,S}$) and successful
 307 breeders with two chicks ($N_{SB2,S}$):

$$308 \quad N_{adtot,S,t} = N_{NB,S,t} + N_{FB,S,t} + N_{SB1,S,t} + N_{SB2,S,t} \quad (22)$$

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

$$312 \quad N_{adtot,P,t} = N_{NB,P,t} + N_{FBE,P,t} + N_{FBC,P,t} + N_{SB,P,t} \quad (23)$$

313 **Count data**

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

318 $Y_{X,t} \sim Norm(N_{adtot,X,t}, \varepsilon_X)$ (24)

319 The likelihood for the population count data is denoted

320 as $L_{CO,S}(Y_S | \phi_{J1,S}, \phi_{J2,S}, \phi_{J3,S}, \phi_{J4,S}, Pr_S, \phi_S, \beta_S, \gamma_S, \delta_S, N_{adtot,S})$ for skuas and

321 as $L_{CO,P}(Y_P | \phi_{J1,P}, \phi_{J2,P}, \phi_{J3,P}, \phi_{J4,P}, Pr_P, \phi_P, \beta_P, \omega_P, \gamma_P, N_{adtot,P})$ for petrels.

322 **Capture-recapture data**

323 For adult CR data, we used multievent capture–recapture models to estimate the demographic
 324 parameters (Pradel 2005). These models take into account the imperfect detectability of the
 325 individuals as well as the uncertainty in the assignment of states to individuals (Gimenez et al.
 326 2012).

327 For skuas, our multievent model includes five states: NB, FB, SB1, SB2, dead, and six events:
 328 not seen, seen as NB, seen as FB, seen as SB1, seen as SB2, seen as C *i.e.* individuals seen with
 329 an uncertain breeding status. For petrels, the five states are: NB, FBE, FBC, SB, dead, and the
 330 six events are: not seen, seen as NB, seen as FBE, seen as FBC, seen as SB, seen as C. The
 331 following demographic parameters were estimated for the two species: the adult apparent
 332 survival probability (ϕ_X), the breeding probability (β_X), the probability of successful
 333 breeding (γ_X). The probability of successful breeding with two chicks (δ_S) was also estimated
 334 for skuas, as well as the probability of hatching (ω_P) for petrels. Two additional parameters were
 335 also estimated: the detection probability (p_X) and the state assignment probability of individuals
 336 with uncertain state (u_X). All parameters were time-varying through a yearly random effect,
 337 except u (Table 1). State transitions were set to be state dependent according to the breeding
 338 status in the previous breeding season (Table 1): Breeder (\tilde{B}) representing birds that attempted to

339 breed the previous breeding season ($FB, SB1, SB2$ for skuas or FBE, FBC, SB for petrels) or
 340 Nonbreeder (\widetilde{NB}) representing birds that already bred previously but did not attempt to breed
 341 during the previous breeding season (NB). The detection probability and the state assignment
 342 probability also depended on the breeding status (Table 1). The likelihood for the CR data for
 343 skuas is denoted as $L_{cr,S}(Ch_S|\phi_S, \beta_S, \gamma_S, \delta_S, p_S, u_S)$ and $L_{cr,P}(Ch_P|\phi_P, \beta_P, \gamma_P, \delta_P, p_P, u_P)$ for
 344 petrels.

345 **Joint likelihood**

346 The joint likelihood of the skua IPM is the product of the likelihood for the count data ($L_{co,S}$)
 347 and CR data ($L_{cr,S}$):

$$\begin{aligned}
 348 \quad & L_{ipm,S}(Y_S, Ch_S|\phi_{J1,S}, \phi_{J2,S}, \phi_{J3,S}, \phi_{J4,S}, Pr_S, \phi_S, \beta_S, \gamma_S, \delta_S, N_{adtot,S}, p_S, u_S) = \\
 349 \quad & L_{co,S}(Y_S|\phi_{J1,S}, \phi_{J2,S}, \phi_{J3,S}, \phi_{J4,S}, Pr_S, \phi_S, \beta_S, \gamma_S, \delta_S, N_{adtot,S}) \times \\
 350 \quad & L_{cr,S}(Ch_S|\phi_S, \beta_S, \gamma_S, \delta_S, p_S, u_S) \qquad \qquad \qquad (25)
 \end{aligned}$$

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

353 **Interspecific relationships, intraspecific density-dependence, and environmental** 354 **covariates**

355 We used different covariates to investigate their effects on the adult demographic parameters
 356 estimated for the two species (Table 2). We focused only on the demographic parameters of adult
 357 individuals because only adults were observed on the field. We tested interspecific predator-prey
 358 relationships between skua and petrel, and intraspecific relationships with density-dependence

359 for both species. Moreover, we considered several climatic covariates that were suspected to
360 affect demographic parameters of skuas and petrels, the Southern Annular Mode (SAM) on a
361 large scale, and the Sea Surface Temperature anomalies (SSTa) and Chlorophyll a concentration
362 (Chla) on a local scale. In the following, we provide more details on covariates and how they
363 may affect the demography of skuas and petrels.

364 **Predator-prey interactions**

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

374 **Intraspecific density-dependence**

375 We investigated the effect of intraspecific density-dependence on the demography of the two
376 species as higher density of individuals on the breeding area can lead to and an increasing
377 competition for food resources or for territories. Skuas are highly territorial and defend their
378 territories vigorously during the whole breeding season. The most violent fights may even lead to
379 their death. Moreover, the limited number of territories could cause emigration of skuas without

380 territory. Thus, we predicted that the apparent survival (ϕ_S), *i.e.* the joint estimation of the
381 mortality and emigration, would be negatively impacted by the number of skuas. This limited
382 number of territories could also lead to a negative density-dependence relationship between
383 breeding probability (β_S) and population density. The energetic cost and the time spent in
384 defending a territory throughout the breeding season may limit the time spent searching for food,
385 potentially limiting energy investment in reproduction. We thus predicted a negative effect of
386 population density on the successful breeding parameter (γ_S) and the probability to have two
387 chicks rather than one for successful breeders (δ_S). For petrels, we also tested the effects of
388 intraspecific competition for food resources, which could affect their adult apparent survival
389 (ϕ_P) and their breeding parameters: breeding probability (β_P), hatching (ω_P) and fledging
390 success (γ_P).

391 **Environmental covariates**

392 Climate variability impacts biological processes in marine ecosystems, which cascade through
393 food webs and are integrated by seabirds (Barbraud and Weimerskirch 2001, Jenouvrier et al.
394 2003). Hence, we considered several covariates that are suspected to affect populations of petrels
395 and skuas through these bottom-up mechanisms. All covariates are used as proxies of food
396 availability at sea at different scales. In the following, we explain how environmental conditions
397 may impact the two species based on their diet and distribution.

398 Because skuas have broad wintering areas (Delord et al. 2018), we tested a large-scale
399 environmental covariate, the SAM. In contrast with their diet during the breeding season
400 specialized on the Blue Petrel, during winter skuas adopt a mixed diet composed of low trophic
401 level preys, such as macrozooplankton and crustaceans (Delord et al. 2018). We hypothesized

402 that availability of food resources at sea during the austral winter might have an effect on the
403 body condition of skuas and then affect the survival of skuas. Moreover, skuas may experience a
404 carry-over effect as the additional energy invested by individuals to maintain themselves during
405 poor wintering conditions may have repercussion on their ability to breed the next breeding
406 season (Harrison et al. 2011, Bogdanova et al. 2017)

407 For petrels, the wintering areas have been determined (Cherel et al. 2016) allowing us to test two
408 covariates used at the local scale, the SSTa and the Chla, in addition to the SAM. As their diet is
409 mainly composed of crustaceans and fish feeding at low trophic levels (Cherel et al. 2002, 2014),
410 the food availability at sea may impact the survival of petrels. Moreover, during the breeding
411 season, male and female petrels take turns, one incubating the egg and fasting and the other
412 foraging at sea, which results in substantial variation in their body mass (Chaurand and
413 Weimerskirch 1994a, 1994b, Weimerskirch et al. 1994, Chastel et al. 1995). Therefore, high
414 food availability at sea may allow a good foraging success of the foraging partner that may return
415 to land after a short stay at sea, allowing a good synchronization of the breeding partners on the
416 nest. In contrast, poor conditions could increase the time spent at sea by the foraging partner,
417 which would increase desertion of the nest by the fasting partner and then, reduce the breeding
418 success. We thus predicted that conditions at sea during the breeding season would also affect
419 the breeding success of petrels.

420 *Southern Annular Mode*

421 The SAM is a large-scale climate index. SAM is the leading mode of climate variability over the
422 Southern Hemisphere. SAM is defined as the difference of atmospheric pressure between the
423 40°S and 65°S latitudes (Marshall 2003). SAM influences surface wind, sea surface temperature

424 (SST) and surface chlorophyll concentration. A large majority of the skuas from Mayes Island
425 overwinter north of the polar front (Delord et al. 2018). In the subtropical zone, SAM positive
426 phases induced warm SSTa, low surface chlorophyll concentration and easterly winds driving
427 Ekman transport (the 90° wind-driven net transport on the sea surface), while in the Subantarctic
428 zone there is a convergence of waters that increase downwelling and positive SSTa (Lovenduski
429 and Gruber 2005). We thus predicted that the positive phases of SAM, potentially leading to
430 poorer food availability in the areas used by skuas during the nonbreeding period, would have
431 negative impacts on skua survival and limit their ability to breed the next breeding season. South
432 of the polar front, where petrels spend the winter, positive phases of the SAM are associated with
433 westerly winds. This induces cold SSTa, increased equatorward Ekman transport and drives
434 increased upwelling (Lovenduski and Gruber 2005). Consequently, the biological productivity
435 and potential prey availability for petrels are higher during positive phases of the SAM. We thus
436 predicted that the positive phases of SAM would be favorable for petrel demographic
437 parameters. Data were obtained from the online database of the British Antarctic Survey
438 (<http://www.nerc-bas.ac.uk/icd/gjma/sam.html>).

439 *Sea Surface Temperature anomalies*

440 SSTa reflect local oceanographic conditions that influence the whole marine trophic food web.
441 High SST generally reduces vertical mixing and provides poor growing conditions for
442 zooplankton communities which, through bottom-up mechanisms, induces reduced trophic
443 resources for seabirds (Barbraud et al. 2012, Sydeman et al. 2015). Consequently, year-to-year
444 variation of SST was previously found to be negatively correlated with petrel body condition
445 (Guinet et al. 1998). Therefore, we predicted that high SSTa would negatively affect overwinter

446 survival and breeding success of petrels. The SSTa data were downloaded from the National
447 Oceanic and Atmospheric Administration (“data: NOAA NCEP EMC CMB GLOBAL
448 Reyn_SmithOlv2 monthly ssta”) from 1996 to 2018.

449 *Chlorophyll a*

450 Chlorophyll a lies at the bottom of the marine food web and provides resources for higher trophic
451 organisms up to seabirds. Because petrel diet is mainly composed of crustaceans and fish feeding
452 at low trophic levels (Cherel et al. 2002, 2014), we predicted that high concentrations of Chla
453 would be favorable to the survival and breeding success of petrels. The Chla data were
454 downloaded from the NASA Ocean Data with a 9km mapped concentration data of chlorophyll a
455 for the years 1997 to 2001 and from the Nasa Earth Observation (NEO AQUA/MODIS data)
456 monthly for the years 2002 to 2018.

457 **Assessing the effect of environmental covariates and population densities**

458 We fitted a single multispecies IPM including all the biologically relevant effects. Logit-linear
459 regressions were used to estimate the effect of environmental (SAM, SSTa and Chla) and inter-
460 and intra-specific interactions on demographic parameters (adult apparent survival, breeding
461 probability, hatching probability, breeding success) (Table 2). We used state variables
462 $N_{adtot,S}$ and $N_{adtot,P}$, respectively the number of adult skuas and petrels, to assess the effects of
463 inter- and intra-specific interactions. For example, we modelled the hatching probability for
464 petrels that bred the previous year ($\omega_{P,\bar{B}}$) using a logit link:

$$465 \text{logit}(\omega_{P,\bar{B},t-1}) = \mu_{\omega,P,\bar{B}} + \alpha_{SAM,\omega,P,\bar{B}} \times SAM_{\omega,P,t} + \alpha_{SSTa,\omega,P,\bar{B}} \times SSTa_{\omega,P,t} +$$
$$466 \alpha_{Chla,\omega,P,\bar{B}} \times Chla_{\omega,P,t} + \alpha_{DD,\omega,P,\bar{B}} \times N_{adtot,P,t} + \alpha_{PP,\omega,P,\bar{B}} \times N_{adtot,S,t} + \varepsilon_{\omega,P,\bar{B},t}$$

467 $\varepsilon_{\omega,P,\bar{B},t} \sim Norm(0, \sigma^2_{\varepsilon,\omega,P,\bar{B}})$ (26)

468 with $\mu_{\omega,P,\bar{B}}$ the intercept, $\alpha_{SAM_{\omega,P,\bar{B}}}$ the slope for the climatic covariate $SAM_{\omega,P}$, $\alpha_{SSTa_{\omega,P,\bar{B}}}$ the
 469 slope for the climatic covariate $SSTa_{\omega,P}$, $\alpha_{Chla_{\omega,P,\bar{B}}}$ the slope for the climatic covariate $Chla_{\omega,P}$,
 470 $\alpha_{DD,\omega,P,\bar{B}}$ the slope indicating the strength of the intraspecific density-dependence with
 471 $N_{adtot,P}$ the number of adult petrels, $\alpha_{PP,\omega,P,\bar{B}}$ the slope indicating the strength of the predator-
 472 prey relationship with $N_{adtot,S}$ the number of adult skuas, $\varepsilon_{\omega,P,\bar{B}}$ is a yearly random effect and
 473 $\sigma^2_{\varepsilon,\omega,P,\bar{B}}$ its temporal variance. This temporal random effect allows to capture residual
 474 environmental stochasticity that is not explained by temporal covariates. The descriptions of all
 475 logit-linear relationships used on demographic parameters are available in Appendix S2 and the
 476 temporal used of covariates is described in Appendix S3: Fig. S1.

477 For local covariates (SSTa and Chla), we calculated the average values of the covariates in the
 478 areas in which petrels were located (Cherel et al. 2016) in a specific time period during which the
 479 environment might affect the demographic parameter under investigation (Table 2). Each
 480 environmental covariate was standardized to have zero mean and unit variance. However, the
 481 inter- and intra-specific covariates were not standardized prior to the analyses because the
 482 population sizes were estimated step by step each year. To compare the relative contribution of
 483 the effects of each covariate, we calculated the standardized effect of population size (for inter-
 484 and intra-specific relationship) posterior to the analyses by multiplying their slopes (α) by the
 485 standard deviation of the estimated population sizes. Then, we compared the relative contribution
 486 of each covariate using the regression estimate which we used as a measure of effect size.

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

490 **Model implementation**

491 To fit the juvenile apparent survival parameters increasing with age, we modelled them as a
492 positive linear function of age by assigning to the slope λ_2 a $U(0,1)$ prior, and by defining the
493 intercept λ_1 with a normal $N(0,1)$ prior. The probability of the first breeding attempt (Pr) is
494 time-dependent with a uniform prior: $Pr_t \sim U(0,1)$. Normal priors $N(0,10^4)$ were assigned to the
495 regression coefficients (α) of the covariate effects. For the variance of the random year
496 effects (σ_ε^2), we used a $U(0,10)$ vague prior. The state assignment probability of individuals
497 with uncertain state parameter (u) was defined *a priori* with a $U(0,10)$ vague prior.

498 Bayesian posterior distributions were approximated *via* Markov chain Monte Carlo (MCMC)
499 algorithms. Two independent MCMC chains of 200,000 iterations were used with a burn-in
500 period of 100,000. One out of five iterations was kept and final inferences were derived from a
501 sample of $2 \times 20,000$ iterations that resulted from merging the two chains. Gelman-Rubin
502 convergence diagnostic (Brooks and Gelman 1998) was below 1.5 for each parameter and the
503 mixing of the chains was satisfactory. We performed the analyses using Nimble (de Valpine et
504 al. 2017 ; version 0.9.1) and program R (R Core Team 2020 ; R version 4.0.3). Code and data are
505 available on GitHub at https://github.com/maudqueroue/MultispeciesIPM_SkuaPetrel.

506 **Results**

507 **Predator-prey relationships**

508 We estimated positive relationships between two breeding parameters of skuas and the number
509 of adult petrels. The breeding success for at least one chick ($\gamma_{S,\bar{B}}$) [slope mean ($\alpha_{PP_{\gamma,S,\bar{B}}}$) = 0.67;
510 95% CRI (0.38, 1.04)] (Fig. 2a) and the breeding success with two chicks ($\delta_{S,\bar{B}}$) [slope mean
511 ($\alpha_{PP_{\delta,S,\bar{B}}}$) = 1.28; 95% CRI (0.67, 2.08)] (Fig. 2b) for skuas that were breeders the previous
512 breeding season increased with an increasing number of prey. Even though the effects were less
513 clear (95% CRI including zero), the breeding success and survival of petrels tended to be
514 positively impacted by the number of predators (Table 3). We detected a positive relationship
515 between the number of adult skuas and the hatching success of petrels that were breeders the
516 previous breeding season ($\omega_{P,\bar{B}}$), with the breeding success ($\gamma_{P,\bar{NB}}$) and with the apparent
517 survival ($\phi_{P,\bar{NB}}$) of petrels that were nonbreeders the previous breeding season. We found no
518 other interspecific relationship on the other parameters (Table 3).

519 **Intraspecific density-dependence**

520 The number of skuas had a clear effect on two demographic parameters, namely the breeding
521 success and the breeding success with two chicks for skuas that were breeders the previous
522 breeding season. We found negative density-dependence for the breeding success ($\gamma_{S,\bar{B}}$) [slope
523 mean ($\alpha_{DD_{\gamma,S,\bar{B}}}$) = -0.40; 95% CRI (-0.66, -0.15)] (Fig. 2c) and for the probability of producing
524 two chicks rather than one ($\delta_{S,\bar{B}}$) [slope mean ($\alpha_{DD_{\delta,S,\bar{B}}}$) = -0.54; 95% CRI (-1.04, -0.13)] (Fig.

525 2d). These two breeding parameters were also affected by interspecific relationships and we
526 observed that the predator-prey effects were stronger than intraspecific effects ($\left| \text{mean } \alpha_{PP_{\gamma,S,\bar{B}}} \right| =$
527 0.67 ; $\left| \text{mean } \alpha_{DD_{\gamma,S,\bar{B}}} \right| = 0.40$ respectively) for the breeding success and ($\left| \text{mean } \alpha_{PP_{\delta,S,\bar{B}}} \right| = 1.28$;
528 $\left| \text{mean } \alpha_{DD_{\delta,S,\bar{B}}} \right| = 0.54$ respectively) for the breeding success with two chicks (Table 3).

529 For petrels, we estimated a positive effect of increased number of adult petrels on the breeding
530 probability for individuals that were breeders the previous breeding season ($\beta_{P,\bar{B}}$) [slope
531 $\text{mean } (\alpha_{DD_{\beta,P,\bar{B}}}) = 0.65$; 95% CRI (0.19, 1.06)] (Fig. 2e). Even though the effects were less clear
532 (95% CRI including zero), the number of petrels tended to negatively affect the apparent survival
533 ($\phi_{P,\bar{N}\bar{B}}$) and the breeding success ($\gamma_{P,\bar{N}\bar{B}}$) of petrels that did not bred the previous breeding
534 season (Table 3).

535 **Environmental covariates**

536 We found ecologically relevant relationships between environmental covariates and
537 demographic parameters of the two species (Table 3). For petrels, we found positive
538 relationships between the two local environmental covariates (SSTa and Chla) and the breeding
539 probability for individuals that were nonbreeders the previous breeding season ($\beta_{P,\bar{N}\bar{B}}$). The
540 effect of these environmental covariates on the breeding probability was stronger for the Chla
541 covariate than for the SSTa covariate ($\left| \text{mean } \alpha_{Chla_{\beta,P,\bar{N}\bar{B}}} \right| = 0.78$; $\left| \text{mean } \alpha_{SSTa_{\beta,P,\bar{N}\bar{B}}} \right| = 0.31$
542 respectively). We estimated a positive relationship between the SAM covariate and the hatching
543 success ($\omega_{P,\bar{B}}$) and breeding success ($\gamma_{P,\bar{B}}$) of petrels that were breeders the previous breeding
544 season and with the hatching success ($\omega_{P,\bar{N}\bar{B}}$) of petrels that were nonbreeders the previous

545 breeding season. For skuas, we also found a positive relationship between the SAM and the
546 breeding probability ($\beta_{S,NB}$) of skuas that were nonbreeders the previous breeding season.
547 In addition to the results above, we also estimated the demographic parameters and the number
548 of individuals in each state for both species from 1996 to 2017 (see Appendix S4: Figs. S1– S6).

549 **Discussion**

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

561 **Effects of predator-prey relationships**

562 The number of prey is a determining factor in the breeding success of skuas according to our
563 results. Food availability is known to be positively related with breeding parameters in seabirds
564 (Cairns 1988, Piatt et al. 2007, Oro et al. 2014). As diet of skuas during the breeding period is

565 dominated by petrels (Mougeot et al. 1998, Pacoureaux et al. 2019c), a large abundance of petrels
566 provides easier conditions for skuas to feed themselves and their chicks resulting in a higher
567 breeding success.

568 Interestingly, we did not find the opposite relationship in the prey dynamics. Our model provided
569 no evidence for a negative effect of the number of skuas on the demographic parameters of the
570 petrel. As skuas prey on both adults and juveniles during the breeding season, we expected a
571 negative effect of the number of skuas on the petrel breeding parameters. This lack of effect
572 could be explained by the large abundance of petrels compared to the skuas on Mayes Island.
573 Oro et al. (2006) reported that in another seabird predator-prey system, the highest breeding
574 success of the prey occurred when the prey/predator ratio was very high. On Mayes Island, the
575 breeding population of petrels is estimated at approximately 142,000 breeding pairs (Barbraud
576 and Delord 2006), and this does not include chicks (around 71,000 each year) and nonbreeders
577 (approximately 30% of the petrels). Hence, there are about 476,000 petrels during a breeding
578 season versus about 200 skuas, resulting in a very high prey/predator ratio. Moreover, Mougeot
579 et al. (1998) showed that skuas breeding at Mayes Island preyed on about 40,000 petrels each
580 breeding season. This corresponds to about 8% of the petrel population of the island. It is
581 therefore possible that skua predation is only a minor factor in shaping petrel demographics, and
582 this effect may be too weak to be detected by our model. Inversely, although the relationships
583 estimated were less clear, our results suggest that the density of skuas tended to increase slightly
584 with the hatching success and breeding success of the prey. However, it is unlikely that the
585 presence of predators increased the reproductive success or survival of petrels. To explain these
586 relationships, we might rely on the other strong effects estimated by our model. Indeed, we found

587 that the number of petrels positively affected the breeding success of skuas and that skuas were
588 sensitive to intraspecific density-dependence. Therefore, years when prey experience a high
589 survival and breeding success correspond to years with particularly abundant food resources for
590 skuas and this until the end of the breeding season as petrels stay longer on the breeding area
591 when they successfully breed. Since skuas are potentially less affected by intraspecific density-
592 dependence than by abundance of prey, they could potentially breed in higher numbers in the
593 breeding area.

594 **Effects of intraspecific density-dependence**

595 For skuas, we found negative density-dependent effects on breeding success and probability to
596 fledge two chicks, in accordance with our predictions. Egg and chick predation by conspecifics
597 has been reported in the Great Skua (*Catharacta skua*) (Hamer et al. 1991, Ratcliffe and Furness
598 1999). Hence, a higher abundance of skuas increases the risk of predation on eggs and chicks,
599 resulting in higher breeding failure. To avoid predation by conspecifics, the skuas start defending
600 their territories from conspecifics just a few days after arrival on a breeding site until the end of
601 the season. This activity is energetically costly and may also limit the time spent searching for
602 food, potentially limiting energy investment in reproduction. The heterogeneous habitat
603 hypothesis already demonstrated in territorial birds (Dhondt et al. 1992, Krüger and Lindström
604 2001, Ferrer and Donazar 2015) could also explain the relationships we found. Indeed, when the
605 population increases, some individuals may be forced to occupy poorer quality habitats, resulting
606 in lower reproductive success. We did not find an effect of density-dependence on the breeding
607 probability of skuas. As skuas are territorial with high site fidelity, we hypothesized that in years
608 with a high abundance of skuas, the breeding probability would decrease, as all the skuas would
30

609 not succeed in acquiring a territory. It is possible that we did not observe this effect because the
610 logistic function used for density-dependence does not accurately model the territory acquisition
611 dynamics by floaters (e.g. van de Pol et al. 2010, Barraquand et al. 2014).

612 We estimated that the breeding success of skuas was affected by both predator-prey relationships
613 and intraspecific density-dependence. Predator-prey relationships had a higher contribution to
614 the variability in breeding success of skuas than the density-dependent effect. Hamer et al.
615 (1991) reported that, following a reduction of sandeel (*Ammodytes marinus*) abundance, great
616 skua increased their foraging effort reducing the adult territorial attendance. In turn, breeding
617 failure increased due to predation from adults of neighboring territories. We then may assume
618 that petrel abundance allowed a suitable territorial attendance for skuas reducing the negative
619 density-dependent effects such as chick predation by conspecifics.

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

631 studies showing that petrels might skip breeding and take sabbatical years when environmental
632 conditions are poor (Warham 1990, Chastel et al. 1995).

633 **Effects of environmental conditions**

634 We detected positive relationships between the hatching and breeding success of petrels and the
635 SAM covariate. South of the polar front, where petrels feed during the breeding season, positive
636 phases of the SAM increase the biological productivity and potential prey availability for petrels
637 (Lovenduski and Gruber 2005) which may have a positive impact on their breeding success.
638 Breeding probability of petrels tended to be impacted by two of the environmental covariates
639 tested, namely SSTa and Chla. This effect of environmental conditions on the breeding
640 probability is in accordance with previous research showing that the body condition of petrels
641 might impact their decision to attempt breeding (Warham 1990, Chastel et al. 1995). High Chla
642 increases resources availability for organisms at higher trophic levels (macrozooplankton,
643 fishes), which are consumed by petrels (Cherel et al. 2002). Consequently, high Chla may
644 increase abundance of petrel prey, with a positive effect on the breeding performances and body
645 condition of petrels. Unexpectedly, we detected a positive effect of SSTa on breeding probability
646 of petrels. This result is surprising as a previous study showed that warm SST events negatively
647 affected the breeding performances and body condition of petrels at Kerguelen Islands (Guinet et
648 al. 1998). Indeed, high SST generally reduces vertical mixing and provides poor growing
649 conditions for zooplankton communities that in turn reduce trophic resources for seabirds
650 (Barbraud et al. 2012, Sydeman et al. 2015). However, it has been showed recently that during
651 the pre-laying period petrels use water masses situated at more northerly latitudes than during the
652 winter period or the breeding period (Quillfeldt et al. 2020), where relationships between SST

32

653 and primary productivity may differ. Indeed, the covariance between SST and Chla depends on
654 location and shows particularly complex patterns in the Southern Ocean (Dunstan et al. 2018).
655 Positive effects of SSTa have already been identified in other subantarctic seabirds (Pinaud and
656 Weimerskirch 2002, Nevoux et al. 2007, Horswill et al. 2014). Furthermore, we estimated that
657 Chla, at the bottom of the trophic food chain, had a higher effect on the breeding probability than
658 SSTa which reflect oceanographic conditions. This indicated that the effect size of
659 environmental covariates increased when the covariates approached the trophic level occupied
660 by the prey of the petrels, suggesting a bottom-up mechanism. This result is consistent with
661 many studies showing that climatic conditions affect seabirds through indirect processes by
662 influencing prey availability and resulting in changes in their dynamics (Frederiksen et al. 2006,
663 Barbraud et al. 2012, Jenouvrier 2013, Lauria et al. 2013).

664 We did not detect any relationship between the breeding success of the skua and the
665 environmental covariates. This lack of effect could be explained by an absence of a direct link
666 between skuas and the environmental covariates tested, as breeding skuas remain on their
667 territory to defend it or to forage. However, we found an effect of SAM on the breeding
668 probability for skuas that were nonbreeders during the previous season. It was proposed that only
669 seabirds attaining a threshold condition decide to breed (Weimerskirch 1992). Therefore,
670 environmental conditions before the breeding period may impact the conditions of skuas and
671 consequently, their breeding decision. Nonbreeders are generally in poorer conditions than
672 breeders (Chastel et al. 1995, Cam et al. 1998) and thus more sensitive to environmental
673 conditions explaining why this effect is only detected on previous nonbreeders. Nevertheless, we
674 found a positive relationship between breeding probability and SAM whereas we expected a

675 negative relationship. Indeed, skuas mainly overwinter north of the polar front (Delord et al.
676 2018) where positive phases of SAM induce warm SST, low surface Chla concentration
677 (Lovenduski and Gruber 2005), and thus potentially poor feeding conditions. However, only
678 breeding skuas were studied in Delord et al. (2018) and nonbreeding individuals may use
679 different wintering areas where the relationships between SAM and oceanographic variables
680 differ. Several studies reviewed in Jenouvrier (2013) highlighted multifaceted effects of climatic
681 conditions on the demography of seabirds involving direct, time-lagged and non-linear effect,
682 which we did not consider here. Therefore, despite the important contribution of our approach in
683 understanding the effect of the environment in our predator-prey system, disentangling the
684 complex mechanisms between environmental covariates and their effects on the demography of
685 the two seabirds remains challenging.

686 **A bottom-up dynamic in a predator-prey system**

687 Overall, our study has highlighted the important role of bottom-up processes in the dynamics of
688 this marine predator-prey system, *i.e.* the dynamics of these two seabirds was mostly driven by
689 food availability. Petrel dynamics were more strongly affected by environmental covariates and
690 the number of petrels impacted the dynamics of skuas. The bottom-up control of demographic
691 rates in oceanic predators have been largely assumed (Jenouvrier 2013). This is because the
692 functioning of oceanic systems is controlled and structured by physical processes impacting
693 nutrient fluxes (Behrenfeld et al. 2006) and then the whole trophic food web. We found no
694 evidence of top-down processes, *i.e.* predation effects, in this system, although these two
695 mechanisms have been found to jointly affect ecosystems (Hunter and Price 1992, Sinclair et al.
696 2003) including other seabird systems (Horswill et al. 2014, 2016, Perkins et al. 2018). Effects of

697 skua predation on petrels were expected, based on their diet during the breeding season.
698 However, given the very large number of petrels present on the island compared to the number
699 of predators, the impact of predation may have been too small to be detected by our model.

700 **Conclusion**

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

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977 **Tables**

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

980 Notations are \widetilde{NB} : Nonbreeder the previous year, \widetilde{B} : Breeder the previous year, NB : Nonbreeder,
 981 FB : Failed Breeder, SBI : Successful Breeder with one fledged chick, $SB2$: Successful Breeder
 982 with two fledged chicks, FBE : Failed Breeder at the Egg stage, FBC : Failed Breeder at the Chick
 983 stage and SB : Successful Breeder.

Species	Parameter	Year random effect	State dependence
Skua	Adult apparent survival ϕ_S	✓	$\widetilde{NB}_S \widetilde{B}_S$
	Breeding probability β_S	✓	$\widetilde{NB}_S \widetilde{B}_S$
	Breeding success γ_S	✓	$\widetilde{NB}_S \widetilde{B}_S$
	Breeding success 2 chicks δ_S	✓	$\widetilde{NB}_S \widetilde{B}_S$
	Detection probability p_S	✓	$\widetilde{NB}_S \widetilde{B}_S$
	Uncertain state assignment probability u_S	✗	$NB_S FB_S SB1_S SB2_S$
Petrel	Adult apparent survival ϕ_P	✓	$\widetilde{NB}_P \widetilde{B}_P$
	Breeding probability β_P	✓	$\widetilde{NB}_P \widetilde{B}_P$
	Hatching success ω_P	✓	$\widetilde{NB}_P \widetilde{B}_P$
	Breeding success γ_P	✓	$\widetilde{NB}_P \widetilde{B}_P$
	Detection probability p_P	✓	$\widetilde{NB}_P \widetilde{B}_P$
	Uncertain state assignment probability u_P	✗	$NB_P FBE_P FBC_P SB_P$

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986 Table 2: Summary of the covariates tested on the demographic parameters of the two species –
 987 the Brown Skua (top) and the Blue Petrel (bottom) – and the time period (in months) considered
 988 for each demographic parameter. Notations are PP: Predator-Prey interactions, DD: intraspecific
 989 Density-Dependence, SAM: Southern Annual Mode, SSTa: Sea Surface Temperature anomalies,
 990 Chla: Chlorophyll a concentration.

Species	Parameter	Covariates tested	Time period
Skua	Adult apparent survival ϕ_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_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)

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993 Table 3: Regression coefficients estimates for the relationships between covariates (DD:
994 intraspecific Density-Dependence, PP: Predator-Prey interactions, SAM: Southern Annular
995 Mode, SSTa: Sea Surface Temperature anomalies, Chla: Chlorophyll a concentration) and
996 demographic parameters (ϕ : adult apparent survival, β : breeding probability, γ : breeding
997 success, δ : breeding success with two chicks, ω : hatching success) for Brown Skuas (top) and
998 Blue Petrels (bottom), \tilde{B} : breeders or \tilde{NB} : non breeders the previous years. 80% credible
999 intervals that do not include zero are in bold.

SKUA	DD				PP				SAM			
Parameters	slope	sd	10%	90%	slope	sd	10%	90%	slope	sd	10%	90%
$\phi_{S,\tilde{B}}$	-0,09	0,11	-0,22	0,06					-0,34	0,34	-0,76	0,07
$\phi_{S,\tilde{NB}}$	-0,12	0,16	-0,29	0,10					0,42	0,65	-0,36	1,16
$\beta_{S,\tilde{B}}$	0,22	0,22	-0,09	0,51					0,28	0,50	-0,35	0,92
$\beta_{S,\tilde{NB}}$	0,09	0,19	-0,18	0,32					0,81	0,52	0,18	1,45
$\gamma_{S,\tilde{B}}$	-0,40	0,13	-0,57	-0,24	0,67	0,17	0,47	0,89	-0,10	0,18	-0,33	0,13
$\gamma_{S,\tilde{NB}}$	-0,26	0,28	-0,59	0,12	0,28	0,40	-0,20	0,77	-0,24	0,60	-0,96	0,48
$\delta_{S,\tilde{B}}$	-0,54	0,23	-0,86	-0,25	1,28	0,36	0,86	1,74	-0,29	0,37	-0,75	0,15
$\delta_{S,\tilde{NB}}$	-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	DD				PP				SAM				SSTa				Chla			
Parameters	slope	sd	10%	90%	slope	sd	10%	90%	slope	sd	10%	90%	slope	sd	10%	90%	slope	sd	10%	90%
$\phi_{P,\tilde{B}}$	-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
$\phi_{P,\tilde{NB}}$	-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
$\beta_{P,\tilde{B}}$	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
$\beta_{P,\tilde{NB}}$	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
$\omega_{P,\tilde{B}}$	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
$\omega_{P,\tilde{NB}}$	-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
$\gamma_{P,\tilde{B}}$	-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
$\gamma_{P,\tilde{NB}}$	-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

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1003 **Figure Legends**

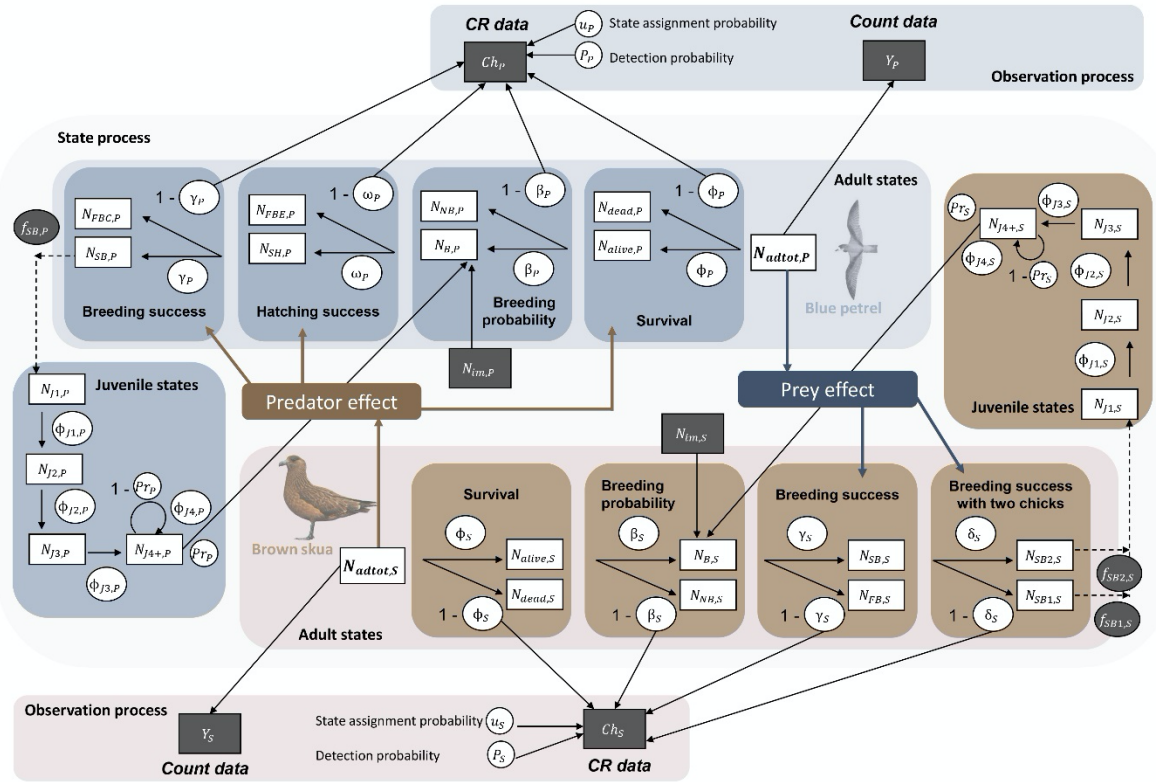
1004 Figure 1: Structure of the multispecies Integrated Population Model. Squares represent the state
1005 variables, circles represent the parameters. Data and fixed values are represented with a dark
1006 background, estimated state variables and parameters with a white background. Two types of
1007 data are used, capture histories (Ch) from capture-recapture data and count data (Y). Adult
1008 apparent survival (ϕ), breeding probability (β), hatching success (ω), breeding success (γ),
1009 breeding success with two chicks (δ), juvenile apparent survival for one to four years old and
1010 older (ϕ_{J1} to ϕ_{J4}), probability of first reproduction (Pr), state assignment probability (u) and
1011 detection probability (p) are parameters estimated in the model. Fecundity (f) is fixed. The
1012 number of adults (N_{adtot}), dead (N_{dead}), alive (N_{alive}), breeders (N_B), nonbreeders (N_{NB}),
1013 failed breeders (N_{FB}), failed breeders at the stage egg (N_{FBE}), breeders with an egg hatched
1014 (N_{SH}), failed breeders at the stage chick (N_{FBC}), successful breeders (N_{SB}), successful breeders
1015 with one chick (N_{SB1}) or with two chicks (N_{SB2}) and the number of juveniles of one year old to
1016 four years old and older (N_{J1} to N_{J4+}) are state variables estimated by the model. The number of
1017 immigrants (N_{im}) is a fixed vector. The blue part is for Blue Petrels and the brown part is for
1018 Brown Skuas. Interspecific relationships are represented with thick arrows.

1019 Figure 2: Effects of predator-prey relationships (top panels) and intraspecific density-dependence
1020 (bottom panel) on adult demographic parameters for the two seabirds, the Brown Skua and the
1021 Blue Petrel. Solid lines represent the estimated relationship between the covariates and the
1022 demographic parameters. Shaded areas are the 50% and 95% credibility intervals. Points
1023 represent demographic parameter estimates each year (21 years) plotted against covariate. Error
1024 bars are standard deviation. Prey effect on (a) the estimated breeding success probability

1025 $(\alpha_{PP_{\gamma,S,\bar{B}}})$ and (b) breeding success with two chicks for skuas that bred the previous breeding
1026 season $(\alpha_{PP_{\delta,S,\bar{B}}})$. Intraspecific density-dependence effect on (c) the breeding success $(\alpha_{DD_{\gamma,S,\bar{B}}})$
1027 and on (d) breeding success of skuas that were breeders the previous breeding season $(\alpha_{DD_{\delta,S,\bar{B}}})$
1028 and (e) on the breeding probability of petrels that bred the previous breeding season $(\alpha_{DD_{\beta,P,\bar{B}}})$.

1029 **Figures**

1030 **Figure 1**



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