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

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1

Abstract

Assessing the effects of climate and interspecific relationships on communities is challenging

because of the complex interplay between species population dynamics, their interactions, and

the need to integrate information across several biological levels (individuals – populations –

communities). Usually used to quantify species interactions, integrated population models

(IPMs) have recently been extended to communities. These models allow fitting multispecies

matrix models to data from multiple sources while simultaneously accounting for various sources

of uncertainty in each data source. 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, the Brown Skua (*Catharacta

lönnbergi*) and its main prey the Blue Petrel (*Halobaena caerulea*) both breeding on the

Kerguelen Islands in the Southern Ocean. Our results showed that climate and predator-prey

interactions drive the demography of skuas and petrels in different ways. The breeding success

of skuas appeared to be largely driven by the number of petrels and to a lesser extent by

intraspecific density-dependence. In contrast, there was no evidence of predation effects on the

demographic parameters of petrels, which were affected by oceanographic factors (chlorophyll a

and sea surface temperature anomalies). We conclude that bottom-up mechanisms are the main

drivers of this skua-petrel system. We discuss the mechanisms by which climate variability and

predator-prey relationships may affect the demographic parameters of these seabirds. Taking into

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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

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

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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

4

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 lönnbergi*) 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*

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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.

Materials and Methods

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

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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 (Pacoureau 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, Pacoureau 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.

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

8

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

9

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.

Integrated Population Model

210

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.

11

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

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

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

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

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

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

12

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

251   where ϕ_J is the juvenile apparent survival, age_i the age of the juvenile state (from N_{J1} to N_{J4}),

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_{J4+}). The individuals that

256   attempted to breed for the first time with a first breeding attempt probability Pr are in the state

257   N_{J4B} and the individuals that did not attempt to breed are in the state N_{J4NB}:

258    $$N_{J4B,X,t} \sim Bin\left(Pr_{X,t}, \phi_{J4,X} \times N_{J4+,X,t-1}\right) \qquad (7)$$

259    $$N_{J4NB,X,t} = \phi_{J4,X} \times N_{J4+,X,t-1} - N_{J4B,X,t} \qquad (8)$$

260   with ϕ_{J4} the apparent survival for the N_{J4+} state. The N_{J4+} state includes individuals that did not

261   attempt to breed (N_{J4NB}) and individuals aged between three and four years (N_{J4}):

262    $$N_{J4+,X,t} = N_{J4,X,t} + N_{J4NB,X,t} \qquad (9)$$

13

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    $N_{alive,X,t} \sim Bin\left(\phi_{X,t-1}, N_{adtot,X,t-1}\right)$ (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    $N_{Balive,X,t} \sim Bin\left(\beta_{X,t-1}, N_{alive,X,t}\right)$ (11)

272    $N_{NB,X,t} = N_{alive,X,t} - N_{Balive,X,t}$ (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    $N_{B,X,t} = N_{Balive,X,t} + N_{J4B,X,t} + N_{im,X,t}$ (13)

14

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    $$N_{SB,S,t} \sim Bin\left(\gamma_{S,t-1}, N_{B,S,t}\right) \tag{14}$$

285    $$N_{FB,S,t} = N_{B,S,t} - N_{SB,S,t} \tag{15}$$

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    $$N_{SB2,S,t} \sim Bin\left(\delta_{S,t-1}, N_{SB,S,t}\right) \tag{16}$$

289    $$N_{SB1,S,t} = N_{SB,S,t} - N_{SB2,S,t} \tag{17}$$

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    $$N_{SH,P,t} \sim Bin\left(\omega_{P,t-1}, N_{B,P,t}\right) \tag{18}$$

298    $$N_{FBE,P,t} = N_{B,P,t} - N_{SH,P,t} \tag{19}$$

15

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 $$N_{SB,P,t} \sim Bin\,(\gamma_{P,t-1}, N_{SH,P,t}) \tag{20}$$

302 $$N_{FBC,P,t} = N_{SH,P,t} - N_{SB,P,t} \tag{21}$$

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 $$N_{adtot,S,t} = N_{NB,S,t} + N_{FB,S,t} + N_{SB1,S,t} + N_{SB2,S,t} \tag{22}$$

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 $$N_{adtot,P,t} = N_{NB,P,t} + N_{FBE,P,t} + N_{FBC,P,t} + N_{SB,P,t} \tag{23}$$

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):

16

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

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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 ($L_{cr,S}$):

348    $L_{ipm,S}(Y_S, Ch_S | \phi_{J1,S}, \phi_{J2,S}, \phi_{J3,S}, \phi_{J4,S}, Pr_S, \phi_S, \beta_S, \gamma_S, \delta_S, N_{adtot,S}, p_S, u_S) =$

349    $L_{co,S}(Y_S | \phi_{J1,S}, \phi_{J2,S}, \phi_{J3,S}, \phi_{J4,S}, Pr_S, \phi_S, \beta_S, \gamma_S, \delta_S, N_{adtot,S}) \times$

350    $L_{cr,S}(Ch_S | \phi_S, \beta_S, \gamma_S, \delta_S, p_S, u_S)$ (25)

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

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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.

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, Pacoureau 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).

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

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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

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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
      21

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

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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_SmithOIv2 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 ($\omega_{P,\tilde{B}}$) using a logit link:

465    $logit(\omega_{P,\tilde{B},t-1}) = \mu_{\omega,P,\tilde{B}} + \alpha_{SAM,\omega,P,\tilde{B}} \times SAM_{\omega,P,t} + \alpha_{SSTa,\omega,P,\tilde{B}} \times SSTa_{\omega,P,t} +$

466    $\alpha_{Chla,\omega,P,\tilde{B}} \times Chla_{\omega,P,t} + \alpha_{DD,\omega,P,\tilde{B}} \times N_{adtot,P,t} + \alpha_{PP,\omega,P,\tilde{B}} \times N_{adtot,S,t} + \varepsilon_{\omega,P,\tilde{B},t}$

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

468 with $\mu_{\omega,P,\tilde{B}}$ the intercept, $\alpha_{SAM_{\omega,P,\tilde{B}}}$ the slope for the climatic covariate $SAM_{\omega,P}$, $\alpha_{SSTa,\omega,P,\tilde{B}}$ the

469 slope for the climatic covariate $SSTa_{\omega,P}$, $\alpha_{Chla,\omega,P,\tilde{B}}$ the slope for the climatic covariate $Chla_{\omega,P}$,

470 $\alpha_{DD,\omega,P,\tilde{B}}$ the slope indicating the strength of the intraspecific density-dependence with

471 $N_{adtot,P}$ the number of adult petrels, $\alpha_{PP,\omega,P,\tilde{B}}$ the slope indicating the strength of the predator-

472 prey relationship with $N_{adtot,S}$ the number of adult skuas, $\varepsilon_{\omega,P,\tilde{B}}$ is a yearly random effect and

473 $\sigma^2_{\varepsilon,\omega,P,\tilde{B}}$ 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.

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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).

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 × 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.

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Results

Predator-prey relationships

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

Intraspecific density-dependence

The number of skuas had a clear 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 ($\gamma_{S,\tilde{B}}$) [slope mean ($\alpha_{DD_{\gamma,S,\tilde{B}}}$) = -0.40; 95% CRI (-0.66, -0.15)] (Fig. 2c) and for the probability of producing two chicks rather than one ($\delta_{S,\tilde{B}}$) [slope mean ($\alpha_{DD_{\delta,S,\tilde{B}}}$) = -0.54; 95% CRI (-1.04, -0.13)] (Fig.

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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 ($\left|\text{mean } \alpha_{PP_{\gamma,S,\tilde{B}}}\right| =$

527   0.67; $\left|\text{mean } \alpha_{DD_{\gamma,S,\tilde{B}}}\right| = 0.40$ respectively) for the breeding success and ($\left|\text{mean } \alpha_{PP_{\delta,S,\tilde{B}}}\right| = 1.28$;

528    $\left|\text{mean } \alpha_{DD_{\delta,S,\tilde{B}}}\right| = 0.54$ 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 ($\beta_{P,\tilde{B}}$) [slope

531   mean ($\alpha_{DD_{\beta,P,\tilde{B}}}$) = 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   ($\phi_{P,\widetilde{NB}}$) and the breeding success ($\gamma_{P,\widetilde{NB}}$) 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 ($\beta_{P,\widetilde{NB}}$). The

540   effect of these environmental covariates on the breeding probability was stronger for the Chla

541   covariate than for the SSTa covariate ($\left|\text{mean } \alpha_{Chla_{\beta,P,\widetilde{NB}}}\right| = 0.78$; $\left|\text{mean } \alpha_{SSTa_{\beta,P,\widetilde{NB}}}\right| = 0.31$

542   respectively). We estimated a positive relationship between the SAM covariate and the hatching

543   success ($\omega_{P,\tilde{B}}$) and breeding success ($\gamma_{P,\tilde{B}}$) of petrels that were breeders the previous breeding

544   season and with the hatching success ($\omega_{P,\widetilde{NB}}$) of petrels that were nonbreeders the previous

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545 breeding season. For skuas, we also found a positive relationship between the SAM and the

546 breeding probability ($\beta_{S,\widetilde{NB}}$) 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).

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.

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

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565   dominated by petrels (Mougeot et al. 1998, Pacoureau 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

29

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.

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

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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

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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

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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

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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.

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

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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.

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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Tables

Table 1: Summary of the demographic parameters and their specificities (year random effect or state dependence) for the two species: the Brown Skua (top) and the Blue Petrel (bottom). 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_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 $\widetilde{NB}$: 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
$\phi_{S,\widetilde{NB}}$	-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
$\beta_{S,\widetilde{NB}}$	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
$\gamma_{S,\widetilde{NB}}$	-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
$\delta_{S,N\tilde{B}}$	-0,41	0,45	-0,96	0,17	0,69	0,96	-0,48	1,71	-0,53	1,65	-2,30	1,33

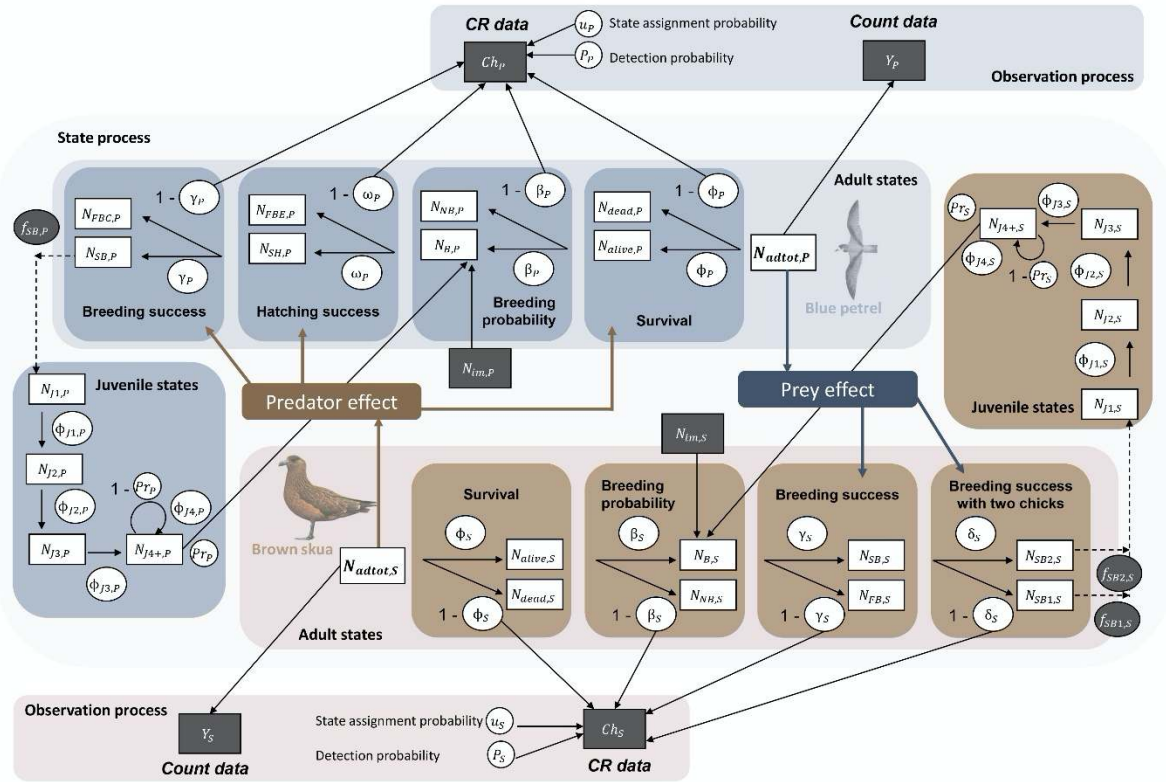| PETREL	DD				PP				SAM				SSTa				Chla			
Parameters	slope	sd	10%	90%	slope	sd	10%	90%	slope	sd	10%	90%	slope	sd	10%	90%	slope	sd	10%	90%
$\phi_{P,\tilde{B}}$	-0,12	0,31	-0,51	0,26	0,27	0,25	-0,05	0,58	-0,05	0,39	-0,54	0,42	-0,16	0,23	-0,45	0,12	-0,57	0,46	-1,14	0,01
$\phi_{P,\widetilde{NB}}$	**-0,99**	**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
$\beta_{P,\widetilde{NB}}$	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
$\omega_{P,\widetilde{NB}}$	-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
$\gamma_{P,\widetilde{NB}}$	**-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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Figure Legends

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

Figure 2: Effects of predator-prey relationships (top panels) and intraspecific density-dependence (bottom panel) on adult demographic parameters for the two seabirds, the Brown Skua and the Blue Petrel. 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 against covariate. Error bars are standard deviation. Prey effect on (a) the estimated breeding success probability

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1025 $(\alpha_{PP_{\gamma,S,\widetilde{B}}})$ and (b) breeding success with two chicks for skuas that bred the previous breeding

1026   season $(\alpha_{PP_{\delta,S,\widetilde{B}}})$. Intraspecific density-dependence effect on (c) the breeding success $(\alpha_{DD_{\gamma,S,\widetilde{B}}})$

1027   and on (d) breeding success of skuas that were breeders the previous breeding season $\left(\alpha_{DD_{\delta,S,\widetilde{B}}}\right)$

1028   and (e) on the breeding probability of petrels that bred the previous breeding season $(\alpha_{DD_{\beta,P,\widetilde{B}}})$.

Figures

Figure 1

Figure 2

Predator−prey relationships

Intraspecific density−dependance