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Seabird- induced natural mortality of forage fish varies with fish abundance: Evidence from five ecosystems

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Abstract :

Forage fish populations often undergo large and rapid fluctuations in abundance. However, most of their
predators are buffered against such fluctuations owing to their slower pace of life, which allows them to
maintain more stable populations, at least during short periods of food scarcity. In this study, we
investigated top-down processes exerted by seabirds on forage fish stocks in five contrasted marine
ecosystems, compiling numerous data sets on seabird counts, diets, energetic needs and prey energy
content and abundance. Off Norway, South Africa, Peru, Sweden and Scotland, we found that predation
pressure—estimated as the proportion of a fish stock consumed by seabirds—was generally low
(median = 1%), but increased sharply at low levels of prey abundance. When prey biomass decreased
below 15–18% of its maximum recorded value, predation by seabirds became a source of important
additional pressure on prey stocks (~20% of prey biomass is consumed by seabirds). An earlier empirical
study advocated for keeping forage stocks from falling below a threshold of 33% of long-term maximum
prey biomass in order to safeguard seabird breeding success, but here we further suggest that a threshold
of 18% should be considered as a limit not to be exceeded for the sake of the forage fish themselves, and
below which extra cautious management of fisheries may be required. Nevertheless, despite

exceptionally high rates of predation on some occasions, predation pressure was not correlated with prey dynamics, suggesting an absence of prey entrapment due to seabirds alone in these five ecosystems.

Keywords : Benguela, Baltic Sea, Humboldt, predator–prey, prey consumption, Shetland

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Introduction

Natural mortality (M) is an understudied aspect of fish population biology and fisheries science. In most fisheries' stock assessments, natural mortality is modeled as constant or as a function of size to account both for predation pressure and age (Gislason, Daan, Rice, & Pope, 2010). However, a growing number of studies suggests that this assumption is incorrect, and that mortality could be density-dependent, or modulated by the environment (Dutil & Lambert, 2000; Fromentin et al., 2001; Pershing et al., 2015). Because fisheries management often relies on stock assessments which compare fishing mortality (F) to natural mortality, understanding fluctuations in natural mortality is of primary importance. For example, a recent study found up to a 40% difference between estimates of spawning stock biomass (SSB), F and recruitment (R) in Atlantic cod (*Gadus morhua,* Gadidae) stock assessments, assuming a constant M versus a variable M linked to body condition (Casini, Eero, Carlshamre, & Lövgren, 2016). Here, we are interested in examining to what degree natural mortality rates of forage fish may be influenced by seabirds, which are widely distributed and abundant forage fish predators on all continental shelf ecosystems around the world (Cury et al., 2011). Additionally, On top of potential improvement of stock assessment, clarifying predator-prey functional relationships between forage fish and seabirds will also inform ecosystem-based management research, e.g. by better understanding how seabird diet relies on forage fish (Dickey-Collas et al., 2014; Peck et al., 2014), and the degree to which mass mortality of seabirds from starvation is exacerbated by low forage abundance and competition with large predatory groundfish for shared prey (Piatt et al., 2020).

Forage fish are consumed by a variety of upper trophic level species in marine ecosystems, including seabirds, marine mammals, and larger piscivorous fish. Typically, and on regional scales, seabirds consume considerably less biomass than marine mammals or especially piscivorous fish (Gaichas et al., 2009) but seabirds can have significant impacts locally (Furness, 1978). In contrast to ectothermic groundfish that need to acquire only about 0.2% to 1.2% of their body mass in food daily (Holsman & Aydin, 2015), endothermic seabirds have high metabolic rates and need to consume

96 upwards of 30-80% of their mass in food daily (Ellis & Gabrielsen, 2002; Furness, 1990). Combined

97 with the fact that seabirds gather to breed in very large colonies in the thousands to millions (Guinet,

98 Jouventin, & Malacamp, 1995), this results in a concentration of high energetic demands in a limited

99 area. As central-place foragers, breeding birds return to breeding sites on land (or occasionally ice) to

100 attend and provision offspring, which concentrates foraging areas closer to breeding locations. As a

101 result, some studies have shown localized prey depletion in proximity to island-based colonies, and

102 this may result in intraspecific competition among birds (Ainley et al., 2003; Birt, Birt, Goulet, Cairns,

103 & Montevecchi, 1987; Lewis, Sherratt, Hamer, & Wanless, 2001; but see Nur & Sydeman, 1999).

104 Additionally, most of the forage fish of importance to seabirds are known to exhibit wide fluctuations

105 in abundance in response to climate (e.g. Lluch-Belda et al., 1992) and are often subjected to high

106 fishing mortality (Hilborn et al., 2017; Schwartzlose et al., 1999). Fish abundance often changes much

107 faster than the abundance of predators, because many forage fish predators, including seabirds,

108 have slower life-history characteristics such as high annual survival and delayed sexual maturity,

109 which buffer their breeding populations from fluctuations in food supply (e.g. Hunt, Furness, & Kerr

110 Building, 1996 and 'canalization hypothesis' Gaillard & Yoccoz, 2003). Thus the relative predation

111 pressure exerted by seabirds should increase with declines in forage fish stocks, except under

112 extreme conditions where adult seabirds are unable to obtain sufficient food for their own

113 maintenance and survival (Cairns, 1988; Crawford et al., 2011; Erikstad, Fauchald, Tveraa, & Steen,

114 1998). Therefore, seabird-induced natural mortality of forage fish could vary strongly with time.

115 If the proportion of a fish stock consumed by predators increases as biomass decreases, the

116 stock in question may become entrapped, whereby populations cannot overcome predation

117 pressures or easily return to previous levels of abundance (Smout, Rindorf, Hammond, Harwood, &

118 Matthiopoulos, 2014). Bakun (2006) theoretically explored the functional responses of predators to

119 biomass variation in small pelagic fish, and suggested that predation pressure should be nil when

120 stocks are collapsed at very low levels of biomass (i.e., "refuge abundance"), but increase

121 substantially when fish biomass reaches a level sufficient for predators to be interested in a

122   population as prey. At low, but not collapsed biomass, Bakun predicted that 'carnage predation' may

123   hold the population at a relatively low biomass, and coined the term "predator pit" for this

124   mechanism. Predator pits may be maintained until the forage fish population reaches a level

125   sufficient to satiate predators and grow larger at the same time. The addition of human fishing

126   pressure on small pelagic fish populations has been shown to increase the probability of stock

127   collapse but not the duration of the collapse (Essington et al., 2015). Although fishing pressure after

128   a collapse usually drops, or is even halted due to fisheries management and/or profitability, with no

129   change, maintaining fishing effort at lower biomass would likely exacerbate the duration small

130   pelagics are held in a predator pit. To date fisheries impacts and empirically estimated predation

131   pressure have yet to be jointly addressed.

132   In this paper, we test the hypothesis of predator-pit dynamics for forage fish by examining

133   (1) whether the proportion of forage fish stocks consumed by seabirds increases in response to drops

134   in prey biomass, and (2) whether such increases in seabird-induced forage fish mortality affect forage

135   fish population dynamics. To test this hypothesis, we model non-linear relationships between seabird

136   consumption and fish biomass across five ecosystems, and determine the biomass thresholds at

137   which seabirds might begin to exert top-down control on their prey populations. By determining such

138   thresholds in five different ecosystems, this work also tests the generality of top-down control of

139   seabirds on forage fish and identifies local differences, as suggested in (Peck et al., 2014).

140

141   **Methods**

142   To estimate seabird predation pressure on forage fish, we use long-term data collected in five

143   contrasted ecosystems on: 1) Atlantic puffin (*Fratercula arctica*, Alcidae) and Atlantic herring (*Clupea*

144   *harengus*, Clupeidae) at Røst off northwest Norway, 2) Cape gannet (*Morus capensis*, Sulidae) and

145   sardine (*Sardinops sagax,* Clupeidae) and anchovy (*Engraulis encrasicolus*, Engraulidae) off western

146   South Africa in the Southern Benguela ecosystem, 3) common murre (*Uria aalge*, Alcidae) and

147   European sprat (*Sprattus sprattus,* Clupeidae) in the Baltic Sea, 4) twelve seabird species and lesser

148   sandeel (*Ammodytes marinus*, Ammodytidae) off Shetland and 5) Peruvian booby (*Sula variegata*,

149   Sulidae), Peruvian pelican (*Pelecanus thagus*, Pelecanidae*)* and Guanay cormorant (*Phalacrocorax*

150   *bougainvillii*, Phalacrocoracidae) and anchovy (*Engraulis ringens*, Engraulidae) in the Northern

151   Humboldt ecosystem (Figure 1). While the methodology used (see below) requires a large number of

152   data and constrains the number of ecosystems on which we could test the hypothesis, these five

153   ecosystems enabled investigation of predation pressure in contrasted environments, ranging from

154   productive upwelling regions (Benguela, Humboldt) to the semi-closed Baltic Sea.

155

156   ***Estimates of seabird consumption and proportion of prey biomass consumed***

157   To estimate seabird predation pressure, we combined several processes (estimation of bird numbers

158   and population structure, bird energy requirements, bird diet and prey energetic values and

159   abundance) based on a large number of datasets (see similar approaches in Queiros, Fromentin,

160   Astruc, Bauer, & Saraux, 2018; Van Beveren et al., 2017). In particular, both the quantity consumed

161   by seabirds and the prey stock size were evaluated. A schematic diagram of the general method used

162   in this study is represented in Figure 2.

163   The main challenge of this study was to estimate the total quantity of a given prey that is extracted

164   by seabirds C_t, meaning that all birds extracting prey should be included, i.e. both adults and chicks,

165   as well as breeders and non-breeders that are present in the area and consume this prey. This was

166   estimated using the formula below:

$$C_t = \frac{P_t}{AE * PreyNRJ} * \begin{pmatrix} DEE_B * N_{B,t} * Nbdays_{BS} \\ +DEE_{NB} * N_{B,t} * Nbdays_{NBS} \\ +DEE_{NB} * N_{NB,t} * Nbdays_{col} \end{pmatrix} * \frac{1}{1000} + C_{chick,t}$$

167   Where

168   1) C_t is the consumption of the given prey (in tonnes). Note that the 1/1000 in the equation is

169   here only to convert from kg to tonnes.

170   2) P_t (unitless) corresponds to the proportion of the given prey in terms of energy in the diet in

171   a given year t. Note that in each ecosystem, we assumed P_t to be independent of bird age

172   class (chick and adult diet assumed to be the same) and breeding status (see Supplementary

173   material for more details and justifications).

174   3) AE (unitless) is the assimilation efficiency.

175   4) $PreyNRJ$ (in kJ.g^{-1}) is the calorific content of the prey

176   5) DEE (in kJ.d^{-1}) is the daily energy expenditure of the birds. As breeding incurs an additional

177   cost, two distinct DEEs were considered: one for breeding birds DEE_B and one for non-

178   breeders or adults in the non-breeding season DEE_{NB}.

179   6) N_t (in thousands of birds) represents the number of birds present in the area in year t, either

180   breeding $N_{B,t}$, or non-breeding $N_{NB,t}$.

181   7) $Nbdays$ (in d) is the number of days during which the prey is consumed by the seabird

182   species in the area. Three periods were distinguished: $Nbdays_{BS}$ corresponds to the number

183   of days in the breeding season, $Nbdays_{NBS}$ the duration of the non-breeding season in

184   which breeding birds are present in the colony and finally $Nbdays_{col}$ the duration in which

185   non-breeding birds (immature or birds skipping reproduction) are present in the area. Note

186   that for some ecosystems, birds are migratory and $Nbdays_{NBS}$ is zero.

187   8) C_{chick} (in tonnes) corresponds to the consumption in tonnes made by chicks. This was either

188   calculated through energy requirements and DEE (in the Benguela, Humboldt and Shetland),

189   i.e. $C_{chick} = \frac{P_t}{AE*PreyNRJ} * \left(DEE_{chick} * N_{chick} * Nbdays_{chickrearing}\right)$ or directly from meal

190   size given to the chicks (in Norwegian and Baltic Seas): $C_{chick} = P_{mass,t} * N_{chick} *$

191        $Nbdays_{chickrearing} * Mealsize$

192   Once the consumption of a prey is estimated, it needs to be compared to the prey stock biomass to

193   estimate the predation pressure. Fish biomass was estimated either through stock assessment

194   models, or from direct acoustic biomass estimates, depending on the ecosystem (see Table 1 Only in

195   the North Sea (case study Shetland Islands), did natural mortality (M) explicitly include bird

196   consumption. Yet, while predator consumption included that of seabirds and marine mammals, the

197   most important predators of sandeels by far are fish - especially mackerel, herring, cod, haddock,

198   whiting, and gurnard, so that there should be little effect of seabird consumption on M (ICES-HAWG,

199   2020; ICES-WKSand, 2016). Further, stock biomass should represent the entire fish biomass present

200   before seabird consumption occurred. Depending on the timing of stock biomass assessment and

201   seabird consumption phenology, stock biomass had to be corrected. In the Humboldt, the production

202   model estimates the biomass available each month, so that no correction was needed. Similarly, no

203   corrections were applied in the Baltic, where stock assessment refers to the start of spawning (i.e.

204   April), just before seabirds start consuming sprats and in the Norwegian Sea, where stock

205   assessments refer to the first of January, i.e. before the predation events. By contrast, acoustic

206   biomass estimates in the Benguela derive from November acoustic surveys and a stock assessment

207   model in the Shetland estimates biomass on the 1st of July. In both cases, most of seabird

208   consumption occurred beforehand, so that stock biomass was corrected by adding seabird

209   consumption. Finally, the fish biomasses presented here represented annual estimates of the stock,

210   and not fish availability within foraging range of the birds around the colonies, so that we are

211   estimating the predation pressure on the stock and not local prey depletion. However, it has to be

212   noted that in some large ecosystems, regional scales were used (e.g. we considered the southern

213   sub-system of the Benguela, located off South-Africa and not the entire Benguela ecosystem). Spatial

214   scales can be found in Table 1 for each ecosystem.

215   Although the approach was the same everywhere, differences appeared in the estimation of these

216   parameters because of species and ecosystem specificity. For instance, gannets in the Southern

217   Benguela are resident seabirds and consumption outside of the breeding period had to be

218 considered in order to estimate the entire predation pressure they exerted on sardine and anchovy

219 stocks, while migrating Atlantic puffins are present in the eastern Norwegian Sea only for a few

220 months in order to breed.

221 As some seabird data were not always available in each ecosystem, some assumptions had to be

222 made (see summary in Table 1). While these were done to best fit our knowledge of the ecosystem

223 or the species at play, they introduce uncertainty in our estimates of consumption and predation

224 pressure. Nevertheless, we applied the same methodology through time within each ecosystem and

225 among ecosystems. This allowed us to investigate temporal trends and compare among ecosystems,

226 and to identify the magnitude of top-down effects. The main assumptions and parameters are

227 summarized for each ecosystem in Table 1 and details about the specificities as well as monitoring

228 methods are detailed in supplementary material. Note that in the case of the Atlantic puffin in the

229 Norwegian Sea, two different scenarios of consumption were run in the absence of diet data outside

230 the chick-rearing period. The first assumed that puffins consumed herring during the entire time they

231 are present at the colony while the minimum consumption scenario assumed herring consumption

232 only during chick-rearing (see Supplementary material).

233 Predation pressure was then estimated as the percentage of the stock consumed by seabirds,

234 calculated as: $Pred_t = 100 * \frac{C_t}{B_t}$.

Relationships between consumption and biomass

236 In order to examine functional responses of seabird diet and aggregated prey consumption C_t to prey

237 biomass, for each relationship we tested a selection of six _a priori_ parametric models (null model

238 assuming no link of seabird diet or consumption with prey biomass $y = a$; linear model assuming a

239 constant increase of seabird diet or consumption with fish biomass $y = a * B + b$; second-order

240 polynomial model assuming an optimum fish biomass for seabirds $y = a * B + b * B + c$; as well as

241 exponential, logarithmic and power models which all assume non-linearities and some sort of

242 thresholds above or below which seabirds react differently to prey $y = a * e^{-b*B}$, $y = a * \ln(B) +$

243 b, $y = a * B^b$). When looking at the relationship between seabird aggregated consumption and

244   stock biomass, we also tested two additional models: type II and III functional responses: $C_t = \frac{a*B}{1+b*B}$

245   and $C_t = \frac{a*B}{1+b*B^2}$). Because data in the Shetland were only collected in 3 years, they are only

246   presented as a qualitative indication and no model was performed for this ecosystem. Also, in the

247   Humboldt, no model was performed for the diet data in the absence of annual estimated diet (diet

248   was estimated by period in this ecosystem). All models were fitted using non-linear least square

249   adjustment and the best fit was selected based on the lowest AICc values to avoid over-

250   parameterization (Piatt et al., 2007). When change in AICc (ΔAICc) was less than 2 between the two

251   best models, the more parsimonious model was chosen. All models within a ΔAICc of 2 are presented

252   along with the null model in Table 2. Once the numerical relationships between stock biomass and

253   the percentage of the stock consumed by seabirds were established, we used a change-point analysis

254   to identify thresholds within non-linear relationships (Andersen, Carstensen, Hernández-García, &

255   Duarte, 2009; Cury et al., 2011). The threshold in biomass was then expressed relatively to the

256   maximum biomass observed in the time-series (*i.e.* % threshold = 100 * $\frac{threshold}{Max\ B}$).

257

258   ***Effect of the predation pressure on-prey dynamics***

259   To investigate whether the predation pressure exerted by seabirds might impact prey dynamics, we

260   examined the correlations between prey biomass and the number of avian predators or the

261   percentage of the stock that was consumed the previous year. Because stock biomass time series are

262   often autocorrelated, residuals were checked for autocorrelation. While autocorrelation was never

263   significant in the Baltic Sea, residuals from the models in the Humboldt and Benguela all displayed

264   positive autocorrelation of order 1 (detected through the pacf function in R). To account for that, a

265   one-year lagged time series of the stock biomass was added as an explanatory variable in the 6

266   models ($B_t \sim N_{t-1} + B_{t-1}$ and $B_t \sim Pred_{t-1} + B_{t-1}$ for sardine and anchovy in the Benguela and for

267   anchovy in the Humboldt). Finally, we also studied the relationship between the change in prey

268   biomass (i.e. $\Delta B = B_t - B_{t-1}$) and the percentage of the stock consumed at t-1 ($\Delta B \sim Pred_{t-1}$). These

269 relationships were not investigated in Shetland due to too few data points and in the Norwegian Sea,

270 where puffins consume age 0 herring that first recruit to the spawning stock at age 3. The

271 relationship between this herring's spawning stock biomass and its recruitment three years later is

272 weak (Sætre, Toresen, & Anker-Nilssen, 2002).

273

274 **Results**

275 *Diet*

276 The percentage contributions of various prey species to the seabird predators included in our study

277 are shown in Figure 3. For Atlantic puffins from 1982–2006, the contribution by mass of age 0 herring

278 to the diet (46 ± 22% [13–89%]) was not significantly related to the biomass of age 0 herring (Figure

279 4a, Table 2). For common murres, the mean contribution by mass of sprat to the diet from 2002–

280 2012 was very high and stable across time (98 ± 2%; range 93–100%), regardless of the biomass of

281 sprat (Figure 4d). In the Humboldt ecosystem, the contribution of anchovy in the diet was usually

282 quite high (81 ± 8%) but dropped significantly in El-Niño years (55% for cormorants and 58% for

283 boobies and pelicans; Figure 3b). For Cape gannets, the mean contribution by mass of sardine to the

284 diet from 1978–2011 was 30 ± 19% (range 2–61%) and that of anchovy 28 ± 16% (range 3–62%;

285 Figure 3e). The average combined contribution of these two prey species to the diet was 58 ± 14%

286 (range 16–77%; Figure 3e). In both cases, the percentage of fish in gannet diet increased with fish

287 stock biomass, although the relationships differed (Table 2; Figure 4e & 4f). Finally, at Shetland the

288 average contribution by mass of sandeel to the diet of 12 seabirds decreased from 88 ± 4 % in 1977

289 and 83 ± 5 % in 1986 to only 45 ± 10 % in 2000 (Figure 3c).

290

291 *Consumption and proportion of prey stock consumed*

292 The consumption of age 0 herring by Atlantic puffins at Røst (regardless of the scenario used) and the

293 consumption of anchovy by boobies, cormorants and pelicans in the Humboldt ecosystem were not

294 significantly related to the prey stock biomass (Figure 5a & 5b, Table 2). However, consumption of

295   sardine and anchovy by Cape gannets in the southern Benguela ecosystem was significantly

296   positively related to the biomasses of these prey species by a type II functional response (Figure 5e &

297   5f). Similarly, the consumption of sandeels by 12 seabird species at Shetland seemed to increase with

298   the biomass of sandeels (Figure 5c). Finally, the consumption of sprats by common murres in the

299   Baltic Sea decreased with sprat biomass following a power model (Figure 5d).

300   The predation pressure, as estimated by the percentage of the fish biomass consumed by seabirds,

301   was generally low (median =1% across all years and ecosystems; Figure 6). While this was true in

302   most cases (≤ 20% in 95% of the cases), the predation pressure increased when fish abundance was

303   low (Figure 6).

304   Further, in four ecosystems (it was not tested for Shetland due to few data points), all relationships

305   were best fitted by power models. While the proportion of the stock consumed remained extremely

306   low in the Baltic Sea (0.5-1.2%; Figure 6d), it increased sharply in other ecosystems once fish biomass

307   decreased below a certain threshold. This threshold was lower than the median biomass observed in

308   the series (Figure 6) and varied between 15 and 18% of the maximum observed prey biomass (15%

309   for herring in the Norwegian Sea regardless of the scenario Figure 6a, 16% for both anchovy and

310   sardine in the Benguela Figure 6e & 6f and 18% for anchovy in the Humboldt Figure 6b).

311

312   ***Effect of the predation pressure on prey dynamics***

313   Autocorrelation in the residuals was positive and of order 1 in all models explaining prey stock

314   biomass, except for the Baltic, where no autocorrelation was detected. Stock biomass at t-1 was thus

315   added as an explanatory variable in the models (except for the Baltic) and had a significant positive

316   effect on prey biomass at t in all relevant models (all $P < 0.009$). In the Humboldt, while prey biomass

317   was positively related to the number of seabirds present at t-1, and negatively to the percentage of

318   the stock consumed by seabirds at t-1, both relationships disappeared after accounting for

319   autocorrelation (Fig. 7 a & d). In the Benguela, the sardine stock biomass was positively related to

320   the number of birds present the previous year (regardless of the autocorrelation, Fig 7c), but not to

321 the percentage of the stock consumed the year before (Fig. 7f). The anchovy stock biomass in the

322 Benguela was not related to either the number of gannets or the proportion of prey consumed by

323 gannets in the previous year (Fig 7c & f). Sprat biomass was negatively related to both the number of

324 murres the previous year and the proportion of stock that they consumed (Fig 7b & e).

325 Finally, the change in fish biomass from one year to another was not related to the percentage of the

326 stock consumed the previous year in any of the ecosystems (Figure 7g & 7h &7i).

327

328 **Discussion**

329 Many studies advocate that seabirds are good bioindicators of marine ecosystems (e.g. Cairns, 1988;

330 Piatt et al., 2007), although an implied assumption and frequent observation is that these

331 ecosystems are regulated by bottom-up processes (Aebischer, Coulson, & Colebrook, 1990;

332 Frederiksen, Edwards, Richardson, Halliday, & Wanless, 2006; Speckman, Piatt, Minte-Vera, &

333 Parrish, 2005). However, aquatic ecosystems are complex and may also be regulated by numerous

334 biological interactions, including predation and competition. For instance, whole-lake experiments

335 showed that trophic cascades could inhibit the response of primary producers to nutrient inputs

336 (Carpenter et al., 2001). The existence of such top-down mechanisms or trophic cascades, which had

337 previously been reported only from terrestrial ecosystems or lakes, has now been demonstrated in

338 marine ecosystems (Ainley, Ballard, & Dugger, 2006), especially after overfishing (Baum & Worm,

339 2009; Casini et al., 2009; Frank, Petrie, Choi, & Leggett, 2005; Österblom, Casini, Olsson, & Bignert,

340 2006). Further studies have proposed that marine ecosystems might be regulated by alternating

341 bottom-up and top-down processes (Cury et al., 2008; Litzow & Ciannelli, 2007), or a "wasp-waist"

342 interaction of the two (Fauchald, Skov, Skern-Mauritzen, Johns, & Tveraa, 2011), and that relative

343 strength of bottom-up and top-down control may vary spatially (Frederiksen, Furness, & Wanless,

344 2007). For example, marine heatwaves can markedly increase metabolic rates and food demands of

345 ectothermic groundfish and trigger temporary top-down control of prey populations and increased

346 competition with seabirds for shared prey (Barbeaux, Holsman, & Zador, 2020; Piatt et al., 2020).

347   Here, we examined one component of top-down processes by estimating the predation

348   pressure exerted by seabirds on forage fish in five different ecosystems. Because this requires a large

349   quantity of data on both seabirds and forage fish, it was necessary to sometimes make assumptions

350   that could have a marked effect on model outcomes. In the Norwegian Sea for instance, due to the

351   absence of diet data outside of the chick-rearing period, we had to consider two extreme scenarios:

352   i.e., either puffins do not eat herring outside the chick-rearing season, or they consume herring

353   during the entire breeding season. The latter scenario (i.e. maximum consumption) yielded some

354   unrealistically high values (>100% of prey stock). However, such outcomes could also result from the

355   uncertainty associated with calculating prey biomass in this ecosystem. Indeed, puffins eat age-0

356   herring, the biomass of which is not directly assessed (see the ESM for more details). Still, we believe

357   the relationships we found likely reflect qualitatively the true relationship (in terms of shape) as we

358   applied our methods consistently between years and between ecosystems but actual estimates

359   under that scenario were less reliable.

360   With respect to seabird diets, we found that different species displayed marked differences

361   in response to fluctuations in prey abundance. Seabird species have different locomotion and

362   foraging strategies which limit the distance that they can forage from colonies, or the depth to which

363   they can feed (e.g. Shealer, 2002). Large seabirds are, for instance, often less vulnerable to prey

364   depletion due to greater travelling capacities and greater energetic efficiencies (Ellis & Gabrielsen,

365   2002; Furness & Tasker, 2000), which might explain the absence of seabird response to prey biomass

366   decrease in the Humboldt system in typical (i.e. non El-Niño) conditions. The non-linear relationships

367   between abundance of sardine and anchovy and the contribution of these species to the diet of Cape

368   gannets off western South Africa suggest that gannets are able to maintain their intake of these

369   species over a wide range of biomass variability. Cape gannets have indeed been shown to be flexible

370   in their foraging effort and duration to track sardines and anchovies, their preferred prey even when

371   abundance decreases or spatial distribution shifts (Green et al., 2015). However, below a certain

372   threshold of prey biomass, gannets were not able to compensate anymore and had to shift their diet

towards other prey. Recent research off the south coast of South Africa has shown that in the post-guard stage (>50 days) of chick-rearing, foraging range is extended and gannet diet may differ from that in the guard stage as a consequence of changes either in prey abundance and distribution, or in the energetic requirements of growing offspring (Botha & Pistorius, 2018). A similar relationship was evident for the average proportion of sandeel in the diets of seabirds at the Shetland Islands. Yet, this masks important differences between species, with Arctic skua (*Stercorarius parasiticus,* Stercorariidae) and Arctic tern (*Sterna paradisaea*, Laridae) maintaining 100% of their sandeel diet in all three periods of study, whereas the sandeel contribution to diet decreased from 70-80% to less than 10% in gannet (*Morus bassanus*, Sulidae), fulmar (*Fulmarus glacialis*, Procellariidae), great skua (*S. skua,* Stercorariidae) and great black-backed gull *(Larus marinus*, Laridae) between 1977 and 2000. Small surface-feeders, such as Arctic terns, are more constrained and, as such, more vulnerable to environmental changes than other species (Baird, 1990; Furness & Tasker, 2000; Shealer, 2002). Seabird diet, body size and the ability to switch to other prey when their favored prey is depleted might then be important components of their sensitivity to environmental or fisheries-induced fluctuations in prey.

These results highlight the importance of forage fish accessibility for seabirds rather than just abundance. Indeed, a decrease in forage fish stock biomass does not automatically translate into a decrease in forage fish availability or catchability for seabirds, or at least not linearly, due to possible changes in spatial distribution. First, the shoaling behaviour of most forage fish means that predation, like fisheries catches, may be maintained even when prey abundance decreases (in fisheries known as hyperstability of catches, Hilborn & Walters, 1992). For example, as stock biomass decreases, forage fish may concentrate in their most suitable habitat (i.e., the basin hypothesis; MacCall, 1990), resulting in habitat contractions, but no decrease in fish density. In this study, the absence of relationships between seabird diet and forage fish abundance in the Humboldt system was in line with previous works which showed that except in the case of extreme El Niño events, seabird behavior, breeding seasonality and population dynamics were affected by fish accessibility

399   rather than fish abundance (Barbraud et al., 2017; Boyd et al., 2015, 2016, 2017; Passuni et al., 2018,

400   2015). Anchovy spatial distribution was shown to be strongly correlated with oxygen levels

401   (Bertrand, Ballón, & Chaigneau, 2010), so that when the oxycline goes up, anchovies are

402   concentrated close to the surface, where they become accessible to shallow divers such as Peruvian

403   boobies and Peruvian pelicans (Weimerskirch, Bertrand, Silva, Bost, & Peraltilla, 2012). This

404   phenomenon may be apparent also in the Benguela with respect to anchovy accessibility to both

405   purse-seine fishers as well as surface-diving predators, since unpublished evidence suggests that

406   anchovy in recent periods are located closer to the sea bed given reduced stratification (and more

407   homogenous oxygen levels) through the water column (SWG-PEL of Department of Environments,

408   Forestry and Fisheries in South Africa 2019).

409   Our results show that the predation pressure from seabirds, *i.e.* the proportion of the stock

410   consumed by seabirds, was generally low (median = 1% and ≤20% of stock size in 95% of cases),

411   confirming that bottom-up processes might be controlling seabird – forage fish interactions most of

412   the time at the population scale. It is important to note that our analyses occurred at a regional or

413   ecosystem scale, so that our results did not consider the potential for local prey depletion (Lewis et

414   al., 2001) or the importance of top-down processes on spatial distribution at a fine scale. The broad

415   scale used in this study might also explain why the estimated predation pressure was lower than that

416   obtained by some previous studies (Furness, 1978). Nonetheless, when prey biomass decreased

417   below a certain threshold (here estimated between 15 and 18% of the maximum biomass depending

418   on the ecosystem and always lower than the median biomass), the predation pressure increased

419   sharply as depicted by power relationships between prey biomass and the percentage of prey

420   biomass consumed by seabirds. While it could not be tested in Shetland due to the small number of

421   years monitored, this held true in the Norwegian Sea, in the Humboldt and in the Benguela. In

422   contrast, the percentage of the sprat stock consumed by common murres in the Baltic Sea remained

423   extremely low (≤1.2%) throughout the study. This could be explained by the high abundance and

424   small variability in sprat biomass during the study period (Eero, 2012), which in fourteen years did

425 not fall below 54% of its maximum value (a value well above the 15% threshold detected in other

426 ecosystems). An increase in the proportion of prey that is consumed by predators when prey

427 abundance is low was not unexpected, because predators need to satisfy their food requirements

428 (Bakun, 2006) and even though some are able to switch their diet to alternative food sources, they

429 may preferentially target energetically-rewarding prey (Adams & Klages, 2010). Due to different life-

430 histories between short-lived prey and long-lived predators, and the canalization of seabird adult

431 survival, *i.e.* the key parameter buffering their population dynamics against temporal fluctuations

432 (Gaillard & Yoccoz, 2003), the number of seabirds can still be high after a decrease in prey biomass,

433 maintaining prey consumption at high levels. In some exceptional cases, the predation pressure we

434 estimated became extremely high, such as in the Norwegian Sea, where this most likely reflected

435 unrealistic survival rates for herring in the modelling for some of the poorest years (cf. ICES, 2012

436 and Supplementary material for further details).

437   A rapid rise in the proportion of forage fish consumed, *i.e.* in predation mortality, once

438 forage fish have been depleted below a certain threshold of abundance, might result in their

439 entrapment in a predator pit (Bakun, 2006). This effect would be exacerbated if proportions of those

440 prey taken by other predators in the ecosystem (*e.g.* other seabirds, seals, cetaceans, predatory fish,

441 see Table S1) increase similarly and fishing mortality is also high. For several fish stocks in the North-

442 West Atlantic, including Atlantic herring, chub mackerel (*Scomber colias*, Scombridae), haddock

443 (*Melanogrammus aeglefinus*, Gadidae) and silver hake (*Merluccius bilinearis*, Merlucciidae) empirical

444 evidence suggested that recruitment remained poor when stocks were reduced to 10% of pristine

445 levels, but that good year-classes were experienced, and stock rebuilding took place when biomass

446 was above about 20% of peak levels of abundance (Brown, Anthony, Anderson, Hennemuth, &

447 Sherman, 1983). Here, we found that predation pressure increased sharply when the stock biomass

448 decreased below 15 to 18% of its maximum abundance. These observations raise the question as to

449 whether such predation pressure might constrain prey stocks and keep them at very low levels.

450   First, positive correlations between prey biomass and the number of seabirds the year before

451   were highlighted in both the Benguela and Humboldt ecosystems. While this might appear

452   surprising, it could be due to temporal autocorrelation in prey biomass time series, i.e. the fact that a

453   high prey biomass in a given year is likely to be followed by another high prey biomass the next year

454   and vice versa (Fréon, Cury, Shannon, & Roy, 2005). If the ecosystem is indeed under bottom-up

455   control, or both prey and predators react the same way to other external variables, then both would

456   endure similar favourable or unfavourable periods, explaining the positive relationship between prey

457   at t+1 and predator at t. Indeed, a partial temporal autocorrelation of lag 1 was present in the

458   residuals of the models in the Benguela and the Humboldt. Once we removed the autocorrelation by

459   adding a one-year lagged time series of the prey biomass as a covariate in the model, both

460   relationships between prey biomass and predator abundance or consumption disappeared in the

461   Humboldt. Further, a negative temporal correlation of predator and prey abundance, despite being

462   the most commonly used approach to investigate predation (e.g. Frank et al., 2005; Worm & Myers,

463   2003), does not allow one to distinguish between predators driving prey dynamics and both

464   populations responding in opposite directions to an external environmental driver (Hunt &

465   McKinnell, 2006; Oken & Essington, 2015). When looking at the effect of the predation pressure,

466   instead of the number of predators, on the prey biomass a year later, no relationship was detected in

467   the Humboldt or Benguela ecosystems. In contrast, a significant negative relationship between prey

468   biomass and the number of birds or the percentage of the stock consumed by seabirds the year

469   before was found in the Baltic Sea. Given the very low predation pressure (<1.2%) estimated in this

470   ecosystem, we suggest that this might be due to a spurious correlation, perhaps attributable to a

471   third variable to which sprat and murres might react differently. Finally, looking at how predation

472   pressure affects the change in prey biomass from one year to another, rather than the absolute value

473   of biomass, should remove the variance explained by temporal autocorrelation and enable an

474   investigation of the immediate effects of predation, whereas the effect on absolute biomass might

475   be delayed (Oken & Essington, 2015). Importantly, no relationships were highlighted between these

476 two variables, suggesting that seabird predation pressure did not drive changes in forage fish

477 abundance.

478   However, it should be borne in mind that we only estimated a portion, often small (e.g.

479 Shannon, Christensen, & Walters, 2004), of the overall natural mortality, as consumption by other

480 predators present in the area (large predatory fish, marine mammals, other seabirds) was not

481 included. Further, predators do not target the entire population, but rather focus on given length- (or

482 age-) classes, making the effect of predation harder to detect (Oken & Essington, 2015). Hence, in

483 years when prey biomass is low and corresponding seabird consumption requires a significant part of

484 the forage fish stock, strong competition might arise between predators and fisheries. During such

485 intense competition, as created in the North Pacific by the massive biennial fluctuations in predatory

486 adult pink salmon (Ruggerone, Springer, Shaul, & van Vliet, 2019; Springer & Van Vliet, 2014) or

487 during the 2014-2016 marine heatwave when all forage fish stocks crashed simultaneously (Jones et

488 al., 2018; Piatt et al., 2020; von Biela et al., 2019), it is increasingly apparent that seabirds may take

489 the brunt of competitive displacement from food supplies (e.g. 10-20% of the NE Pacific population

490 of common murres died en masse from starvation during the heatwave; Piatt et al., 2020).In the

491 California current, seabirds whose diet is mainly forage fish, especially anchovy, respond negatively

492 to forage fisheries (Koehn et al., 2017). While economic consequences of fishing forage fish are

493 unclear for piscivorous fisheries (Engelhard et al., 2014), the impact on conservation of seabirds and

494 marine mammals might tip the scales towards keeping forage fish at sea being more valuable than

495 fishing them out (Koehn et al., 2017). Many seabirds have an unfavourable conservation status.

496 Seabirds are more threatened, and declining faster, than other groups of birds (Dias et al., 2019). For

497 example, nine of 15 seabird species (60%) that breed in the Benguela ecosystem are classified, in

498 terms of criteria of the International Union for the Conservation of Nature (IUCN), as Endangered,

499 Vulnerable or Near-threatened; these include three that feed mainly on sardine and anchovy,

500 whereas several seabirds that do not compete with fisheries for food have a Red List status of Least

501 Concern (Crawford, 2013; IUCN, 2019). Cury et al. (2011) identified a threshold of approximately

one-third of maximum prey biomass below which seabird breeding success was consistently reduced and more variable. Similarly, when the biomass of sardine spawners fell below c. 25% of its maximum observed value, survival of adult African penguins (*Spheniscus demersus*, Spheniscidae) decreased markedly (Robinson, Butterworth, & Plagányi, 2015) and survival and numbers breeding decreased for three Benguela seabirds when a forage availability index reached low values (Crawford, Sydeman, Thompson, Sherley, & Makhado, 2019). There may be a still lower ecological threshold (15 to 18% according to our study) where prey species, or at least spatial components of prey stocks (e.g. west coast vs. south coast in the Benguela), suffer high rates of natural and fishing mortality. Interestingly, 20% of maximum biomass is often used in fishery management as a limit biomass (B_{lim}) below which a stock should not fall or a recovery plan should be put in place. Here, we confirm a similar threshold and advise fishery managers to exercise due care in allocating allowable catches or fishing licenses, *etc.* at low levels of abundance.

To conclude, our study is important as it contributes to the growing literature in support of an ecosystem approach to fisheries (EAF; Dickey-Collas et al., 2014; Hill et al., 2020; Koehn et al., 2017; Pikitch et al., 2004). While top-down processes due to predation of forage fish by seabirds did not seem to control forage fish dynamics in any of the five ecosystems we considered, the predation pressure sometimes attained high levels, which signals the need for fisheries management to account for ecosystem constraints when setting catch limits in periods of low forage fish biomass. Finally, our results (and in particular the differences of sensitivity of seabird diet to prey biomass among species) also suggest that forage fish accessibility might be more important than forage fish abundance depending on the ecophysiological constraints that apply to seabirds (e.g. depth to which they can dive). As a consequence, fish stock management should not only ensure a safe level of fish biomass for the stock to be sustainable and the predators to feed (Cury et al., 2011), but also focus on safeguarding predator foraging grounds. Measures such as spatial enclosure around breeding sites have for instance been used in different areas (see (Sydeman et al., 2017) for more on the

527   subject). Spatial planning is thus an extremely important component of human activity (and

528   especially fishery) management in order to safeguard all components of the ecosystem.

529

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548   **Data Availability Statement**

549   The data that support the findings of this study are openly available in Mendeley data at

550   http://dx.doi.org/10.17632/5bb8nhb6hr.1

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	Proportion of prey in diet in terms of energy P_t	Assimilation Efficiency AE	Prey energetic value $PreyNRJ$	Daily Energy Expenditure DEE	Bird numbers N_t	Number of days $Nbdays$	Chick consumption C_{chick}	Fish biomass
Atlantic puffin in the Norwegian Sea	Chick=Adult diet Annual values (Anker-Nilssen & Aarvak, 2006; updated with www.seapop.no/en)	0.7 (Brekke & Gabrielsen, 1994)	3.7 kJ.g^{-1} (Anker-Nilssen & Øyan, 1995)	Average body mass = 460g (Barrett, Gabrielsen, & Fauchald, 1995) FMR_B = 1.84 kJ.g^{-1}.d^{-1} (Ellis & Gabrielsen, 2002) DEE_{NB} =2.25*BMR = 745.2 kJ.d^{-1} (Ellis & Gabrielsen, 2002)	Røst population $N_{B,t}$ estimated from counts (Anker-Nilssen & Aarvak, 2006; updated with www.seapop.no/en) $N_{NB,t}$= nb of immature from 1 to 5 (estimated from number of fledglings and juvenile survival; Sandvik, Erikstad, Fauchald, & Tveraa, 2008) + 25% of mature birds skipping reproduction	2 scenarios: 1) $Nbdays_B$ estimated annually equal to chick-rearing duration 2) $Nbdays_B = 152\ d$ $Nbdays_{NB} = 0$ $Nbdays_{col} = Nbdays_B$	Meal size = 108 g.chick^{-1}.day^{-1}, (Øyan & Anker-Nilssen, 1996) Nb of chicks estimated from counts	Age 0 fraction of the stock. Estimated using back-calculations from recruitment indices (i.e. age class 3) obtained through VPA (ICES, 2012; Toresen & Østvedt, 2000)

Cape gannet in the southern Benguela	Chick=Adult diet Annual values (average from all months and 2 localities) (Crawford et al., 2019)	0.74 (Crawford, Ryan, & Williams, 1991)	8.59 and 6.74 kJ.g^{-1} for sardine and anchovy respectively (Batchelor & Ross, 1984)	DEE_B = 3380 kJ.d^{-1} DEE_{NB} = 2767 kJ.d^{-1} (Adams, Abrams, Siegfried, Nagy, & Kaplan, 1991; Berruti, Underhill, Shelton, Moloney, & Crawford, 1993)	Lambert's Bay + Malgas Island populations (South Africa west coast) $N_{B,t}$ estimated from occupied breeding area sizes and densities of nests (Crawford et al., 2007 updated) $N_{NB,t}$= nb of immature from 1 to 4 (estimated from number of chicks and age-dependent survival)	$Nbdays_B$ = 165. $Nbdays_{NB}$ = 140 $Nbdays_{col}$ dependent on age-class (Jarvis, 1974)	Nb of chicks = nb of breeding pairs * 0.45 DEE_{chick} = 2236 kJ.d^{-1} (Cooper, 1978) Nbdays$_{chick}$ = 97 (Jarvis, 1974)	Spawning stock biomass West of Cape Agulhas Estimated based on hydro-acoustic surveys (Augustyn et al., 2018; Coetzee et al., 2008)

Common murre in the Baltic Sea	Chick = adult diet Annual values (Kadin, Österblom, Hentati-Sundberg, & Olsson, 2012)	0.78(Hilton, Furness, & Houston, 2000)	5.46 kJ.g^{-1} (Enekvist, 2003)	DEE_B = 1530 kJ.d^{-1} DEE_{NB} = 1392 kJ.d^{-1} (Roth, Nur, Warzybok, & Sydeman, 2008)	Entire Baltic Sea population $N_{B,t}$ = 100/65 * $N_{B,t}$ at Stora Karlsö (Olsson & Hentati-Sundberg, 2017) from annual counts at Stora Karlsö $N_{NB,t}$ = 0.5 * $N_{B,t}$	$Nbdays_B = 90$ (Hedgren, 1975) $Nbdays_{NB} = 275$ $Nbdays_{col} = 365$	Meal size = 4*10.26 = 41 g.chick^{-1}.day^{-1}, (Enekvist, 2003; Kadin et al., 2012) Nb of chicks = annual breeding success * nb of breeding pairs (Kadin et al., 2012) Nb of days = 18d (Kadin, Olsson, Hentati-Sundberg, Ehrning, & Blenckner, 2016)	Spawning Stock biomass Entire baltic Sea Estimated through XSA using acoustics and landings as inputs (ICES, 2018)

| Shetland Islands | Chick = adult diet

Period values (Furness, 1990; Furness & Tasker, 2000; Martin, 1989) | 0.80 (Hilton et al., 2000) | 6 kJ.g^{-1} (Pedersen & Hislop, 2001) | DEE$_B$ estimated from allometric equations per order

DEE$_{NB}$ = 2.25 BMR

(Ellis & Gabrielsen, 2002) | Shetland populations

N$_{B,t}$ estimated from counts (Mitchell, Newton, Ratcliffe, & Dunn, 2004; Walsh et al., 1995)

N$_{NB,t}$= 25% of breeding birds | $Nbdays_B$ for each species (122d for great skua, 106 for arctic skua, common murre and razorbill, 78 artic tern, 108 puffin, 136 kittiwake, great blacked-back gull, black guillemot, fulmar, shag and gannet) (Furness, 1990)

$Nbdays_{NB} = 0$

$Nbdays_{col} = Nbdays_B$ | Nb of chicks = Breeding success * nb of breeding pairs

DEE from the same equation as non-breeding adult with M$_{chick}$ = 0.5 M$_{adult}$

Nb of days = chick-rearing duration | Total biomass

Shetland stock

Estimated from VPA using landings and experimental trawl surveys as inputs |

Northern Humboldt	Chick = adult diet Period values (Goya, 2000; Jahncke, Checkley, & Hunt, 2004)	0.75 (Dunn, 1975; Laugksch & Duffy, 1984)	6.37 kJ.g^{-1} (Cooper, 1978; Laugksch & Duffy, 1984)	DEE$_B$ estimated from allometric equations of pelecaniform DEE$_{NB}$ = 2.25 BMR (Ellis & Gabrielsen, 2002)	Entire Northern Humboldt populations (31 islands) Monthly counts of total number of birds. N$_{B, t}$ and N$_{NB, t}$ derived from monthly average proportions of breeders vs non-breeders based on the 2003-2014 observations.	$Nbdays_{col} = 365.$	DEE from the same equation as non-breeding adult with M$_{chick}$ = 0.5 M$_{adult}$ Nb chick = brood size * nb of breeding pairs Duration: 86d, 133d and 110d for cormorant, booby and pelican	Production biomass Northern Humboldt (7-18°S) from the coast to 100km offshore Estimated from acoustic estimates and monthly length structure (Oliveros-Ramos & Peña, 2011)

Table 1. Main parameters and assumptions used in the estimation of seabird consumption in each ecosystem.

Variables	Ecosystem/Species	Model type	AICc	ΔAICc	n
Diet ~ Stock biomass	Norwegian Sea – Puffins – Age 0 herring	**null**	**211.1**	**0**	23
		Logarithmic	212.0	0.9	
		Power	212.3	1.2	
	Benguela – Gannets - Sardines	**Logarithmic**	**253.4**	**0**	37
		Power	254.0	0.6	
		null	324.9	71.5	
	Benguela – Gannets - Anchovies	**Power**	**205.4**	**0**	37
		Logarithmic	205.8	0.4	
		null	311.9	106.5	
	Baltic Sea – Murres - Sprats	**null**	**64.1**	**0**	14
Consumption ~ Stock biomass	Norwegian Sea – Puffins – Age 0 herring	**null**	**445.8**	**0**	22
		Type III functional response	447.0	1.2	
		Type II functional response	447.4	1.6	
	Benguela – Gannets - Sardines	**Type II functional response**	**590.8**	**0**	31
		Type III functional response	591.1	0.3	
		Logarithmic	591.4	0.6	
		Power	592.0	1.2	
		null	615.3	24.5	
	Benguela – Gannets - Anchovies	**Type II functional response**	**503.0**	**0**	31
		Power	503.1	0.1	
		Type III functional response	504.1	1.1	
		Logarithmic	504.3	1.4	
		Linear	504.6	1.7	

	Region – Species	Model	AICc	ΔAICc	n
		null	589.5	86.5	
		Power	**230.9**	**0**	
	Baltic Sea – Murres - Sprats	Logarithmic	231.1	0.2	
		Exponential	231.3	0.4	14
		Linear	231.5	0.6	
		null	234.0	3.1	
		Power	1374.4	0	
		Logarithmic	1374.6	0.2	
		Type II functional response	1374.8	0.4	
	Humboldt – All 3 species - Anchovies	Quadratic	1374.9	0.5	
		Linear	1374.9	0.5	48
		Null	**1375.6**	**1.2**	
		Exponential	1375.6	1.2	
		Type III functional response	1376.46	2.0	
% consumed ~ stock biomass	Norwegian Sea – Puffins – Age 0 herring	**Power**	**196.9**	**0**	22
		null	218.6	21.7	
	Benguela – Gannets - Sardines	**Power**	**135.8**	**0**	31
		null	155.0	19.2	
	Benguela – Gannets - Anchovies	**Power**	**39.2**	**0**	31
		null	74.3	35.2	
	Baltic Sea – Murres - Sprats	**Power**	**-22.7**	**0**	
		Exponential	-21.6	1.1	14
		null	1.2	25.3	
	Humboldt – All 3 species - Anchovies	**Power**	**209.1**	**0**	48
		null	254.7	45.6	

Table 2. Seabird diet and consumption according to prey biomass. Six a priori parametric models were fitted using non-linear least square adjustment (null model assuming no link of seabird diet or consumption with prey biomass, linear model assuming a constant increase of seabird diet or

consumption with fish biomass, second-order polynomial models assuming an optimum fish biomass for seabirds, as well as exponential, logarithmic and power models which all assume non-linearities and some sort of thresholds above or below which seabirds react differently to prey). Additionally, functional responses of type II and III were also tested for the relationship between seabird consumption and prey biomass. Results of the most supported models (ΔAICc ≤ 2) are presented along with the null model. Results are not presented in the Shetland system, where too few data points hindered quantitative analyses. Also, for the Humboldt, no model was performed on the diet data and consumption was estimated as the sum of the consumption made by the three seabird species.

Figures

Figure 1. Ecosystems under study along with the studied seabird and fish species.

Figure 2. Schematics of the method used to quantify the proportion of a fish stock that is consumed by seabirds.

Figure 3. Trends in the annual contributions of the main fish prey to the diet of seabird species at Røst from 1982 to 2006 (Atlantic herring in puffin diet), in the Baltic Sea from 1985 to 1995 (sprat in murre diet), in the Northern Humboldt from 1961 to 2008 (anchovy in the diet of three bird species), on the west coast of South Africa from 1985 to 2011 (sardine and anchovy in gannet diet), and at Shetland in 1977, 1986 and 2000 (sandeel in the diet of 12 bird species).

Figure 4. Relationships between the stock biomass of prey (thousand tonnes) and the percentage contribution of prey to the diet of seabirds for each of the five ecosystems. As 12 seabird species were considered at Shetland, we present the mean ± SE for that locality. When two variables were significantly related, dashed lines represent the fit of the best relationship between these variables (see Table 2). Note that for the Benguela, the two candidate models (i.e. ΔAIC ≤ 2) gave very similar predictions, so that just one was plotted for clarity purposes.

Figure 5. Relationships between the stock biomass of prey (thousand tonnes) and the consumption of prey (thousand tonnes) by seabirds. When two variables were significantly related, dashed lines represent the fit of the best relationship between these variables (see Table 2). Note that for the Benguela and the Baltic, the different candidate models (i.e. ΔAIC ≤ 2) gave very similar predictions, so that just one was plotted for clarity purposes.

Figure 6. Relationships between the stock biomass of prey (thousand tonnes) and the percentage of the stock consumed by seabirds. When two variables were significantly related, dashed lines represent the fit of the best relationship between these variables (see Table 2). The thresholds in the

non-linear relationships between stock biomass and the percentage of the stock consumed by seabirds were calculated from change-point analyses and are indicated by vertical solid lines, while the median stock biomass is indicated by a dashed vertical line. Note that for the Baltic, the different candidate models (i.e. ΔAIC ≤ 2) gave very similar predictions, so that just one was plotted for clarity purposes.

Figure 7. Relationships between fish stock biomass at year t and the number of seabirds (in thousands) present at year t-1 (left) or the percentage of the stock consumed by seabirds at year t-1 (middle). To account for autocorrelation in the Benguela and Humboldt ecosystems, the stock biomass at t-1 was added as an explanatory variable in all 6 models run for these two ecosystems. Lines depicting the relationships are drawn in the case of significant relations (linear model with the stock biomass at t-1 as a co-variable). On the right are represented the relationships between the change in fish stock biomass from year t-1 to year t and the percentage of the stock consumed by seabirds at year t-1. Such analyses were not considered for the Norwegian Sea ecosystem, as puffins there consume age 0 herring, which reach maturity at age 3, nor for Shetland were seabirds were not monitored on an annual basis.

Supplementary material

ESM1: Methods: details on data collection in each ecosystem

Atlantic puffin at Røst

Puffin chick diet was available for all years 1982–2006, except for 1987 and 1995, from (Anker-Nilssen & Aarvak, 2006) and unpublished data of SEAPOP (www.seapop.no/en, the Norwegian seabird program). Further, because there appears to be no significant differences in the diet of chicks and adults (Albertsen, 1996) chick diet was used to estimate the proportional contribution by mass of herring *Clupea harengus* of age zero regardless of puffin life stages. Calorific values of the main prey (3.7 kJ.g^{-1} wet mass for age 0 herring; Anker-Nilssen & Øyan, 1995) enabled us to calculate the proportional contribution by energy of age 0 herring in the diet, i.e. P_t. Assimilation efficiency was set at 70% as recommended for prey this lean (Brekke & Gabrielsen, 1994).

Daily energy expenditure of breeding puffins was entered at 848 kJ.d^{-1} as reported from a study in another Norwegian colony (Barrett, Gabrielsen, & Fauchald, 1995; Ellis & Gabrielsen, 2002) for the same average adult body mass as at Røst (460 g, Barrett et al., 1995). Given the general lack of empirical data on FMR for non-breeding auks, we conservatively set DEE_{NB} at two times the basal metabolic rate (BMR), which is about three quarters of the FMR/BMR ratio of 2.7 reported for breeding Atlantic puffins (Ellis & Gabrielsen, 2002). As BMR of Atlantic puffins equals 331 kJ.d^{-1} for 460 g birds (Barrett et al., 1995; Ellis & Gabrielsen, 2002), this results in a DEE_{NB} of 662 kJ.d^{-1} using average body mass at Røst, i.e. a decrease of 22% in DEE compared to breeding birds.

The number of Atlantic puffins breeding at Røst in year t, $N_{B,t}$, as calculated using the method developed by (Anker-Nilssen & Røstad, 1993) and applied to all the islands as reported by (Anker-Nilssen & Øyan, 1995) was available for all years 1982–2012 (Anker-Nilssen & Aarvak, 2006; unpublished data of SEAPOP). We estimated non-breeders on site (i.e. immature and adults skipping reproduction) by assuming that mean age at first breeding is 5 to 7 years (Anker-Nilssen & Aarvak, 2006). Birds at each age class from 1 to 5 were thus considered immature and their numbers

estimated from cohort survival rates, given a constant survival rate of 75% in their first year of life and an immature survival thereafter equal to that of breeding birds (Sandvik, Erikstad, Fauchald, & Tveraa, 2008). As most 1-year old birds do not visit the colony (Sandvik et al., 2008), we excluded this class of immature birds from our calculations. Finally, we assumed that 25% of mature adults skip reproduction or fail before hatching.

As puffins are present on Røst only during the breeding season, $Nbdays_{NB}$ was considered to be null and $Nbdays_{col} = Nbdays_B$. Further, age 0 herring are known to be a key prey for these puffins during the chick-rearing period (Albertsen, 1996; Anker-Nilssen, 1992; Anker-Nilssen & Aarvak, 2006). However, little data on diet is available outside this time window. Due to this uncertainty, we considered a precautionary approach based on the use of two extreme scenarios, where the number of days spent in the colony feeding on age 0-herring was minimum and maximum, in order to have a range of consumption estimation. First, in the minimum consumption scenario, the period considered was restricted to chick-rearing, so that $Nbdays_{NB} = 0$ and $Nbdays_{col} = Nbdays_B = Nbdays_{chickrearing}$. The duration of the chick-rearing period varied from year to year, and was thus estimated annually. The second scenario considered the maximum time spent by puffins in the area. Indeed, although no diet study confirmed a direct link, some indications of the impact of age 0 herring abundance on puffin condition prior to egg-laying have been highlighted (Barrett, Anker-Nilssen, Gabrielsen, & Chapdelaine, 2002; Barrett, Nilsen, & Anker-Nilssen, 2012). In order to account for this pre-laying period, the calculation started from 1st of May. Then a few studies also support the assumption of herring consumption beyond the breeding season (see (Gimenez, Anker-Nilssen, & Grosbois, 2012) for the effect of age 0 herring abundance on adult survival and (Anker-Nilssen & Aarvak, 2009; Fayet et al., 2017) on post-breeding movements by telemetry and geolocators). The calculation thus included August and September, so that the entire duration was set to 152 days.

Chick's consumption was calculated directly from meal size and feeding rates (108 g.chick^{-1}.day^{-1}; Øyan & Anker-Nilssen, 1996) and the annual number of chicks estimated through counts of active nests.

Because breeding puffins in Røst do not feed on herring older than age 0, which stay out of reach in the nursery areas in the SE Barents Sea before becoming too large as prey for puffins, we used the biomass of age 0 herring to estimate the proportion consumed (Toresen & Østvedt, 2000). The biomass of age 0 herring arriving at their nursery grounds in the Barents Sea a few months later was not directly derived from spawning stock size, as this relationship seems weak for the Norwegian spring-spawning stock (Toresen & Østvedt, 2000). Rather it was estimated for all years up to 2011 from back-calculation in virtual population analysis (VPA) from recruitment indices (i.e. age class 3) assuming a fixed larval mortality rate (ICES, 2012). This enabled the proportion of the biomass consumed by Atlantic puffins during the nestling period to be estimated for all 23 years that had information on the contribution of herring to the diet of puffins. It should be noted that the true proportions consumed by puffins in the nestling period were most likely overestimated, as the actual biomass of age 0 herring drifting past the colony in the nestling period was probably significantly higher to an unknown extent (P. Fossum, Norwegian Institute of Marine Research, pers. comm.). As the day-to-day survival of drifting age 0 herring during summer is not known in detail, this bias is difficult to account for.

Cape gannet in the southern Benguela ecosystem

Cape gannets are one of the seabirds in the Benguela ecosystem that subsist mainly on sardine and anchovy (Berruti, Underhill, Shelton, Moloney, & Crawford, 1993). They breed at three localities in Namibia, and at three in South Africa, of which two, Lambert's Bay and Malgas Island, are off South Africa's west coast (Berruti et al., 1993). This study focuses on these two colonies.

The average proportional contribution by mass of five prey categories: sardine, anchovy, saury, Cape hake and other, was available for Cape gannets off western South Africa for 1978–2014 from information in (Crawford, Sydeman, Thompson, Sherley, & Makhado, 2019). The proportional contribution by energy of each of these prey categories was then calculated from the calorific content of prey category i in $kJ.g^{-1}$ (values from (Batchelor & Ross, 1984): sardine 8.59, anchovy 6.74,

saury 6.20, hakes 4.07 and other 5.60 $kJ.g^{-1}$). Details on the sampling method can be found in (Crawford et al., 2019). The assimilation efficiency was set at 74% according to a previous study (Crawford, Ryan, & Williams, 1991). The daily energy expenditure of a breeding Cape gannet (DEE_B) is 3380 $kJ.d^{-1}$ (N. J. Adams, Abrams, Siegfried, Nagy, & Kaplan, 1991; Ellis & Gabrielsen, 2002). That for a non-breeding Cape gannet (DEE_{NB}) was taken to be 2767 $kJ.d^{-1}$ based on a similar contribution of prey species to the diet but an 18% smaller meal size for non-breeding than breeding Cape gannets at Malgas Island (Berruti et al., 1993).

Numbers of Cape gannets breeding at Lambert's Bay and Malgas Island in year t ($N_{B,t}$) were available for 1978–2014 from information in (Crawford et al., 2007) updated. We assumed that all mature birds breed at some point during the year, so that non-breeders come down to immatures only, i.e. birds of age 1 to 4 (Crawford, 1999). Numbers at each age class, from 1 to 4, were estimated by following cohorts, using the number of chicks in each year and age-dependent survival. Cape gannets in their first two years (aged 0 and 1 years) have a mean annual survival of 0.71 (Crawford, 1999) and thereafter birds along western South Africa have an average adult survival of 0.86 (Distiller, Altwegg, Crawford, Klages, & Barham, 2012).

The proportion of a year that birds of different ages remained in western South Africa was estimated from the proportion of recoveries and resightings of banded birds that occurred within 400 km of a breeding colony (Klages, 1994) as follows: < 1 year old 40%; 1–2 years old 44%, 3 years old 70%, > 4 years old 100% of the breeding period and 70% of the non-breeding period. The breeding season of Cape gannets lasts c. 165 days, c. 150days for incubation and chick rearing (Jarvis, 1974) plus c. 15 days for pairing and nest building, so that the non-breeding season is about 200 days.

Finally, chick number was estimated through the number of breeding pairs and breeding success. Over 17 seasons at Lambert's Bay and 22 at Malgas Island between 1988 and 2010 Cape gannets had a mean annual breeding success of 0.45 chicks per pair (Cury et al., 2011). Chicks spend on average 97 days at nests before fledging (Jarvis, 1974). The average daily energy requirement of chicks that fledge is 2236 $kJ.d^{-1}$ (Cooper, 1978).

Estimates for the two localities were summed to obtain an overall amount of consumption by Cape gannets breeding on the west coast in tonnes. Cape gannets at Lambert's Bay and Malgas Island forage offshore of Lambert's Bay to the west of Cape Agulhas when breeding (Pichegru et al., 2007). Estimates of the biomass of sardine and anchovy to the west of Cape Agulhas were available for each year from 1985–2014, based on hydro-acoustic surveys undertaken from late October to early December, centered in November (Augustyn et al., 2018; Coetzee et al., 2008).

Common murre in the Baltic Sea

Adult and juvenile common murre in the Baltic Sea feed predominately on sprat, with limited options for prey switching. Previous studies have estimated percentages of sprat in the adult and chick diet to be higher than 90%, whether in mass or numbers (Hedgren, 1976; Lyngs & Durinck, 1998; Österblom & Olsson, 2002). In this study, the % in mass was estimated for the 2002–2015 period (Kadin, Österblom, Hentati-Sundberg, & Olsson, 2012; HÖ and JHS unpublished monitoring data). This percentage was really high (between 92 and 99 %), the rest being a few three-spined sticklebacks *Gasterosteus aculeatus* and sandeels *Ammodytes* spp. Sprat and small herring are extremely difficult to distinguish in the field, and this (and previous) studies may have underestimated the potential contribution of herring in the diet. This may have led to an over-estimation of the sprat consumption in the analysis. Data on species proportions in the diet were available for all years except 2003; for that year, the average for 2002 and 2004 was used.

The assimilation efficiency was taken as 78%, the true metabolisable energy coefficient estimated for this species elsewhere (Hilton, Furness, & Houston, 2000). We assumed an energy density for sprat of 5.46 kJ.g^{-1} wet mass (Enekvist, 2003). Using previously published estimates of the energy requirements of common murres from the Arctic (Ellis & Gabrielsen, 2002) and California (Roth, Nur, Warzybok, & Sydeman, 2008), we estimated the average daily energy expenditure for non-breeders to be 1392 kJ.d^{-1} and for breeders to be 1530 kJ.d^{-1}.

The population of common murres in the Baltic Sea was 13 000–17 000 pairs, of which approximately 65% breed at Stora Karlsö (Olsson & Hentati-Sundberg, 2017). Numbers of pairs breeding at Stora Karlsö were estimated annually during 2002–2015 based on direct observations. These numbers were doubled and multiplied by 100/65 to estimate the total number of common murres breeding in the Baltic Sea in year t ($N_{B,t}$). We assumed that the number of non-breeders in the population was equivalent to 50% of numbers breeding (i.e. 1/3 of the entire population), based on observations at the Stora Karlsö colony and unpublished modeling results that indicate a high pre-breeding survival and a high proportion of non-breeding birds in the population. The length of the breeding season was set to 90 days, representing the period from the stabilization of the presence of the breeding population in late April to the departure in mid-late July (Hedgren, 1975).

Regarding chick consumption, it was estimated using a combination of number of chicks, number of days feeding, number of feeding events per day and chick meal size. The number of chicks was estimated based on annual monitoring of breeding success, which varied between 0.67 and 0.86 (Kadin et al., 2012; updated), and the number of breeding pairs. Data were not available for 2002 – 2004, so for these years the average for the whole time series 2005 – 2015 was used. The number of days during which chicks are fed was set to 18 d (Kadin, Olsson, Hentati-Sundberg, Ehrning, & Blenckner, 2016), while the meal size was estimated from the number of fish fed per day (4; Kadin et al., 2012) and the average weight of fish fed (0.01026kg; Enekvist, 2003).

We used estimates of sprat biomass for the entire Baltic Sea as determined by ICES (International Council for the Exploration of the Seas) through XSA (Extended Survival Analysis) which uses a combination of reported landings and acoustic surveys as input data (ICES, 2018). In this model, M is calculated through a model (SMS, Stochastic Multi-Species model) using cod predation as time-varying factor. Seabirds are not included in the M estimate. Because bird consumption is so low in this ecosystem, using fisherman catch or fisherman + seabird catch in the catch equation should not

change any result in biomass estimates (C_t = 7021 ± 891 *vs.* Catches = 326,200 ± 62,682 tonnes, *i.e.* 46 times less consumption than catches).

Seabirds at Shetland

Several seabird species breed sympatrically in Shetland. In order to estimate the predation pressure exerted on fish stocks, we estimated the consumption of the entire seabird population, by working on 12 species: 9 charadriiforms (Great and Arctic skua *Stercorarius skua and S. parasiticus*, Arctic tern *Sterna paradisaea*, black-legged kittiwake *Rissa tridactyla,* great black-backed gull *Larus marinus,* black guillemot *Cepphus grylle*, razorbill *Alca torda,* common murre, Atlantic puffin), 1 procellariform (northern fulmar *Fulmarus glacialis),* and 2 pelecaniforms *(*northern gannet *M. bassanus* and European shag *Phalacrocorax aristotelis).*

Diet composition data were collected either as voluntary regurgitates by chicks or adults handled for ringing (great skua, Arctic skua, northern fulmar, black-legged kittiwake, northern gannet and shag), or as cast pellets found near nests (great skua, great black-backed gull and shag), or as fish observed or photographed being carried by adults or sampled from birds caught by mist net, hand net, or noose and pole (Arctic tern, common murre, black guillemot, razorbill and Atlantic puffin). Diet sampling was primarily conducted at Foula, where samples were obtained annually from 1975 to 2004, except for gannets which were sampled only in a few years from Hermaness. Data on gannet diet from (Martin, 1989) were included to supplement unpublished data on gannet diet collected during ringing at the Hermaness colony. Diet sampling spanned both the incubation and chick-rearing periods, but with larger numbers of samples during chick-rearing. Because sample sizes in individual years were not always large and because comprehensive seabird population censuses were only available for three time periods, for estimation of sandeel consumption diet, data were amalgamated for the periods 1975–1983, 1984–1989 and 2000–2004 and related to population sizes in 1977, 1986 and 2000. Diet data for 1975–1983 were previously reported in (Furness, 1990) and for 1990–1996 in (Furness & Tasker, 2000). We assumed the proportion in terms of energy to be the

same as the proportion in mass, as most items in the diet would be likely to be similar in energy content to sandeels (slightly higher for herring and mackerel, slightly lower for whiting and haddock) and the difference between prey taxa likely to be no higher than the seasonal or interannual variability in sandeel energy content.

An assimilation efficiency of 80% was assumed (Hilton et al., 2000), and a calorific content of 6 kJ.g^{-1} for sandeels (Pedersen & Hislop, 2001). Daily energy expenditure of breeding birds was estimated from data on body mass presented in (Furness, 1990) and the bioenergetics equations of (Ellis & Gabrielsen, 2002) estimating field metabolic rate of breeding birds for each order (i.e. DEE = 11.49*m$^{0.718}$ for charadriiforms, DEE = 22.06*m$^{0.594}$ for procellariforms and DEE = 3.9*m$^{0.871}$ for pelecaniforms). Similarly, DEE_{NB} was estimated as 2.25 times the basal metabolic rate (BMR), where BMR was estimated through allometric equations per order according to (Ellis & Gabrielsen, 2002) (i.e. BMR = 2.149*m$^{0.804}$ for charadriiforms, BMR = 2.763*m$^{0.726}$ for procellariforms and BMR = 1.392*m$^{0.823}$ for pelecaniforms).

Numbers of each seabird species breeding at Shetland were taken from surveys using standard census methods (Mitchell, Newton, Ratcliffe, & Dunn, 2004; Walsh et al., 1995). Data were converted from census units to equivalent numbers of breeding pairs (Mitchell et al., 2004), and tabulated for 1977, 1986, and 2000. Additionally, we assumed that non-breeders (i.e. immature birds and mature adults that skip reproduction) represented a further addition of 25% to the breeders.

For seabirds that are only present in Shetland for a short period in spring and summer, dates of arrival and departure were taken from (Furness, 1990). For seabirds remaining in Shetland for longer, we assumed that sandeels were eaten only between 1 April and 15 August, since sandeels tend to remain within the sand at other times of year and are largely unavailable to seabirds, although common murres and shags may sometimes dig sandeels out of the sand during winter.

Regarding chick consumption, the number of chicks was estimated by multiplying the number of breeding pairs by the species-specific breeding success in each of the 3 periods. The average DEE of chicks was then derived from the same equation as for adults, considering the average chicks' weight was half that of adults. Finally, the number of days used to estimate chick consumption corresponded to chick rearing duration.

Estimates of Shetland sandeel total stock biomass on 1st of July each year were obtained by VPA combined with fishery-independent experimental trawl surveys (Wright & Bailey, 1992). In this model, M estimate is not a constant but is re-estimated each year based on diet composition and key predator abundance using a multispecies model. Still, while predator consumption includes that of seabirds and marine mammals, the most important predators of sandeels by far are fish - especially mackerel, herring, cod, haddock, whiting, and gurnard. Because predator consumption is included in M, the catch equation should not include seabird consumption. Abundance in 1977 (123 000 tonnes) was similar to that in 1976 and 1978 (103 000 and 106 000 tonnes). Abundance in 1986 was lower (65 000 tonnes) but similar to 1985 and 1987 (76 000 and 36 000 tonnes). Abundance in 2000 (15 000 tonnes) was similar to that in 1999 and 2001 (25 000 and 17 000 tonnes), considerably lower than in 1986, and an order of magnitude lower than in 1977.

Seabirds in the Humboldt ecosystem

Adult and juvenile Peruvian boobies, Guanay cormorants and Peruvian pelicans feed predominantly on anchovies. Owing to their greater diving capacity, Guanay cormorants are also able to feed on demersal species, while shallower-foraging boobies and pelicans are more restricted to the surface. Diet was estimated through stomach content samplings and analysis of otoliths collected within rejection pellets (cormorants) along the period 1974-2008. As sampling could not be performed

every year at each of the 31 islands and headlands used for breeding (Passuni et al., 2015), some assumptions had to be made. In particular, four types of periods were distinguished: (i) during strong El-Niño periods (1973, 1983, 1998), when small pelagic populations are highly impacted, the proportion of anchovy in the diet was estimated to be 55% for the Guanay cormorant and 58% for boobies and pelicans (Goya, 2000), (ii) during sardine-favoured periods (1974-1982, 1984-1990), the proportion of anchovy in the diet was set to 80% for all three species (Jahncke, Checkley, & Hunt, 2004), (iii) during anchovy-favoured periods and when fishing was regulated (1991-1997, 1999-2008), the proportion of anchovy in the diet was fixed to 81% for cormorants and 93% for boobies and pelicans (Goya, 2000), (iv) during anchovy-favoured periods and when fishing was not regulated (1961-1972), the proportion of anchovy in the diet was fixed to 70% for all three species (Jahncke et al., 2004). Because no detailed data were available on the rest of diet, we assumed the proportion in terms of energy to be the same as the proportion in mass. Indeed, the second prey for these seabirds are sardines, a very closely related species.

Finally, an assimilation efficiency of 75% was assumed (Dunn, 1975; Laugksch & Duffy, 1984) and a calorific content of 6.37 kJ.g^{-1} for anchovies (Cooper, 1978; Laugksch & Duffy, 1984).

Daily energy expenditure of breeding birds was estimated from data on average body mass and the bioenergetics equations of (Ellis & Gabrielsen, 2002) estimating field metabolic rate for pelecaniforms (DEE = $3.9*m^{0.871}$). This resulted in an estimation of 3074 kJ.d^{-1} for Guanay cormorant, 2353 kJ.d^{-1} for Peruvian booby and 6753 kJ.d^{-1} for Peruvian pelican. Similarly, daily energy expenditure of non-breeding birds was estimated as 2.25* BMR, BMR being obtained from the allometric equation BMR = $1.392*m^{0.823}$ valid for pelecaniforms (Ellis & Gabrielsen, 2002), giving values comparable to what had previously been used .

Numbers of individuals of the three species were derived from counts made monthly on the 31 islands and headlands used for breeding by AGRORURAL over the 1961-2014 period. Even if breeding

synchrony exists in this area (Passuni et al., 2015), the phenological patterns are not as sharp as in temperate region, and a small fraction of birds may breed any month of the year. Also, breeding seasonality was showed to change over the long term, at least for cormorants and pelicans, according to the regime shifts of the Humboldt Current System (Passuni et al., 2018). As a consequence, we used monthly counts to estimate the energy needed for the colony each month before summing it over the year. Based on the 2003-2014 period, when breeding and non-breeding birds were distinguished in the counts, we estimated the average proportion of breeders across the year to be 24% [21-31%] for guanay cormorants, 21% [14-28%] for boobies and 25% [19-38%] for pelicans. These proportions were then applied to the 1961-2002 period.

The three species are resident in the North Humboldt Current System and were thus assumed to consume prey all-year round ($Nbdays_{col} = 365$). Breeding period duration ($Nbdays_B$) was respectively set to 142, 203 and 161 days for cormorant, booby and pelican (Nelson, 2005; Tovar & Cabrera, 2005).

Regarding chick consumption, the number of chicks was estimated by multiplying the number of breeding pairs to the mean species-specific brood size (2.19, 1.87 and 1.99 respectively for cormorant, booby and pelican; S. Bertrand et al., 2012; Nelson, 2005). The average DEE of chicks was then derived from the same equation as for non-breeding adults assuming the average chicks' weight was half that of adults (S. Bertrand et al., 2012). Finally, the number of days used to estimate chick consumption corresponded to the sum of chick rearing duration and post-fledging duration (86, 133 and 110 respectively for cormorant, booby and pelican).

We used anchovy production from an integrated assessment model (Oliveros-Ramos & Peña, 2011) as a measure of potential anchovy abundance available to seabirds and the fishery. Anchovy production is the increase in population biomass due to somatic growth and birth rate

without considering natural and fishing mortality and was estimated at monthly time steps.

Anchovy production was built using acoustic estimates of biomass and anchovy length structure

from scientific surveys and fishery landings between 7° and 18°S and from the coast to 100 km

offshore. In the model, M is set as constant (M=0.7 yr^{-1}) based on the estimations made by Imarpe of

0.6 to 0.8 for the years 1974 and 2010. Adjusting the catch equation with bird consumption instead

of just fishermen catches should not change much the stock assessment results, as catches are an

order of magnitude higher than seabird consumption (C_t = 472,489 ± 390,792 *vs.* Catches = 5,199,381

± 342,858, *i.e.* 11 times less consumption than catches).

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ESM2: Supplementary tables

Table S1. Annual consumption of anchovy and sardine (combined) and proportion of diet comprised of anchovy and sardine, for key predators in the Southern Benguela. Estimates are those from a base-case model developed for 1978, from which dynamic simulations and model fitting has been performed (Lockerbie & Shannon, 2019; Shannon et al., 2020).

		Consumption of anchovy and sardine (tonnes/year)	Combined % anchovy and sardine in the diet of the predators
Seabirds	Cape cormorant	77 000	98%
	African penguins	31 000	79%
	Cape gannet	30 000	58%
Fish	Snoek	Close to 100 000	46%
	Hake	756 000	10-40% depending on size class
	Yellowtail	10 000	30%
	Geelbek	4 000	20%
Cetaceans	Cetaceans	67 000	37%
	Bryde's Whales	7000	Based on Gwen Penry's (pers. comm.) calculations and Best *et al.*'s (1984) diet estimate of around 82 % comprised of small pelagics
Marine mammals	Seals	145 000	30%
Squids	Chokka squid	31 000	3%