

1 Seabird-induced natural mortality of forage fish varies with fish abundance: evidence from 5
2 ecosystems

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27 **Running title:** seabird-induced natural mortality of forage fish

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31

32 **Abstract**

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

50

51 **Keywords:** predator-prey, predator pit, prey entrapment, predation pressure, prey consumption

52 Introduction

53 Natural mortality (M) is an understudied aspect of fish population biology and fisheries
54 science. In most fisheries' stock assessments, natural mortality is modeled as constant or as a
55 function of size to account both for predation pressure and age (Gislason, Daan, Rice, & Pope, 2010).
56 However, a growing number of studies suggests that this assumption is incorrect, and that mortality
57 could be density-dependent, or modulated by the environment (Dutil & Lambert, 2000; Fromentin et
58 al., 2001; Pershing et al., 2015). Because fisheries management often relies on stock assessments
59 which compare fishing mortality (F) to natural mortality, understanding fluctuations in natural
60 mortality is of primary importance. For example, a recent study found up to a 40% difference
61 between estimates of spawning stock biomass (SSB), F and recruitment (R) in cod (*Gadus morhua*)
62 stock assessments, assuming a constant M versus a variable M linked to body condition (Casini, Eero,
63 Carlshamre, & Lövgren, 2016). Here, we are interested in examining to what degree natural mortality
64 rates of forage fish may be influenced by seabirds, which are widely distributed and abundant forage
65 fish predators on all continental shelf ecosystems around the world (Cury et al., 2011). Additionally,
66 On top of potential improvement of stock assessment, clarifying predator-prey functional
67 relationships between forage fish and seabirds will also inform ecosystem-based management
68 research, e.g. by better understanding how seabird diet relies on forage fish (Dickey-Collas et al.,
69 2014; Peck et al., 2014), and the degree to which mass mortality of seabirds from starvation is
70 exacerbated by low forage abundance and competition with large predatory groundfish for shared
71 prey (Piatt et al., 2020).

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

78 upwards of 30-80% of their mass in food daily (Ellis & Gabrielsen, 2002; Furness, 1990). Combined
79 with the fact that seabirds gather to breed in very large colonies in the thousands to millions (Guinet,
80 Jouventin, & Malacamp, 1995), this results in a concentration of high energetic demands in a limited
81 area. As central-place foragers, breeding birds return to breeding sites on land (or occasionally ice) to
82 attend and provision offspring, which concentrates foraging areas closer to breeding locations. As a
83 result, some studies have shown localized prey depletion in proximity to island-based colonies, and
84 this may result in intraspecific competition among birds (Ainley et al., 2003; Birt, Birt, Goulet, Cairns,
85 & Montevecchi, 1987; Lewis, Sherratt, Hamer, & Wanless, 2001; but see Nur & Sydeman, 1999).
86 Additionally, most of the forage fish of importance to seabirds are known to exhibit wide fluctuations
87 in abundance in response to climate (e.g. Lluch-Belda et al., 1992) and are often subjected to high
88 fishing mortality (Hilborn et al., 2017; Schwartzlose et al., 1999). Fish abundance often changes much
89 faster than the abundance of predators, because many forage fish predators, including seabirds,
90 have slower life-history characteristics such as high annual survival and delayed sexual maturity,
91 which buffer their breeding populations from fluctuations in food supply (e.g. Hunt, Furness, & Kerr
92 Building, 1996 and 'canalization hypothesis' Gaillard & Yoccoz, 2003). Thus the relative predation
93 pressure exerted by seabirds should increase with declines in forage fish stocks, except under
94 extreme conditions where adult seabirds are unable to obtain sufficient food for their own
95 maintenance and survival (Cairns, 1988; Crawford et al., 2011; Erikstad, Fauchald, Tveraa, & Steen,
96 1998). Therefore, seabird-induced natural mortality of forage fish could vary strongly with time.

97 If the proportion of a fish stock consumed by predators increases as biomass decreases, the
98 stock in question may become entrapped, whereby populations cannot overcome predation
99 pressures or easily return to previous levels of abundance (Smout, Rindorf, Hammond, Harwood, &
100 Matthiopoulos, 2014). Bakun (2006) theoretically explored the functional responses of predators to
101 biomass variation in small pelagic fish, and suggested that predation pressure should be nil when
102 stocks are collapsed at very low levels of biomass (i.e., "refuge abundance"), but increase
103 substantially when fish biomass reaches a level sufficient for predators to be interested in a

104 population as prey. At low, but not collapsed biomass, Bakun predicted that ‘carnage predation’ may
105 hold the population at a relatively low biomass, and coined the term “predator pit” for this
106 mechanism. Predator pits may be maintained until the forage fish population reaches a level
107 sufficient to satiate predators and grow larger at the same time. The addition of human fishing
108 pressure on small pelagic fish populations has been shown to increase the probability of stock
109 collapse but not the duration of the collapse (Essington et al., 2015). Although fishing pressure after
110 a collapse usually drops, or is even halted due to fisheries management and/or profitability, with no
111 change, maintaining fishing effort at lower biomass would likely exacerbate the duration small
112 pelagics are held in a predator pit. To date fisheries impacts and empirically estimated predation
113 pressure have yet to be jointly addressed.

114 In this paper, we test the hypothesis of predator-pit dynamics for forage fish by examining
115 (1) whether the proportion of forage fish stocks consumed by seabirds increases in response to drops
116 in prey biomass, and (2) whether such increases in seabird-induced forage fish mortality affect forage
117 fish population dynamics. To test this hypothesis, we model non-linear relationships between seabird
118 consumption and fish biomass across five ecosystems, and determine the biomass thresholds at
119 which seabirds might begin to exert top-down control on their prey populations. By determining such
120 thresholds in five different ecosystems, this work also tests the generality of top-down control of
121 seabirds on forage fish and identifies local differences, as suggested in (Peck et al., 2014).

122

123 **Methods**

124 To estimate seabird predation pressure on forage fish, we use long-term data collected in five
125 contrasted ecosystems on: 1) Atlantic puffin *Fratercula arctica* and Atlantic herring *Clupea harengus*
126 at Røst off northwest Norway, 2) Cape gannet *Morus capensis* and sardine *Sardinops sagax* and
127 anchovy *Engraulis encrasicolus* off western South Africa in the Southern Benguela ecosystem, 3)
128 common murre *Uria aalge* and European sprat *Sprattus sprattus* in the Baltic Sea, 4) twelve seabird
129 species and lesser sandeel *Ammodytes marinus* off Shetland and 5) Peruvian booby *Sula variegata*,

130 Peruvian pelican *Pelecanus thagus* and Guanay cormorant *Phalacrocorax bougainvillii* and anchovy
 131 *Engraulis ringens* in the Northern Humboldt ecosystem (Figure 1). While the methodology used (see
 132 below) requires a large number of data and constrains the number of ecosystems on which we could
 133 test the hypothesis, these five ecosystems enabled investigation of predation pressure in contrasted
 134 environments, ranging from productive upwelling regions (Benguela, Humboldt) to the semi-closed
 135 Baltic Sea.

136

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

138 To estimate seabird predation pressure, we combined several processes (estimation of bird numbers
 139 and population structure, bird energy requirements, bird diet and prey energetic values and
 140 abundance) based on a large number of datasets (see similar approaches in Queiros, Fromentin,
 141 Astruc, Bauer, & Saraux, 2018; Van Beveren et al., 2017). In particular, both the quantity consumed
 142 by seabirds and the prey stock size were evaluated. A schematic diagram of the general method used
 143 in this study is represented in Figure 2.

144 The main challenge of this study was to estimate the total quantity of a given prey that is extracted
 145 by seabirds C_t , meaning that all birds extracting prey should be included, i.e. both adults and chicks,
 146 as well as breeders and non-breeders that are present in the area and consume this prey. This was
 147 estimated using the formula below:

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

148 Where

149 1) C_t is the consumption of the given prey (in tonnes). Note that the 1/1000 in the equation is
 150 here only to convert from kg to tonnes.

151 2) P_t (unitless) corresponds to the proportion of the given prey in terms of energy in the diet in
 152 a given year t. Note that in each ecosystem, we assumed P_t to be independent of bird age

153 class (chick and adult diet assumed to be the same) and breeding status (see Supplementary
154 material for more details and justifications).

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

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

157 5) EE (in kJ.d^{-1}) is the daily energy expenditure of the birds. As breeding incurs an additional
158 cost, two distinct DEEs were considered: one for breeding birds DEE_B and one for non-
159 breeders or adults in the non-breeding season DEE_{NB} .

160 6) N_t (in thousands of birds) represents the number of birds present in the area in year t , either
161 breeding $N_{B,t}$ or non-breeding $N_{NB,t}$.

162 7) (in d) is the number of days during which the prey is consumed by the seabird
163 species in the area. Three periods were distinguished: corresponds to the number
164 of days in the breeding season, the duration of the non-breeding season in
165 which breeding birds are present in the colony and finally the duration in which
166 non-breeding birds (immature or birds skipping reproduction) are present in the area. Note
167 that for some ecosystems, birds are migratory and $N_{days_{NB}}$ is zero.

168 8) (in tonnes) corresponds to the consumption in tonnes made by chicks. This was either
169 calculated through energy requirements and DEE (in the Benguela, Humboldt and Shetland),
170 *i.e.* $C_{chick} = \frac{t}{t} * (DEE_{chick} * N_{chick} * N_{days_{chickrearing}})$ or directly from meal
171 size given to the chicks (in Norwegian and Baltic Seas): C

172

173 Once the consumption of a prey is estimated, it needs to be compared to the prey stock biomass to
174 estimate the predation pressure. Fish biomass was estimated either through stock assessment
175 models, or from direct acoustic biomass estimates, depending on the ecosystem (see Table 1 Only in

176 the North Sea (case study Shetland Islands), did natural mortality (M) explicitly include bird
177 consumption. Yet, while predator consumption included that of seabirds and marine mammals, the
178 most important predators of sandeels by far are fish - especially mackerel, herring, cod, haddock,
179 whiting, and gurnard, so that there should be little effect of seabird consumption on M (ICES-HAWG,
180 2020; ICES-WKSand, 2016). Further, stock biomass should represent the entire fish biomass present
181 before seabird consumption occurred. Depending on the timing of stock biomass assessment and
182 seabird consumption phenology, stock biomass had to be corrected. In the Humboldt, the production
183 model estimates the biomass available each month, so that no correction was needed. Similarly, no
184 corrections were applied in the Baltic, where stock assessment refers to the start of spawning (i.e.
185 April), just before seabirds start consuming sprats and in the Norwegian Sea, where stock
186 assessments refer to the first of January, i.e. before the predation events. By contrast, acoustic
187 biomass estimates in the Benguela derive from November acoustic surveys and a stock assessment
188 model in the Shetland estimates biomass on the 1st of July. In both cases, most of seabird
189 consumption occurred beforehand, so that stock biomass was corrected by adding seabird
190 consumption. Finally, the fish biomasses presented here represented annual estimates of the stock,
191 and not fish availability within foraging range of the birds around the colonies, so that we are
192 estimating the predation pressure on the stock and not local prey depletion. However, it has to be
193 noted that in some large ecosystems, regional scales were used (e.g. we considered the southern
194 sub-system of the Benguela, located off South-Africa and not the entire Benguela ecosystem). Spatial
195 scales can be found in Table 1 for each ecosystem.

196 Although the approach was the same everywhere, differences appeared in the estimation of these
197 parameters because of species and ecosystem specificity. For instance, gannets in the Southern
198 Benguela are resident seabirds and consumption outside of the breeding period had to be
199 considered in order to estimate the entire predation pressure they exerted on sardine and anchovy
200 stocks, while migrating Atlantic puffins are present in the eastern Norwegian Sea only for a few
201 months in order to breed.

202 As some seabird data were not always available in each ecosystem, some assumptions had to be
203 made (see summary in Table 1). While these were done to best fit our knowledge of the ecosystem
204 or the species at play, they introduce uncertainty in our estimates of consumption and predation
205 pressure. Nevertheless, we applied the same methodology through time within each ecosystem and
206 among ecosystems. This allowed us to investigate temporal trends and compare among ecosystems,
207 and to identify the magnitude of top-down effects. The main assumptions and parameters are
208 summarized for each ecosystem in Table 1 and details about the specificities as well as monitoring
209 methods are detailed in supplementary material. Note that in the case of the Atlantic puffin in the
210 Norwegian Sea, two different scenarios of consumption were run in the absence of diet data outside
211 the chick-rearing period. The first assumed that puffins consumed herring during the entire time they
212 are present at the colony while the minimum consumption scenario assumed herring consumption
213 only during chick-rearing (see Supplementary material).

214 Predation pressure was then estimated as the percentage of the stock consumed by seabirds,
215 calculated as: $Pred_t = 100 * \frac{C_t}{B_t}$.

216 ***Relationships between consumption and biomass***

217 In order to examine functional responses of seabird diet and aggregated prey consumption C_t to prey
218 biomass, for each relationship we tested a selection of six *a priori* parametric models (null model
219 assuming no link of seabird diet or consumption with prey biomass $y = a$; linear model assuming a
220 constant increase of seabird diet or consumption with fish biomass $y = a * B + b$; second-order
221 polynomial model assuming an optimum fish biomass for seabirds $y = a * B + b * B + c$; as well as
222 exponential, logarithmic and power models which all assume non-linearities and some sort of
223 thresholds above or below which seabirds react differently to prey $y = a * e^{-b*B}$, $y = a * \ln(B) +$
224 b , $y = a * B^b$). When looking at the relationship between seabird aggregated consumption and
225 stock biomass, we also tested two additional models: type II and III functional responses: $C_t = \frac{a*B}{1+b*B}$
226 and $C_t = \frac{a*B}{1+b*B^2}$). Because data in the Shetland were only collected in 3 years, they are only

227 presented as a qualitative indication and no model was performed for this ecosystem. Also, in the
228 Humboldt, no model was performed for the diet data in the absence of annual estimated diet (diet
229 was estimated by period in this ecosystem). All models were fitted using non-linear least square
230 adjustment and the best fit was selected based on the lowest AICc values to avoid over-
231 parameterization (Piatt et al., 2007). When change in AICc ($\Delta AICc$) was less than 2 between the two
232 best models, the more parsimonious model was chosen. All models within a $\Delta AICc$ of 2 are presented
233 along with the null model in Table 2. Once the numerical relationships between stock biomass and
234 the percentage of the stock consumed by seabirds were established, we used a change-point analysis
235 to identify thresholds within non-linear relationships (Andersen, Carstensen, Hernández-García, &
236 Duarte, 2009; Cury et al., 2011). The threshold in biomass was then expressed relatively to the
237 maximum biomass observed in the time-series (i.e. % threshold = $100 * \frac{\text{threshold}}{\text{max biomass}}$).

238

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

240 To investigate whether the predation pressure exerted by seabirds might impact prey dynamics, we
241 examined the correlations between prey biomass and the number of avian predators or the
242 percentage of the stock that was consumed the previous year. Because stock biomass time series are
243 often autocorrelated, residuals were checked for autocorrelation. While autocorrelation was never
244 significant in the Baltic Sea, residuals from the models in the Humboldt and Benguela all displayed
245 positive autocorrelation of order 1 (detected through the pacf function in R). To account for that, a
246 one-year lagged time series of the stock biomass was added as an explanatory variable in the 6
247 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
248 anchovy in the Humboldt). Finally, we also studied the relationship between the change in prey
249 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
250 relationships were not investigated in Shetland due to too few data points and in the Norwegian Sea,
251 where puffins consume age 0 herring that first recruit to the spawning stock at age 3. The

252 relationship between this herring's spawning stock biomass and its recruitment three years later is
253 weak (Sætre, Toresen, & Anker-Nilssen, 2002).

254

255 **Results**

256 ***Diet***

257 The percentage contributions of various prey species to the seabird predators included in our study
258 are shown in Figure 3. For Atlantic puffins from 1982–2006, the contribution by mass of age 0 herring
259 to the diet ($46 \pm 22\%$ [13–89%]) was not significantly related to the biomass of age 0 herring (Figure
260 4a, Table 2). For common murrelets, the mean contribution by mass of sprat to the diet from 2002–
261 2012 was very high and stable across time ($98 \pm 2\%$; range 93–100%), regardless of the biomass of
262 sprat (Figure 4d). In the Humboldt ecosystem, the contribution of anchovy in the diet was usually
263 quite high ($81 \pm 8\%$) but dropped significantly in El-Niño years (55% for cormorants and 58% for
264 boobies and pelicans; Figure 3b). For Cape gannets, the mean contribution by mass of sardine to the
265 diet from 1978–2011 was $30 \pm 19\%$ (range 2–61%) and that of anchovy $28 \pm 16\%$ (range 3–62%;
266 Figure 3e). The average combined contribution of these two prey species to the diet was $58 \pm 14\%$
267 (range 16–77%; Figure 3e). In both cases, the percentage of fish in gannet diet increased with fish
268 stock biomass, although the relationships differed (Table 2; Figure 4e & 4f). Finally, at Shetland the
269 average contribution by mass of sandeel to the diet of 12 seabirds decreased from $88 \pm 4\%$ in 1977
270 and $83 \pm 5\%$ in 1986 to only $45 \pm 10\%$ in 2000 (Figure 3c).

271

272 ***Consumption and proportion of prey stock consumed***

273 The consumption of age 0 herring by Atlantic puffins at Røst (regardless of the scenario used) and the
274 consumption of anchovy by boobies, cormorants and pelicans in the Humboldt ecosystem were not
275 significantly related to the prey stock biomass (Figure 5a & 5b, Table 2). However, consumption of
276 sardine and anchovy by Cape gannets in the southern Benguela ecosystem was significantly
277 positively related to the biomasses of these prey species by a type II functional response (Figure 5e &

278 5f). Similarly, the consumption of sandeels by 12 seabird species at Shetland seemed to increase with
279 the biomass of sandeels (Figure 5c). Finally, the consumption of sprats by common murrens in the
280 Baltic Sea decreased with sprat biomass following a power model (Figure 5d).

281 The predation pressure, as estimated by the percentage of the fish biomass consumed by seabirds,
282 was generally low (median =1% across all years and ecosystems; Figure 6). While this was true in
283 most cases ($\leq 20\%$ in 95% of the cases), the predation pressure increased when fish abundance was
284 low (Figure 6).

285 Further, in four ecosystems (it was not tested for Shetland due to few data points), all relationships
286 were best fitted by power models. While the proportion of the stock consumed remained extremely
287 low in the Baltic Sea (0.5-1.2%; Figure 6d), it increased sharply in other ecosystems once fish biomass
288 decreased below a certain threshold. This threshold was lower than the median biomass observed in
289 the series (Figure 6) and varied between 15 and 18% of the maximum observed prey biomass (15%
290 for herring in the Norwegian Sea regardless of the scenario Figure 6a, 16% for both anchovy and
291 sardine in the Benguela Figure 6e & 6f and 18% for anchovy in the Humboldt Figure 6b).

292

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

294 Autocorrelation in the residuals was positive and of order 1 in all models explaining prey stock
295 biomass, except for the Baltic, where no autocorrelation was detected. Stock biomass at t-1 was thus
296 added as an explanatory variable in the models (except for the Baltic) and had a significant positive
297 effect on prey biomass at t in all relevant models (all $P < 0.009$). In the Humboldt, while prey biomass
298 was positively related to the number of seabirds present at t-1, and negatively to the percentage of
299 the stock consumed by seabirds at t-1, both relationships disappeared after accounting for
300 autocorrelation (Fig. 7 a & d). In the Benguela, the sardine stock biomass was positively related to
301 the number of birds present the previous year (regardless of the autocorrelation, Fig 7c), but not to
302 the percentage of the stock consumed the year before (Fig. 7f). The anchovy stock biomass in the
303 Benguela was not related to either the number of gannets or the proportion of prey consumed by

304 gannets in the previous year (Fig 7c & f). Sprat biomass was negatively related to both the number of
305 murrelets the previous year and the proportion of stock that they consumed (Fig 7b & e).
306 Finally, the change in fish biomass from one year to another was not related to the percentage of the
307 stock consumed the previous year in any of the ecosystems (Figure 7g & 7h & 7i).

308

309 **Discussion**

310 Many studies advocate that seabirds are good bioindicators of marine ecosystems (e.g. Cairns, 1988;
311 Piatt et al., 2007), although an implied assumption and frequent observation is that these
312 ecosystems are regulated by bottom-up processes (Aebischer, Coulson, & Colebrook, 1990;
313 Frederiksen, Edwards, Richardson, Halliday, & Wanless, 2006; Speckman, Piatt, Minto-Vera, &
314 Parrish, 2005). However, aquatic ecosystems are complex and may also be regulated by numerous
315 biological interactions, including predation and competition. For instance, whole-lake experiments
316 showed that trophic cascades could inhibit the response of primary producers to nutrient inputs
317 (Carpenter et al., 2001). The existence of such top-down mechanisms or trophic cascades, which had
318 previously been reported only from terrestrial ecosystems or lakes, has now been demonstrated in
319 marine ecosystems (Ainley, Ballard, & Dugger, 2006), especially after overfishing (Baum & Worm,
320 2009; Casini et al., 2009; Frank, Petrie, Choi, & Leggett, 2005; Österblom, Casini, Olsson, & Bignert,
321 2006). Further studies have proposed that marine ecosystems might be regulated by alternating
322 bottom-up and top-down processes (Cury et al., 2008; Litzow & Ciannelli, 2007), or a “wasp-waist”
323 interaction of the two (Fauchald, Skov, Skern-Mauritzen, Johns, & Tveraa, 2011), and that relative
324 strength of bottom-up and top-down control may vary spatially (Frederiksen, Furness, & Wanless,
325 2007). For example, marine heatwaves can markedly increase metabolic rates and food demands of
326 ectothermic groundfish and trigger temporary top-down control of prey populations and increased
327 competition with seabirds for shared prey (Barbeaux, Holsman, & Zador, 2020; Piatt et al., 2020).

328 Here, we examined one component of top-down processes by estimating the predation
329 pressure exerted by seabirds on forage fish in five different ecosystems. Because this requires a large

330 quantity of data on both seabirds and forage fish, it was necessary to sometimes make assumptions
331 that could have a marked effect on model outcomes. In the Norwegian Sea for instance, due to the
332 absence of diet data outside of the chick-rearing period, we had to consider two extreme scenarios:
333 i.e., either puffins do not eat herring outside the chick-rearing season, or they consume herring
334 during the entire breeding season. The latter scenario (i.e. maximum consumption) yielded some
335 unrealistically high values (>100% of prey stock). However, such outcomes could also result from the
336 uncertainty associated with calculating prey biomass in this ecosystem. Indeed, puffins eat age-0
337 herring, the biomass of which is not directly assessed (see the ESM for more details). Still, we believe
338 the relationships we found likely reflect qualitatively the true relationship (in terms of shape) as we
339 applied our methods consistently between years and between ecosystems but actual estimates
340 under that scenario were less reliable.

341 With respect to seabird diets, we found that different species displayed marked differences
342 in response to fluctuations in prey abundance. Seabird species have different locomotion and
343 foraging strategies which limit the distance that they can forage from colonies, or the depth to which
344 they can feed (e.g. Shealer, 2002). Large seabirds are, for instance, often less vulnerable to prey
345 depletion due to greater travelling capacities and greater energetic efficiencies (Ellis & Gabrielsen,
346 2002; Furness & Tasker, 2000), which might explain the absence of seabird response to prey biomass
347 decrease in the Humboldt system in typical (i.e. non El-Niño) conditions. The non-linear relationships
348 between abundance of sardine and anchovy and the contribution of these species to the diet of Cape
349 gannets off western South Africa suggest that gannets are able to maintain their intake of these
350 species over a wide range of biomass variability. Cape gannets have indeed been shown to be flexible
351 in their foraging effort and duration to track sardines and anchovies, their preferred prey even when
352 abundance decreases or spatial distribution shifts (Green et al., 2015). However, below a certain
353 threshold of prey biomass, gannets were not able to compensate anymore and had to shift their diet
354 towards other prey. Recent research off the south coast of South Africa has shown that in the post-
355 guard stage (>50 days) of chick-rearing, foraging range is extended and gannet diet may differ from

356 that in the guard stage as a consequence of changes either in prey abundance and distribution, or in
357 the energetic requirements of growing offspring (Botha & Pistorius, 2018). A similar relationship was
358 evident for the average proportion of sandeel in the diets of seabirds at the Shetland Islands. Yet,
359 this masks important differences between species, with Arctic skua *Stercorarius parasiticus* and
360 Arctic tern *Sterna paradisaea* maintaining 100% of their sandeel diet in all three periods of study,
361 whereas the sandeel contribution to diet decreased from 70-80% to less than 10% in gannet *Morus*
362 *bassanus*, fulmar *Fulmarus glacialis*, great skua *S. skua* and great black-backed gull *Larus marinus*
363 between 1977 and 2000. Small surface-feeders, such as Arctic terns, are more constrained and, as
364 such, more vulnerable to environmental changes than other species (Baird, 1990; Furness & Tasker,
365 2000; Shealer, 2002). Seabird diet, body size and the ability to switch to other prey when their
366 favored prey is depleted might then be important components of their sensitivity to environmental
367 or fisheries-induced fluctuations in prey.

368 These results highlight the importance of forage fish accessibility for seabirds rather than just
369 abundance. Indeed, a decrease in forage fish stock biomass does not automatically translate into a
370 decrease in forage fish availability or catchability for seabirds, or at least not linearly, due to possible
371 changes in spatial distribution. First, the shoaling behaviour of most forage fish means that
372 predation, like fisheries catches, may be maintained even when prey abundance decreases (in
373 fisheries known as hyperstability of catches, Hilborn & Walters, 1992). For example, as stock biomass
374 decreases, forage fish may concentrate in their most suitable habitat (i.e., the basin hypothesis;
375 MacCall, 1990), resulting in habitat contractions, but no decrease in fish density. In this study, the
376 absence of relationships between seabird diet and forage fish abundance in the Humboldt system
377 was in line with previous works which showed that except in the case of extreme El Niño events,
378 seabird behavior, breeding seasonality and population dynamics were affected by fish accessibility
379 rather than fish abundance (Barbraud et al., 2017; Boyd et al., 2015, 2016, 2017; Passuni et al., 2018,
380 2015). Anchovy spatial distribution was shown to be strongly correlated with oxygen levels
381 (Bertrand, Ballón, & Chaigneau, 2010), so that when the oxycline goes up, anchovies are

382 concentrated close to the surface, where they become accessible to shallow divers such as Peruvian
383 boobies *Sula variegata* and Peruvian pelicans *Pelecanus thagus* (Weimerskirch, Bertrand, Silva, Bost,
384 & Peraltila, 2012). This phenomenon may be apparent also in the Benguela with respect to anchovy
385 accessibility to both purse-seine fishers as well as surface-diving predators, since unpublished
386 evidence suggests that anchovy in recent periods are located closer to the sea bed given reduced
387 stratification (and more homogenous oxygen levels) through the water column (SWG-PEL of
388 Department of Environments, Forestry and Fisheries in South Africa 2019).

389 Our results show that the predation pressure from seabirds, *i.e.* the proportion of the stock
390 consumed by seabirds, was generally low (median = 1% and $\leq 20\%$ of stock size in 95% of cases),
391 confirming that bottom-up processes might be controlling seabird – forage fish interactions most of
392 the time at the population scale. It is important to note that our analyses occurred at a regional or
393 ecosystem scale, so that our results did not consider the potential for local prey depletion (Lewis et
394 al., 2001) or the importance of top-down processes on spatial distribution at a fine scale. The broad
395 scale used in this study might also explain why the estimated predation pressure was lower than that
396 obtained by some previous studies (Furness, 1978). Nonetheless, when prey biomass decreased
397 below a certain threshold (here estimated between 15 and 18% of the maximum biomass depending
398 on the ecosystem and always lower than the median biomass), the predation pressure increased
399 sharply as depicted by power relationships between prey biomass and the percentage of prey
400 biomass consumed by seabirds. While it could not be tested in Shetland due to the small number of
401 years monitored, this held true in the Norwegian Sea, in the Humboldt and in the Benguela. In
402 contrast, the percentage of the sprat stock consumed by common murrelets in the Baltic Sea remained
403 extremely low ($\leq 1.2\%$) throughout the study. This could be explained by the high abundance and
404 small variability in sprat biomass during the study period (Eero, 2012), which in fourteen years did
405 not fall below 54% of its maximum value (a value well above the 15% threshold detected in other
406 ecosystems). An increase in the proportion of prey that is consumed by predators when prey
407 abundance is low was not unexpected, because predators need to satisfy their food requirements

408 (Bakun, 2006) and even though some are able to switch their diet to alternative food sources, they
409 may preferentially target energetically-rewarding prey (Adams & Klages, 2010). Due to different life-
410 histories between short-lived prey and long-lived predators, and the canalization of seabird adult
411 survival, *i.e.* the key parameter buffering their population dynamics against temporal fluctuations
412 (Gaillard & Yoccoz, 2003), the number of seabirds can still be high after a decrease in prey biomass,
413 maintaining prey consumption at high levels. In some exceptional cases, the predation pressure we
414 estimated became extremely high, such as in the Norwegian Sea, where this most likely reflected
415 unrealistic survival rates for herring in the modelling for some of the poorest years (cf. ICES, 2012
416 and Supplementary material for further details).

417 A rapid rise in the proportion of forage fish consumed, *i.e.* in predation mortality, once
418 forage fish have been depleted below a certain threshold of abundance, might result in their
419 entrapment in a predator pit (Bakun, 2006). This effect would be exacerbated if proportions of those
420 prey taken by other predators in the ecosystem (*e.g.* other seabirds, seals, cetaceans, predatory fish,
421 see Table S1) increase similarly and fishing mortality is also high. For several fish stocks in the North-
422 West Atlantic, including Atlantic herring, chub mackerel *Scomber colias*, haddock *Melanogrammus*
423 *aeglefinus* and silver hake *Merluccius bilinearis*, empirical evidence suggested that recruitment
424 remained poor when stocks were reduced to 10% of pristine levels, but that good year-classes were
425 experienced, and stock rebuilding took place when biomass was above about 20% of peak levels of
426 abundance (Brown, Anthony, Anderson, Hennemuth, & Sherman, 1983). Here, we found that
427 predation pressure increased sharply when the stock biomass decreased below 15 to 18% of its
428 maximum abundance. These observations raise the question as to whether such predation pressure
429 might constrain prey stocks and keep them at very low levels.

430 First, positive correlations between prey biomass and the number of seabirds the year before
431 were highlighted in both the Benguela and Humboldt ecosystems. While this might appear
432 surprising, it could be due to temporal autocorrelation in prey biomass time series, *i.e.* the fact that a
433 high prey biomass in a given year is likely to be followed by another high prey biomass the next year

434 and vice versa (Fréon, Cury, Shannon, & Roy, 2005). If the ecosystem is indeed under bottom-up
435 control, or both prey and predators react the same way to other external variables, then both would
436 endure similar favourable or unfavourable periods, explaining the positive relationship between prey
437 at $t+1$ and predator at t . Indeed, a partial temporal autocorrelation of lag 1 was present in the
438 residuals of the models in the Benguela and the Humboldt. Once we removed the autocorrelation by
439 adding a one-year lagged time series of the prey biomass as a covariate in the model, both
440 relationships between prey biomass and predator abundance or consumption disappeared in the
441 Humboldt. Further, a negative temporal correlation of predator and prey abundance, despite being
442 the most commonly used approach to investigate predation (e.g. Frank et al., 2005; Worm & Myers,
443 2003), does not allow one to distinguish between predators driving prey dynamics and both
444 populations responding in opposite directions to an external environmental driver (Hunt &
445 McKinnell, 2006; Oken & Essington, 2015). When looking at the effect of the predation pressure,
446 instead of the number of predators, on the prey biomass a year later, no relationship was detected in
447 the Humboldt or Benguela ecosystems. In contrast, a significant negative relationship between prey
448 biomass and the number of birds or the percentage of the stock consumed by seabirds the year
449 before was found in the Baltic Sea. Given the very low predation pressure (<1.2%) estimated in this
450 ecosystem, we suggest that this might be due to a spurious correlation, perhaps attributable to a
451 third variable to which sprat and murre might react differently. Finally, looking at how predation
452 pressure affects the change in prey biomass from one year to another, rather than the absolute value
453 of biomass, should remove the variance explained by temporal autocorrelation and enable an
454 investigation of the immediate effects of predation, whereas the effect on absolute biomass might
455 be delayed (Oken & Essington, 2015). Importantly, no relationships were highlighted between these
456 two variables, suggesting that seabird predation pressure did not drive changes in forage fish
457 abundance.

458 However, it should be borne in mind that we only estimated a portion, often small (e.g.
459 Shannon, Christensen, & Walters, 2004), of the overall natural mortality, as consumption by other

460 predators present in the area (large predatory fish, marine mammals, other seabirds) was not
461 included. Further, predators do not target the entire population, but rather focus on given length- (or
462 age-) classes, making the effect of predation harder to detect (Oken & Essington, 2015). Hence, in
463 years when prey biomass is low and corresponding seabird consumption requires a significant part of
464 the forage fish stock, strong competition might arise between predators and fisheries. During such
465 intense competition, as created in the North Pacific by the massive biennial fluctuations in predatory
466 adult pink salmon (Ruggerone, Springer, Shaul, & van Vliet, 2019; Springer & Van Vliet, 2014) or
467 during the 2014-2016 marine heatwave when all forage fish stocks crashed simultaneously (Jones et
468 al., 2018; Piatt et al., 2020; von Biela et al., 2019), it is increasingly apparent that seabirds may take
469 the brunt of competitive displacement from food supplies (e.g. 10-20% of the NE Pacific population
470 of common murrens died en masse from starvation during the heatwave; Piatt et al., 2020). In the
471 California current, seabirds whose diet is mainly forage fish, especially anchovy, respond negatively
472 to forage fisheries (Koehn et al., 2017). While economic consequences of fishing forage fish are
473 unclear for piscivorous fisheries (Engelhard et al., 2014), the impact on conservation of seabirds and
474 marine mammals might tip the scales towards keeping forage fish at sea being more valuable than
475 fishing them out (Koehn et al., 2017). Many seabirds have an unfavourable conservation status.
476 Seabirds are more threatened, and declining faster, than other groups of birds (Dias et al., 2019). For
477 example, nine of 15 seabird species (60%) that breed in the Benguela ecosystem are classified, in
478 terms of criteria of the International Union for the Conservation of Nature (IUCN), as Endangered,
479 Vulnerable or Near-threatened; these include three that feed mainly on sardine and anchovy,
480 whereas several seabirds that do not compete with fisheries for food have a Red List status of Least
481 Concern (Crawford, 2013; IUCN, 2019). Cury et al. (2011) identified a threshold of approximately
482 one-third of maximum prey biomass below which seabird breeding success was consistently reduced
483 and more variable. Similarly, when the biomass of sardine spawners fell below c. 25% of its maximum
484 observed value, survival of adult African penguins *Spheniscus demersus* decreased markedly
485 (Robinson, Butterworth, & Plagányi, 2015) and survival and numbers breeding decreased for three

486 Benguela seabirds when a forage availability index reached low values (Crawford, Sydeman,
487 Thompson, Sherley, & Makhado, 2019). There may be a still lower ecological threshold (15 to 18%
488 according to our study) where prey species, or at least spatial components of prey stocks (e.g. west
489 coast vs. south coast in the Benguela), suffer high rates of natural and fishing mortality. Interestingly,
490 20% of maximum biomass is often used in fishery management as a limit biomass (B_{lim}) below which
491 a stock should not fall or a recovery plan should be put in place. Here, we confirm a similar threshold
492 and advise fishery managers to exercise due care in allocating allowable catches or fishing licenses,
493 *etc.* at low levels of abundance.

494 To conclude, our study is important as it contributes to the growing literature in support of
495 an ecosystem approach to fisheries (EAF; Dickey-Collas et al., 2014; Hill et al., 2020; Koehn et al.,
496 2017; Pikitch et al., 2004). While top-down processes due to predation of forage fish by seabirds did
497 not seem to control forage fish dynamics in any of the five ecosystems we considered, the predation
498 pressure sometimes attained high levels, which signals the need for fisheries management to
499 account for ecosystem constraints when setting catch limits in periods of low forage fish biomass.
500 Finally, our results (and in particular the differences of sensitivity of seabird diet to prey biomass
501 among species) also suggest that forage fish accessibility might be more important than forage fish
502 abundance depending on the ecophysiological constraints that apply to seabirds (e.g. depth to which
503 they can dive). As a consequence, fish stock management should not only ensure a safe level of fish
504 biomass for the stock to be sustainable and the predators to feed (Cury et al., 2011), but also focus
505 on safeguarding predator foraging grounds. Measures such as spatial enclosure around breeding
506 sites have for instance been used in different areas (see (Sydeman et al., 2017) for more on the
507 subject). Spatial planning is thus an extremely important component of human activity (and
508 especially fishery) management in order to safeguard all components of the ecosystem.

509

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528 **Data Availability Statement**

529 Should the manuscript be accepted for publication in Fish and Fisheries, the dataset would be made
530 available through a public website such as figshare or dryad.

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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) $FMR_B = 1.84 \text{ kJ.g}^{-1}.\text{d}^{-1}$ (Ellis & Gabrielsen, 2002) $DEE_{NB} = 2.25 * BMR = 745.2 \text{ kJ.d}^{-1}$ (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) $Nbdays_B = 152 \text{ d}$ $Nbdays_{NB} = 0$ $Nbdays_{col} = Nbdays_B$	Meal size = $108 \text{ g.chick}^{-1}.\text{day}^{-1}$, (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)

<p>Cape gannet in the southern Benguela</p>	<p>Chick=Adult diet Annual values (average from all months and 2 localities) (Crawford et al., 2019)</p>	<p>0.74 (Crawford, Ryan, & Williams, 1991)</p>	<p>8.59 and 6.74 kJ.g^{-1} for sardine and anchovy respectively (Batchelor & Ross, 1984)</p>	<p>$DEE_B = 3380 \text{ kJ.d}^{-1}$ $DEE_{NB} = 2767 \text{ kJ.d}^{-1}$ (Adams, Abrams, Siegfried, Nagy, & Kaplan, 1991; Berruti, Underhill, Shelton, Moloney, & Crawford, 1993)</p>	<p>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)</p>	<p>$Nbdays_B = 165.$ $Nbdays_{NB} = 140$ $Nbdays_{col}$ dependent on age-class (Jarvis, 1974)</p>	<p>Nb of chicks = nb of breeding pairs * 0.45 $DEE_{chick} = 2236 \text{ kJ.d}^{-1}$ (Cooper, 1978) $Nbdays_{chick} = 97$ (Jarvis, 1974)</p>	<p>Spawning stock biomass West of Cape Agulhas Estimated based on hydro-acoustic surveys (Augustyn et al., 2018; Coetzee et al., 2008)</p>
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<p>Common murre in the Baltic Sea</p>	<p>Chick = adult diet</p> <p>Annual values (Kadin, Österblom, Hentati-Sundberg, & Olsson, 2012)</p>	<p>0.78(Hilton, Furness, & Houston, 2000)</p>	<p>5.46 kJ.g⁻¹ (Enekvist, 2003)</p>	<p>DEE_B = 1530 kJ.d⁻¹</p> <p>DEE_{NB} = 1392 kJ.d⁻¹ (Roth, Nur, Warzybok, & Sydeman, 2008)</p>	<p>Entire Baltic Sea population</p> <p>$N_{B,t} = 100/65 * N_{B,t}$ at Stora Karlsö (Olsson & Hentati-Sundberg, 2017) from annual counts at Stora Karlsö</p> <p>$N_{NB,t} = 0.5 * N_{B,t}$</p>	<p>$Nbdays_B = 90$ (Hedgren, 1975)</p> <p>$Nbdays_{NB} = 275$</p> <p>$Nbdays_{col} = 365$</p>	<p>Meal size = $4 * 10.26 = 41$ g.chick⁻¹.day⁻¹, (Enekvist, 2003; Kadin et al., 2012)</p> <p>Nb of chicks = annual breeding success * nb of breeding pairs (Kadin et al., 2012)</p> <p>Nb of days = 18d (Kadin, Olsson, Hentati-Sundberg, Ehrning, & Blenckner, 2016)</p>	<p>Spawning Stock biomass</p> <p>Entire baltic Sea</p> <p>Estimated through XSA using acoustics and landings as inputs (ICES, 2018)</p>
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<p>Shetland Islands</p>	<p>Chick = adult diet</p> <p>Period values (Furness, 1990; Furness & Tasker, 2000; Martin, 1989)</p>	<p>0.80 (Hilton et al., 2000)</p>	<p>6 kJ.g⁻¹ (Pedersen & Hislop, 2001)</p>	<p>DEE_B estimated from allometric equations per order</p> <p>DEE_{NB} = 2.25 BMR</p> <p>(Ellis & Gabrielsen, 2002)</p>	<p>Shetland populations</p> <p>N_{B,t} estimated from counts (Mitchell, Newton, Ratcliffe, & Dunn, 2004; Walsh et al., 1995)</p> <p>N_{NB,t} = 25% of breeding birds</p>	<p><i>Nbdays_B</i> for each species (122d for great skua, 106 for arctic skua, common murre and razorbill, 78 arctic tern, 108 puffin, 136 kittiwake, great blacked-back gull, black guillemot, fulmar, shag and gannet) (Furness, 1990)</p> <p><i>Nbdays_{NB}</i> = 0</p> <p><i>Nbdays_{col}</i> = <i>Nbdays_B</i></p>	<p>Nb of chicks = Breeding success * nb of breeding pairs</p> <p>DEE from the same equation as non-breeding adult with M_{chick} = 0.5 M_{adult}</p> <p>Nb of days = chick-rearing duration</p>	<p>Total biomass</p> <p>Shetland stock</p> <p>Estimated from VPA using landings and experimental trawl surveys as inputs</p>
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<p>Northern Humboldt</p>	<p>Chick = adult diet</p> <p>Period values (Goya, 2000; Jahncke, Checkley, & Hunt, 2004)</p>	<p>0.75 (Dunn, 1975; Laugksch & Duffy, 1984)</p>	<p>6.37 kJ.g⁻¹ (Cooper, 1978; Laugksch & Duffy, 1984)</p>	<p>DEE_B estimated from allometric equations of pelecaniform</p> <p>DEE_{NB} = 2.25 BMR</p> <p>(Ellis & Gabrielsen, 2002)</p>	<p>Entire Northern Humboldt populations (31 islands)</p> <p>Monthly counts of total number of birds.</p> <p>N_{B, t} and N_{NB, t} derived from monthly average proportions of breeders vs non-breeders based on the 2003-2014 observations.</p>	<p>$Nbdays_{col} = 365.$</p>	<p>DEE from the same equation as non-breeding adult with $M_{chick} = 0.5 M_{adult}$</p> <p>Nb chick = brood size * nb of breeding pairs</p> <p>Duration: 86d, 133d and 110d for cormorant, booby and pelican</p>	<p>Production biomass</p> <p>Northern Humboldt (7-18°S) from the coast to 100km offshore</p> <p>Estimated from acoustic estimates and monthly length structure (Oliveros-Ramos & Peña, 2011)</p>
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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			

		null	589.5	86.5	
		Power	230.9	0	
		Logarithmic	231.1	0.2	
	Baltic Sea – Murres - Sprats	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	48
		Linear	1374.9	0.5	
		Null	1375.6	1.2	
		Exponential	1375.6	1.2	
		Type III functional response	1376.46	2.0	
		Power	196.9	0	
	Norwegian Sea – Puffins – Age 0 herring	null	218.6	21.7	22
		Power	135.8	0	
	Benguela – Gannets - Sardines	null	155.0	19.2	31
		Power	39.2	0	
	Benguela – Gannets - Anchovies	null	74.3	35.2	31
		Power	-22.7	0	
	Baltic Sea – Murres - Sprats	Exponential	-21.6	1.1	14
		null	1.2	25.3	
		Power	209.1	0	
	Humboldt – All 3 species - Anchovies	null	254.7	45.6	48

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 ($\Delta AICc \leq 2$) 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 \pm 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. $\Delta\text{AIC} \leq 2$) 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. $\Delta\text{AIC} \leq 2$) 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. $\Delta AIC \leq 2$) 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 where seabirds were not monitored on an annual basis.

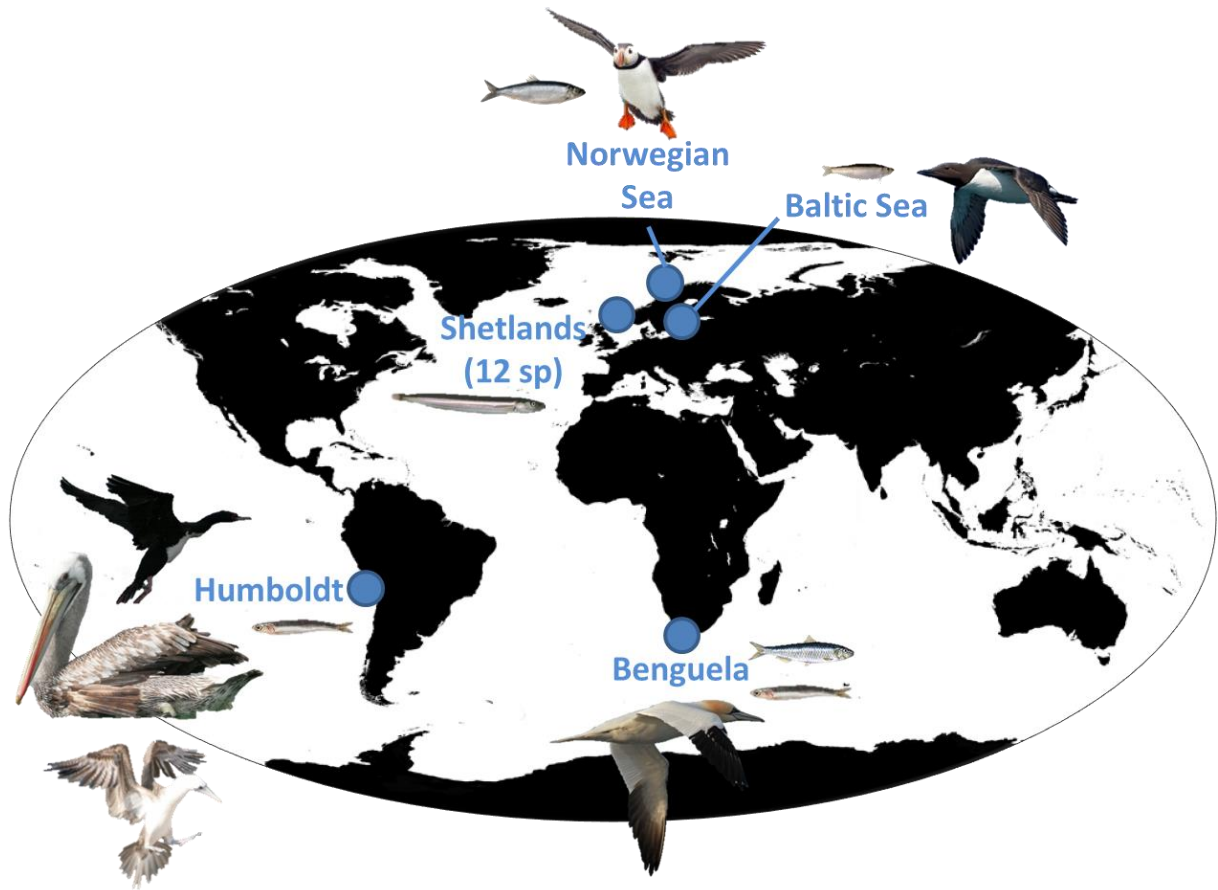


Figure 1.

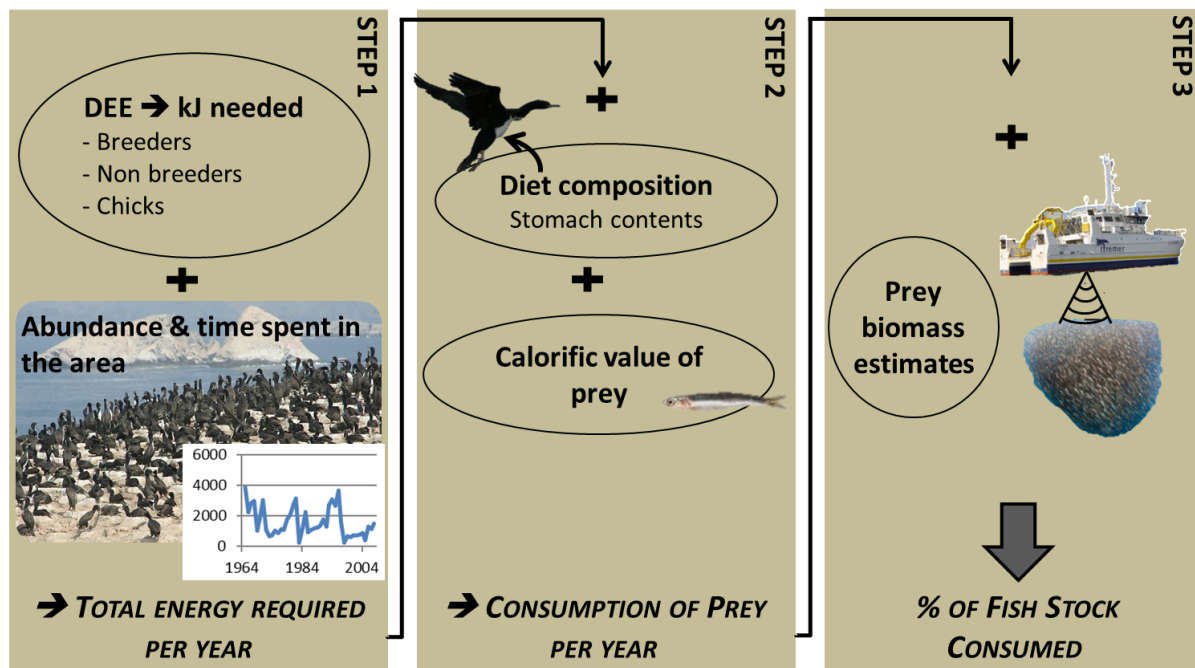


Figure 2.

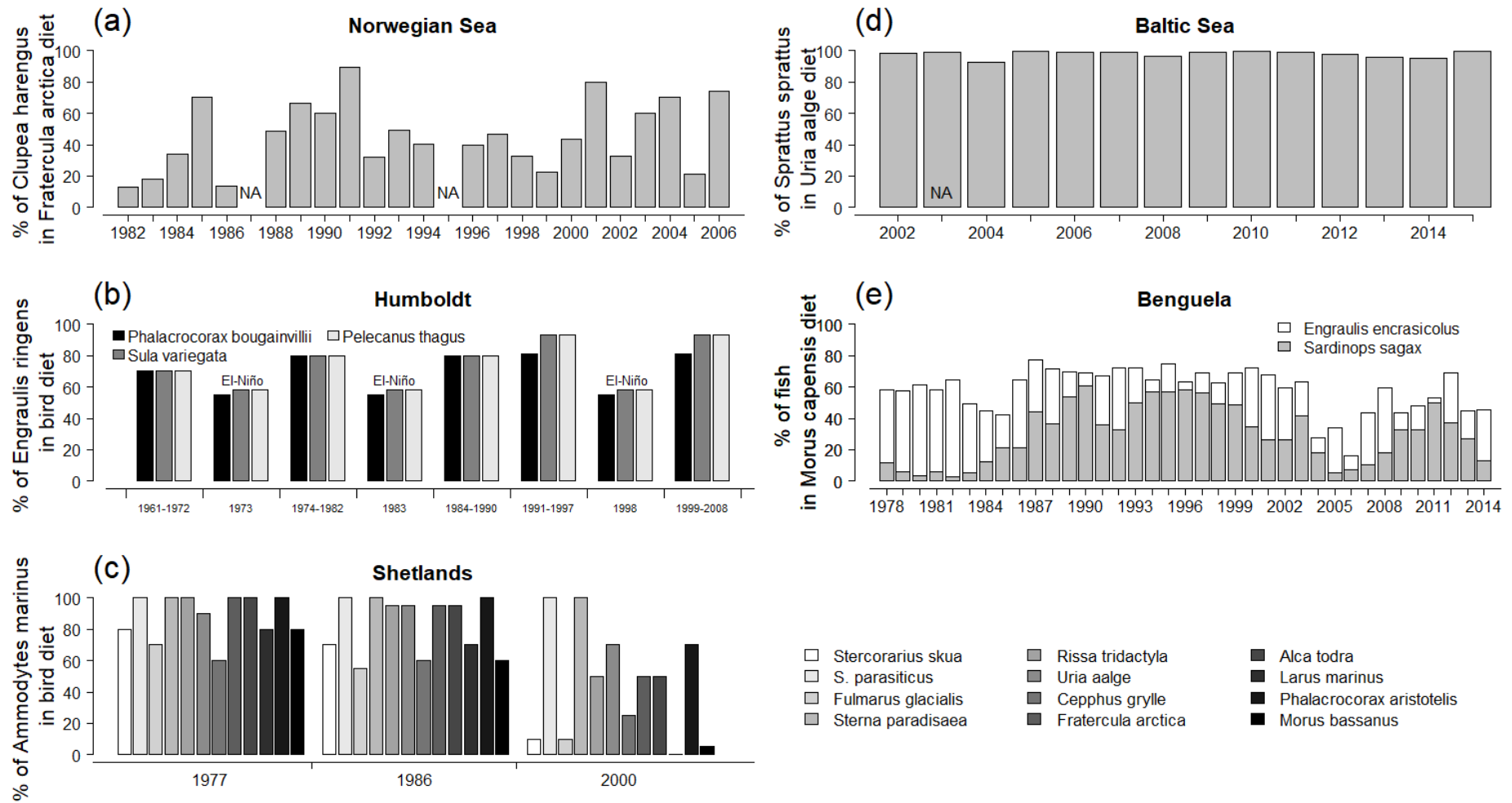


Fig 3

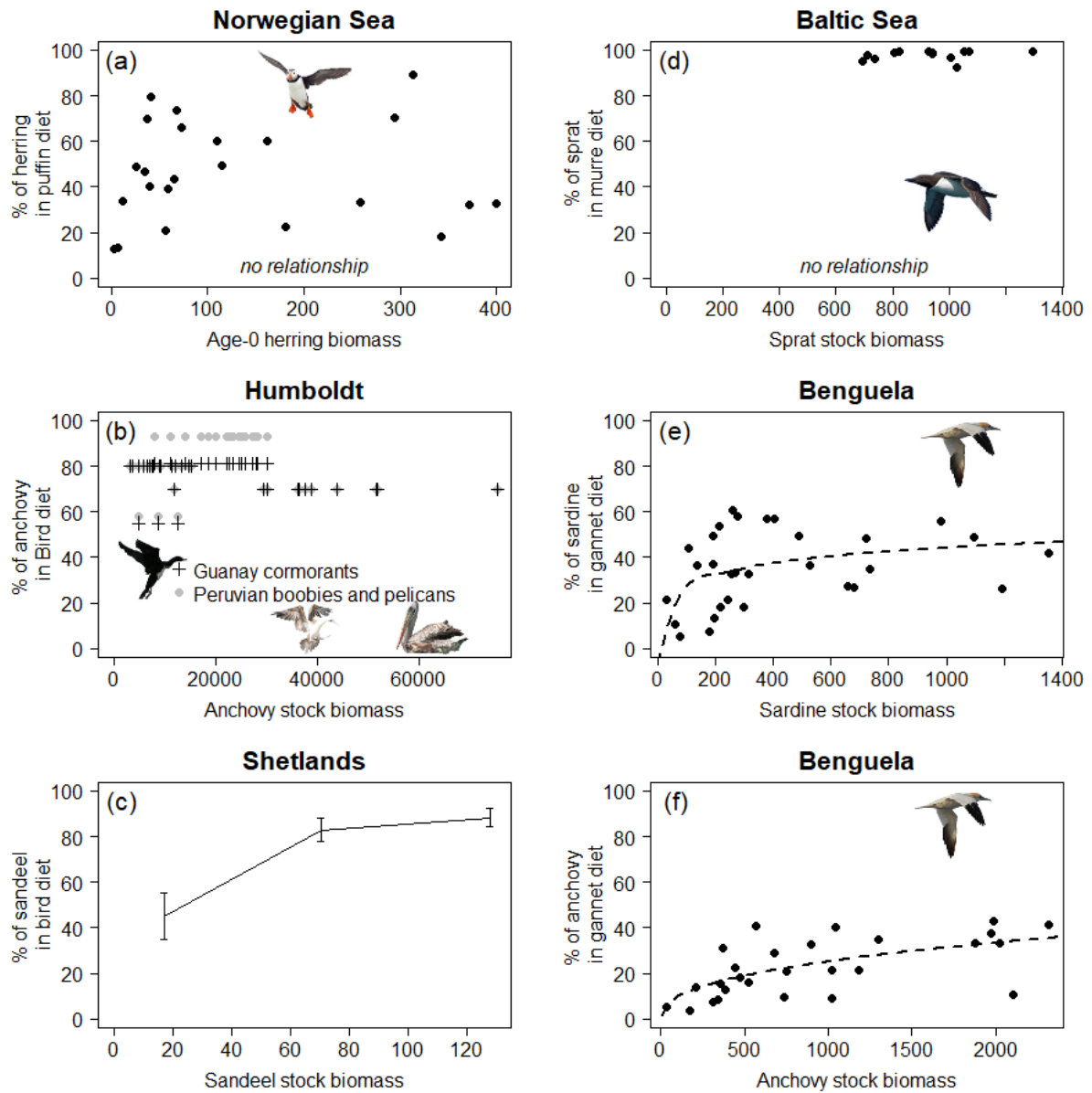


Figure 4

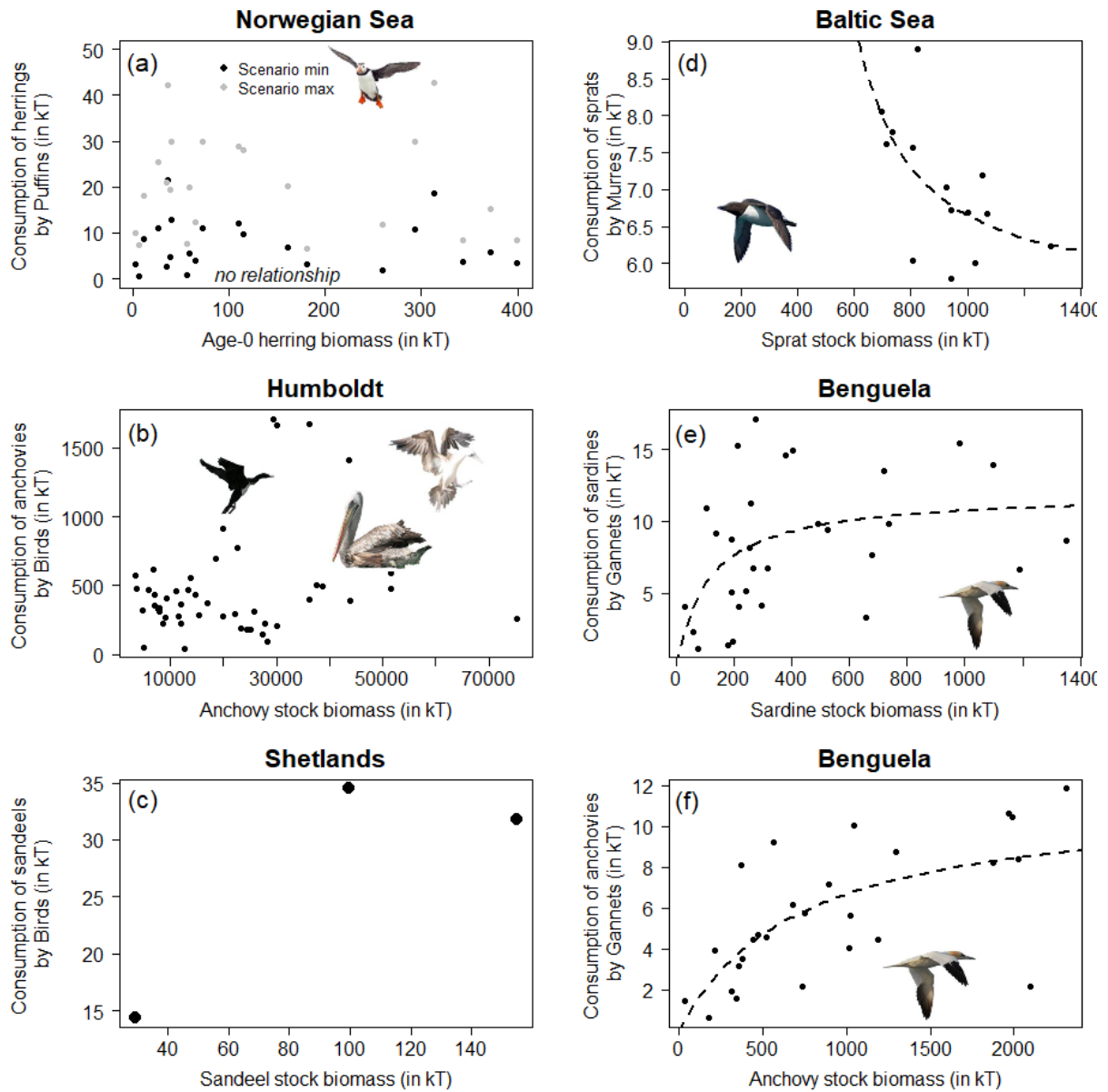


Figure 5

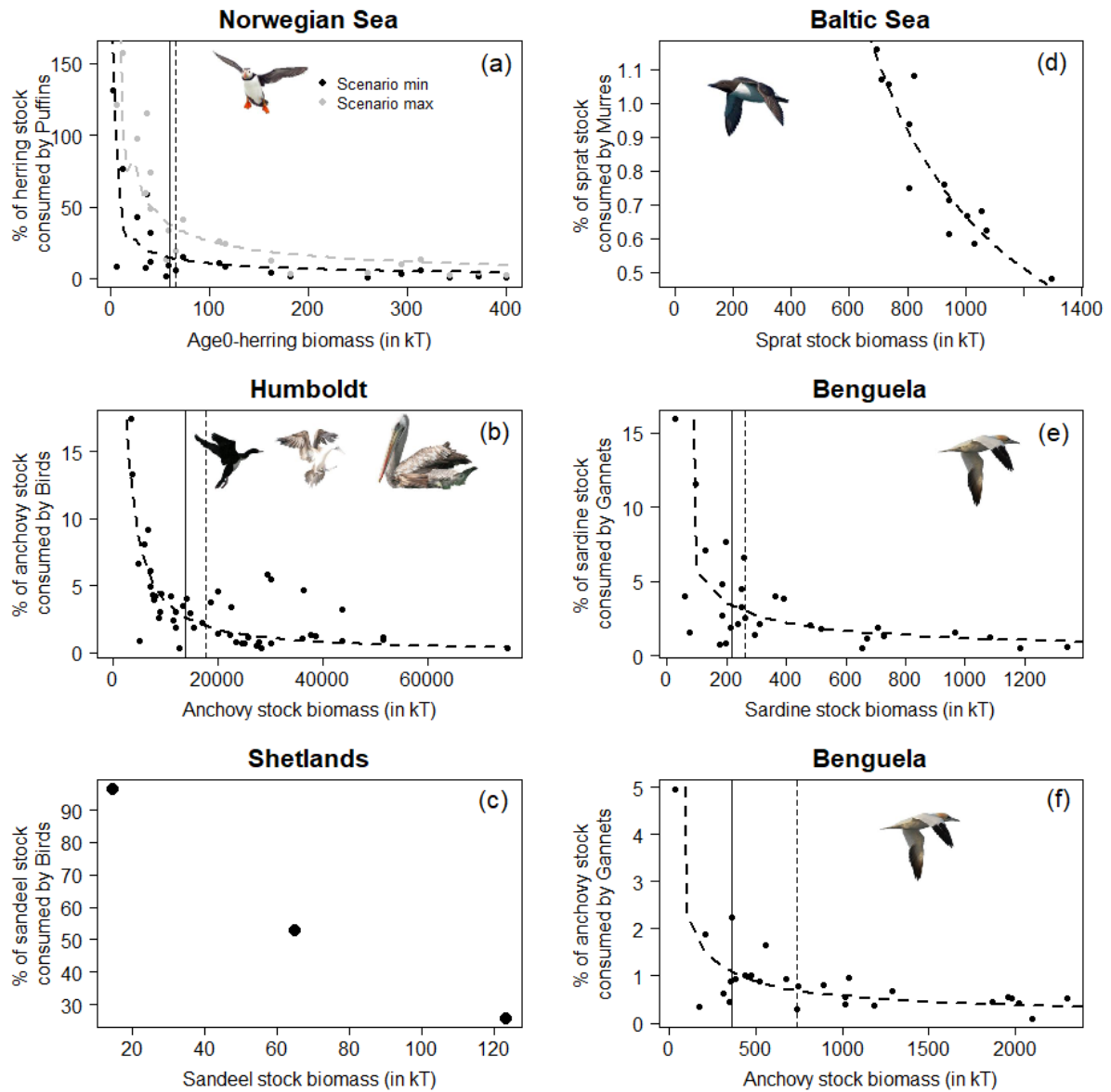


Figure 6

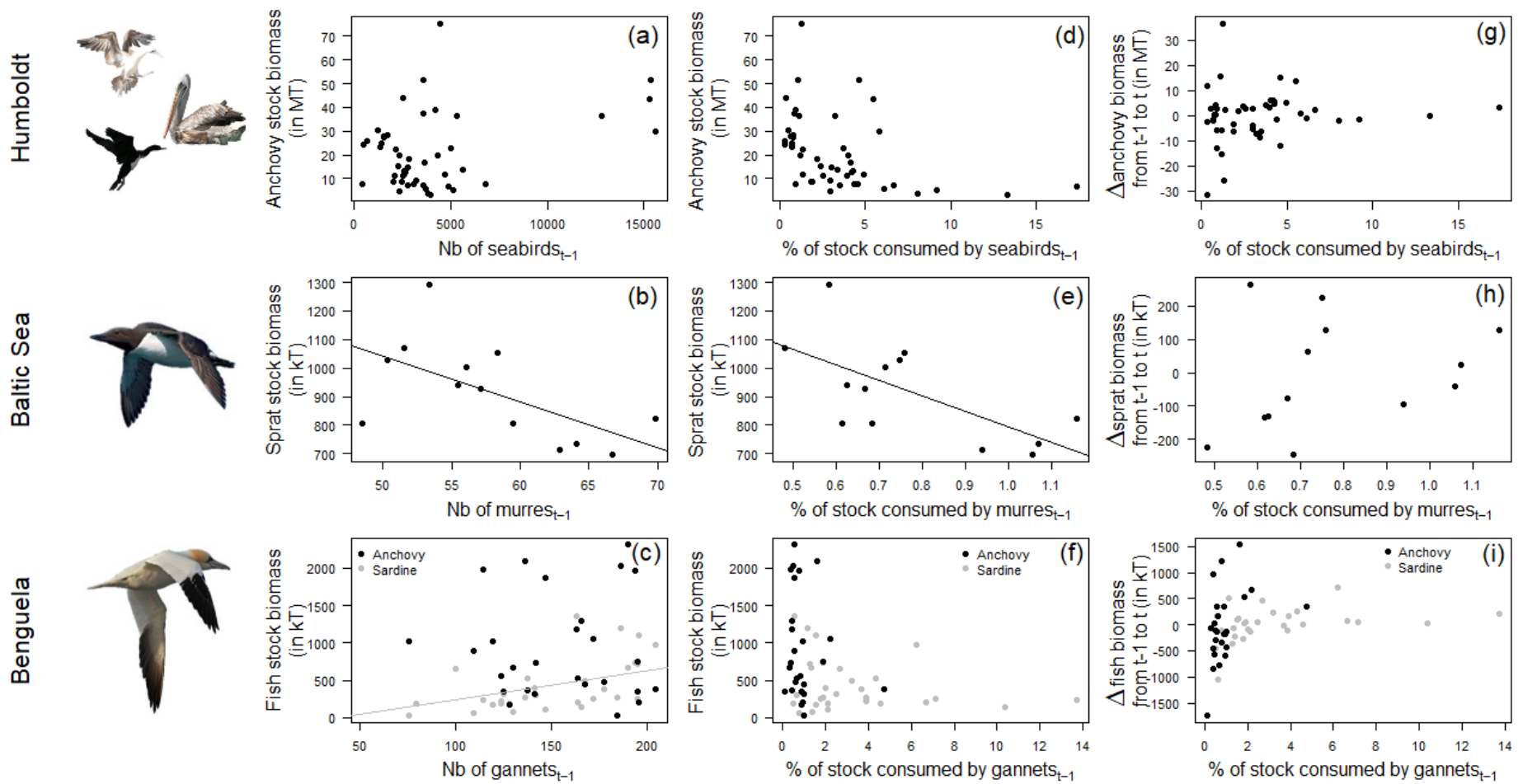


Figure 7

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

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

32 As puffins are present on Røst only during the breeding season, $Nbdays_{NB}$ was considered to be null
33 and $Nbdays_{col} = Nbdays_B$. Further, age 0 herring are known to be a key prey for these puffins
34 during the chick-rearing period (Albertsen, 1996; Anker-Nilssen, 1992; Anker-Nilssen & Aarvak,
35 2006). However, little data on diet is available outside this time window. Due to this uncertainty, we
36 considered a precautionary approach based on the use of two extreme scenarios, where the number
37 of days spent in the colony feeding on age 0-herring was minimum and maximum, in order to have a
38 range of consumption estimation. First, in the minimum consumption scenario, the period
39 considered was restricted to chick-rearing, so that $Nbdays_{NB} = 0$ and $Nbdays_{col} = Nbdays_B =$
40 $Nbdays_{chickrearing}$. The duration of the chick-rearing period varied from year to year, and was thus
41 estimated annually. The second scenario considered the maximum time spent by puffins in the area.
42 Indeed, although no diet study confirmed a direct link, some indications of the impact of age 0
43 herring abundance on puffin condition prior to egg-laying have been highlighted (Barrett, Anker-
44 Nilssen, Gabrielsen, & Chapdelaine, 2002; Barrett, Nilsen, & Anker-Nilssen, 2012). In order to account
45 for this pre-laying period, the calculation started from 1st of May. Then a few studies also support the
46 assumption of herring consumption beyond the breeding season (see (Gimenez, Anker-Nilssen, &
47 Grosbois, 2012) for the effect of age 0 herring abundance on adult survival and (Anker-Nilssen &
48 Aarvak, 2009; Fayet et al., 2017) on post-breeding movements by telemetry and geolocators). The
49 calculation thus included August and September, so that the entire duration was set to 152 days.
50 Chick's consumption was calculated directly from meal size and feeding rates ($108 \text{ g.chick}^{-1}.\text{day}^{-1}$;
51 Øyan & Anker-Nilssen, 1996) and the annual number of chicks estimated through counts of active
52 nests.

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

68

69 ***Cape gannet in the southern Benguela ecosystem***

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

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

79 saury 6.20, hakes 4.07 and other 5.60 kJ.g^{-1}). Details on the sampling method can be found in
80 (Crawford et al., 2019). The assimilation efficiency was set at 74% according to a previous study
81 (Crawford, Ryan, & Williams, 1991). The daily energy expenditure of a breeding Cape gannet (DEE_B) is
82 3380 kJ.d^{-1} (N. J. Adams, Abrams, Siegfried, Nagy, & Kaplan, 1991; Ellis & Gabrielsen, 2002). That for a
83 non-breeding Cape gannet (DEE_{NB}) was taken to be 2767 kJ.d^{-1} based on a similar contribution of prey
84 species to the diet but an 18% smaller meal size for non-breeding than breeding Cape gannets at
85 Malgas Island (Berruti et al., 1993).

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

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

100 Finally, chick number was estimated through the number of breeding pairs and breeding success.
101 Over 17 seasons at Lambert's Bay and 22 at Malgas Island between 1988 and 2010 Cape gannets had
102 a mean annual breeding success of 0.45 chicks per pair (Cury et al., 2011). Chicks spend on average
103 97 days at nests before fledging (Jarvis, 1974). The average daily energy requirement of chicks that
104 fledge is 2236 kJ.d^{-1} (Cooper, 1978).

105

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

112

113 ***Common murre in the Baltic Sea***

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

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

131 The population of common murrelets in the Baltic Sea was 13 000–17 000 pairs, of which approximately
132 65% breed at Stora Karlsö (Olsson & Hentati-Sundberg, 2017). Numbers of pairs breeding at Stora
133 Karlsö were estimated annually during 2002–2015 based on direct observations. These numbers
134 were doubled and multiplied by 100/65 to estimate the total number of common murrelets breeding in
135 the Baltic Sea in year t ($N_{B,t}$). We assumed that the number of non-breeders in the population was
136 equivalent to 50% of numbers breeding (i.e. 1/3 of the entire population), based on observations at
137 the Stora Karlsö colony and unpublished modeling results that indicate a high pre-breeding survival
138 and a high proportion of non-breeding birds in the population. The length of the breeding season
139 was set to 90 days, representing the period from the stabilization of the presence of the breeding
140 population in late April to the departure in mid-late July (Hedgren, 1975).

141 Regarding chick consumption, it was estimated using a combination of number of chicks, number of
142 days feeding, number of feeding events per day and chick meal size. The number of chicks was
143 estimated based on annual monitoring of breeding success, which varied between 0.67 and 0.86
144 (Kadin et al., 2012; updated), and the number of breeding pairs. Data were not available for 2002 –
145 2004, so for these years the average for the whole time series 2005 – 2015 was used. The number of
146 days during which chicks are fed was set to 18 d (Kadin, Olsson, Hentati-Sundberg, Ehrning, &
147 Blenckner, 2016), while the meal size was estimated from the number of fish fed per day (4; Kadin et
148 al., 2012) and the average weight of fish fed (0.01026kg; Enekvist, 2003).

149
150 We used estimates of sprat biomass for the entire Baltic Sea as determined by ICES (International
151 Council for the Exploration of the Seas) through XSA (Extended Survival Analysis) which uses a
152 combination of reported landings and acoustic surveys as input data (ICES, 2018). In this model, M is
153 calculated through a model (SMS, Stochastic Multi-Species model) using cod predation as time-
154 varying factor. Seabirds are not included in the M estimate. Because bird consumption is so low in
155 this ecosystem, using fisherman catch or fisherman + seabird catch in the catch equation should not

156 change any result in biomass estimates ($C_t = 7021 \pm 891$ vs. Catches = 326,200 \pm 62,682 tonnes, *i.e.*
157 46 times less consumption than catches).

158

159 ***Seabirds at Shetland***

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

167 Diet composition data were collected either as voluntary regurgitates by chicks or adults handled for
168 ringing (great skua, Arctic skua, northern fulmar, black-legged kittiwake, northern gannet and shag),
169 or as cast pellets found near nests (great skua, great black-backed gull and shag), or as fish observed
170 or photographed being carried by adults or sampled from birds caught by mist net, hand net, or
171 noose and pole (Arctic tern, common murre, black guillemot, razorbill and Atlantic puffin). Diet
172 sampling was primarily conducted at Foula, where samples were obtained annually from 1975 to
173 2004, except for gannets which were sampled only in a few years from Hermaness. Data on gannet
174 diet from (Martin, 1989) were included to supplement unpublished data on gannet diet collected
175 during ringing at the Hermaness colony. Diet sampling spanned both the incubation and chick-rearing
176 periods, but with larger numbers of samples during chick-rearing. Because sample sizes in individual
177 years were not always large and because comprehensive seabird population censuses were only
178 available for three time periods, for estimation of sandeel consumption diet, data were amalgamated
179 for the periods 1975–1983, 1984–1989 and 2000–2004 and related to population sizes in 1977, 1986
180 and 2000. Diet data for 1975–1983 were previously reported in (Furness, 1990) and for 1990–1996 in
181 (Furness & Tasker, 2000). We assumed the proportion in terms of energy to be the same as the

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

186 An assimilation efficiency of 80% was assumed (Hilton et al., 2000), and a calorific content of 6 kJ.g^{-1}
187 for sandeels (Pedersen & Hislop, 2001). Daily energy expenditure of breeding birds was estimated
188 from data on body mass presented in (Furness, 1990) and the bioenergetics equations of (Ellis &
189 Gabrielsen, 2002) estimating field metabolic rate of breeding birds for each order (i.e. $DEE =$
190 $11.49 * m^{0.718}$ for charadriiforms, $DEE = 22.06 * m^{0.594}$ for procellariiforms and $DEE = 3.9 * m^{0.871}$ for
191 pelecaniforms). Similarly, DEE_{NB} was estimated as 2.25 times the basal metabolic rate (BMR),
192 where BMR was estimated through allometric equations per order according to (Ellis & Gabrielsen,
193 2002) (i.e. $BMR = 2.149 * m^{0.804}$ for charadriiforms, $BMR = 2.763 * m^{0.726}$ for procellariiforms and $BMR =$
194 $1.392 * m^{0.823}$ for pelecaniforms).

195

196 Numbers of each seabird species breeding at Shetland were taken from surveys using standard
197 census methods (Mitchell, Newton, Ratcliffe, & Dunn, 2004; Walsh et al., 1995). Data were converted
198 from census units to equivalent numbers of breeding pairs (Mitchell et al., 2004), and tabulated for
199 1977, 1986, and 2000. Additionally, we assumed that non-breeders (i.e. immature birds and mature
200 adults that skip reproduction) represented a further addition of 25% to the breeders.

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

206

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

212

213 Estimates of Shetland sandeel total stock biomass on 1st of July each year were obtained by
214 VPA combined with fishery-independent experimental trawl surveys (Wright & Bailey,
215 1992). In this model, M estimate is not a constant but is re-estimated each year based on
216 diet composition and key predator abundance using a multispecies model. Still, while
217 predator consumption includes that of seabirds and marine mammals, the most important
218 predators of sandeels by far are fish - especially mackerel, herring, cod, haddock, whiting,
219 and gurnard. Because predator consumption is included in M, the catch equation should not
220 include seabird consumption. Abundance in 1977 (123 000 tonnes) was similar to that in
221 1976 and 1978 (103 000 and 106 000 tonnes). Abundance in 1986 was lower (65 000 tonnes)
222 but similar to 1985 and 1987 (76 000 and 36 000 tonnes). Abundance in 2000 (15 000 tonnes)
223 was similar to that in 1999 and 2001 (25 000 and 17 000 tonnes), considerably lower than in
224 1986, and an order of magnitude lower than in 1977.

225

226 ***Seabirds in the Humboldt ecosystem***

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

232 every year at each of the 31 islands and headlands used for breeding (Passuni et al., 2015), some
233 assumptions had to be made. In particular, four types of periods were distinguished: (i) during strong
234 El-Niño periods (1973, 1983, 1998), when small pelagic populations are highly impacted, the
235 proportion of anchovy in the diet was estimated to be 55% for the Guanay cormorant and 58% for
236 boobies and pelicans (Goya, 2000), (ii) during sardine-favoured periods (1974-1982, 1984-1990), the
237 proportion of anchovy in the diet was set to 80% for all three species (Jahncke, Checkley, & Hunt,
238 2004), (iii) during anchovy-favoured periods and when fishing was regulated (1991-1997, 1999-2008),
239 the proportion of anchovy in the diet was fixed to 81% for cormorants and 93% for boobies and
240 pelicans (Goya, 2000), (iv) during anchovy-favoured periods and when fishing was not regulated
241 (1961-1972), the proportion of anchovy in the diet was fixed to 70% for all three species (Jahncke et
242 al., 2004). Because no detailed data were available on the rest of diet, we assumed the proportion in
243 terms of energy to be the same as the proportion in mass. Indeed, the second prey for these seabirds
244 are sardines, a very closely related species.

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

247

248 Daily energy expenditure of breeding birds was estimated from data on average body mass and the
249 bioenergetics equations of (Ellis & Gabrielsen, 2002) estimating field metabolic rate for
250 pelecaniforms ($\text{DEE} = 3.9 * m^{0.871}$). This resulted in an estimation of 3074 kJ.d^{-1} for Guanay cormorant,
251 2353 kJ.d^{-1} for Peruvian booby and 6753 kJ.d^{-1} for Peruvian pelican. Similarly, daily energy
252 expenditure of non-breeding birds was estimated as $2.25 * \text{BMR}$, BMR being obtained from the
253 allometric equation $\text{BMR} = 1.392 * m^{0.823}$ valid for pelecaniforms (Ellis & Gabrielsen, 2002), giving
254 values comparable to what had previously been used .

255

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

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

267

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

272

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

280

281 We used anchovy production from an integrated assessment model (Oliveros-Ramos & Peña,
282 2011) as a measure of potential anchovy abundance available to seabirds and the fishery.

283 Anchovy production is the increase in population biomass due to somatic growth and birth rate

284 without considering natural and fishing mortality and was estimated at monthly time steps.
285 Anchovy production was built using acoustic estimates of biomass and anchovy length structure
286 from scientific surveys and fishery landings between 7° and 18°S and from the coast to 100 km
287 offshore. In the model, M is set as constant ($M=0.7 \text{ yr}^{-1}$) based on the estimations made by Imarpe of
288 0.6 to 0.8 for the years 1974 and 2010. Adjusting the catch equation with bird consumption instead
289 of just fishermen catches should not change much the stock assessment results, as catches are an
290 order of magnitude higher than seabird consumption ($C_t = 472,489 \pm 390,792$ vs. Catches = 5,199,381
291 $\pm 342,858$, *i.e.* 11 times less consumption than catches).

292

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477 ESM2: Supplementary tables

478 Table S1. Annual consumption of anchovy and sardine (combined) and proportion of diet
479 comprised of anchovy and sardine, for key predators in the Southern Benguela. Estimates
480 are those from a base-case model developed for 1978, from which dynamic simulations and
481 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 <i>et al.</i> 's (1984) diet estimate of around 82 % comprised of small pelagics
Marine mammals	Seals	145 000	30%
Squids	Chokka squid	31 000	3%

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