



HAL
open science

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

Claire Saraux, William J Sydeman, John Piatt, Tycho Anker-nilssen, Jonas Hentati-sundberg, Sophie Bertrand, Philippe Cury, Robert W Furness, James A Mills, Henrik Österblom, et al.

► To cite this version:

Claire Saraux, William J Sydeman, John Piatt, Tycho Anker-nilssen, Jonas Hentati-sundberg, et al.. Seabird-induced natural mortality of forage fish varies with fish abundance: evidence from 5 ecosystems. *Fish and Fisheries*, 2020, 10.1111/faf.12517 . hal-02985435

HAL Id: hal-02985435

<https://hal.science/hal-02985435>

Submitted on 2 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3 Claire Saraux^{1,2}, William J. Sydeman³, John Piatt⁴, Tycho Anker-Nilssen⁵, Jonas Hentati-Sundberg⁶,
4 Sophie Bertrand⁷, Philippe Cury⁷, Robert W. Furness⁸, James A. Mills^{9,10}, Henrik Österblom¹¹, Giannina
5 Passuni¹², Jean-Paul Roux^{13,14}, Lynne J. Shannon¹⁵, Robert J.M. Crawford¹⁶

6
7 ¹ IPHC, Université de Strasbourg, CNRS, 23 rue Becquerel, 67037 Strasbourg, France

8 ² MARBEC, Université de Montpellier, CNRS, IRD, IFREMER, Sète, France

9 ³ Farallon Institute for Advanced Ecosystem Research, Petaluma, California, USA

10 ⁴ US Geological Survey, Alaska Science Center, Anchorage, Alaska, USA

11 ⁵ Norwegian Institute for Nature Research, PO Box 5685 Torgarden, 7485 Trondheim, Norway

12 ⁶ Department of Aquatic Resources, Swedish University of Agricultural Sciences, Turistgatan 5, 45330
13 Lysekil, Sweden

14 ⁷ IRD, UMR MARBEC (Université de Montpellier/CNRS/IRD/IFREMER), Sète, France

15 ⁸ University of Glasgow, UK

16 ⁹ 3 Miromiro Drive, Kaikoura 7300, New Zealand

17 ¹⁰ 10527A Skyline Drive, Corning, New York, USA

18 ¹¹ Stockholm Resilience centre, Stockholm University, 106 91 Stockholm, Sweden

19 ¹² Institute of Hydrobiology and Fisheries Science, University of Hamburg, Grosse Elbstrasse 129,
20 22767 Hamburg, Germany

21 ¹³ Namibia Nature Foundation and SEACODE, PO Box 583, Lüderitz, Namibia

22 ¹⁴ Ministry of Fisheries and Marine Resources, PO Box 394, Lüderitz, Namibia

23 ¹⁵ Department of Biological Sciences, University of Cape Town, South Africa

24 ¹⁶ Branch Oceans and Coasts, Department of Environment, Forestry and Fisheries, Cape Town, South
25 Africa

26

27 Corresponding author: Claire Saraux, IPHC, Université de Strasbourg, CNRS, 23 rue Becquerel, 67037

28 Strasbourg, France, claire.saraux@iphc.cnrs.fr

29

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

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:** Benguela, Humboldt, predator-prey, prey consumption, prey entrapment, Shetland

52

53

54	Table of contents
55	
56	Introduction
57	Methods
58	<i>Estimates of seabird consumption and proportion of prey biomass consumed</i>
59	<i>Relationships between consumption and biomass</i>
60	<i>Effect of the predation pressure on-prey dynamics</i>
61	Results
62	<i>Diet</i>
63	<i>Consumption and proportion of prey stock consumed</i>
64	<i>Effect of the predation pressure on prey dynamics</i>
65	Discussion
66	Acknowledgements
67	Data Availability Statement
68	References
69	

70 **Introduction**

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

90 Forage fish are consumed by a variety of upper trophic level species in marine ecosystems,
91 including seabirds, marine mammals, and larger piscivorous fish. Typically, and on regional scales,
92 seabirds consume considerably less biomass than marine mammals or especially piscivorous fish
93 (Gaichas et al., 2009) but seabirds can have significant impacts locally (Furness, 1978). In contrast to
94 ectothermic groundfish that need to acquire only about 0.2% to 1.2% of their body mass in food daily
95 (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:

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

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.* $C_{chick} = \frac{P_t}{AE * PreyNRJ} * (DEE_{chick} * N_{chick} * Nbdays_{chickrearing})$ or directly from meal
190 size given to the chicks (in Norwegian and Baltic Seas): $C_{chick} = P_{mass,t} * N_{chick} * Nbdays_{chickrearing} * Mealsize$

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

235 ***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 ($\Delta AICc$) was less than 2 between the two
251 best models, the more parsimonious model was chosen. All models within a $\Delta AICc$ 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 ($46 \pm 22\%$ [13–89%]) was not significantly related to the biomass of age 0 herring (Figure
279 4a, Table 2). For common murrelets, the mean contribution by mass of sprat to the diet from 2002–
280 2012 was very high and stable across time ($98 \pm 2\%$; 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 ($81 \pm 8\%$) 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 $30 \pm 19\%$ (range 2–61%) and that of anchovy $28 \pm 16\%$ (range 3–62%;
285 Figure 3e). The average combined contribution of these two prey species to the diet was $58 \pm 14\%$
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 $88 \pm 4\%$ in 1977
289 and $83 \pm 5\%$ in 1986 to only $45 \pm 10\%$ 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 murrelets 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 ($\leq 20\%$ 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 murrelets 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

373 towards other prey. Recent research off the south coast of South Africa has shown that in the post-
374 guard stage (>50 days) of chick-rearing, foraging range is extended and gannet diet may differ from
375 that in the guard stage as a consequence of changes either in prey abundance and distribution, or in
376 the energetic requirements of growing offspring (Botha & Pistorius, 2018). A similar relationship was
377 evident for the average proportion of sandeel in the diets of seabirds at the Shetland Islands. Yet,
378 this masks important differences between species, with Arctic skua (*Stercorarius parasiticus*,
379 Stercorariidae) and Arctic tern (*Sterna paradisaea*, Laridae) maintaining 100% of their sandeel diet in
380 all three periods of study, whereas the sandeel contribution to diet decreased from 70-80% to less
381 than 10% in gannet (*Morus bassanus*, Sulidae), fulmar (*Fulmarus glacialis*, Procellariidae), great skua
382 (*S. skua*, Stercorariidae) and great black-backed gull (*Larus marinus*, Laridae) between 1977 and
383 2000. Small surface-feeders, such as Arctic terns, are more constrained and, as such, more vulnerable
384 to environmental changes than other species (Baird, 1990; Furness & Tasker, 2000; Shealer, 2002).
385 Seabird diet, body size and the ability to switch to other prey when their favored prey is depleted
386 might then be important components of their sensitivity to environmental or fisheries-induced
387 fluctuations in prey.

388 These results highlight the importance of forage fish accessibility for seabirds rather than just
389 abundance. Indeed, a decrease in forage fish stock biomass does not automatically translate into a
390 decrease in forage fish availability or catchability for seabirds, or at least not linearly, due to possible
391 changes in spatial distribution. First, the shoaling behaviour of most forage fish means that
392 predation, like fisheries catches, may be maintained even when prey abundance decreases (in
393 fisheries known as hyperstability of catches, Hilborn & Walters, 1992). For example, as stock biomass
394 decreases, forage fish may concentrate in their most suitable habitat (i.e., the basin hypothesis;
395 MacCall, 1990), resulting in habitat contractions, but no decrease in fish density. In this study, the
396 absence of relationships between seabird diet and forage fish abundance in the Humboldt system
397 was in line with previous works which showed that except in the case of extreme El Niño events,
398 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 $\leq 20\%$ 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 murrelets in the Baltic Sea remained
423 extremely low ($\leq 1.2\%$) 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 murre 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 murrelets 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

502 one-third of maximum prey biomass below which seabird breeding success was consistently reduced
503 and more variable. Similarly, when the biomass of sardine spawners fell below c. 25% of its maximum
504 observed value, survival of adult African penguins (*Spheniscus demersus*, Spheniscidae) decreased
505 markedly (Robinson, Butterworth, & Plagányi, 2015) and survival and numbers breeding decreased
506 for three Benguela seabirds when a forage availability index reached low values (Crawford, Sydeman,
507 Thompson, Sherley, & Makhado, 2019). There may be a still lower ecological threshold (15 to 18%
508 according to our study) where prey species, or at least spatial components of prey stocks (e.g. west
509 coast vs. south coast in the Benguela), suffer high rates of natural and fishing mortality. Interestingly,
510 20% of maximum biomass is often used in fishery management as a limit biomass (B_{lim}) below which
511 a stock should not fall or a recovery plan should be put in place. Here, we confirm a similar threshold
512 and advise fishery managers to exercise due care in allocating allowable catches or fishing licenses,
513 *etc.* at low levels of abundance.

514 To conclude, our study is important as it contributes to the growing literature in support of
515 an ecosystem approach to fisheries (EAF; Dickey-Collas et al., 2014; Hill et al., 2020; Koehn et al.,
516 2017; Pikitch et al., 2004). While top-down processes due to predation of forage fish by seabirds did
517 not seem to control forage fish dynamics in any of the five ecosystems we considered, the predation
518 pressure sometimes attained high levels, which signals the need for fisheries management to
519 account for ecosystem constraints when setting catch limits in periods of low forage fish biomass.
520 Finally, our results (and in particular the differences of sensitivity of seabird diet to prey biomass
521 among species) also suggest that forage fish accessibility might be more important than forage fish
522 abundance depending on the ecophysiological constraints that apply to seabirds (e.g. depth to which
523 they can dive). As a consequence, fish stock management should not only ensure a safe level of fish
524 biomass for the stock to be sustainable and the predators to feed (Cury et al., 2011), but also focus
525 on safeguarding predator foraging grounds. Measures such as spatial enclosure around breeding
526 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

530 **Acknowledgements**

531 This work was partly funded by the Baltic Sea Ecosystem Adaptive Management program, Benguela
532 Current Commission, Department of Environment, Forestry and Fisheries (DEFFA, South Africa), by
533 the cooperative agreement between the Institut de Recherche pour le Développement (IRD, France),
534 the Peruvian Sea Institute (IMARPE), and the International Joint Laboratory DISCOH, by a grant from
535 MISTRA to the Stockholm Resilience Centre, the National Research Foundation (NRF, South Africa,
536 through its incentive programme), the Norwegian Environment Agency and the SEAPOP programme
537 (Norwegian Research Council, grant 192141), the South African Research Chair Initiative funded
538 through the South African Department of Science and Technology and administered by the NRF, and
539 the USGS Alaska Science Center. We thank J. C. Coetzee (Department of Agriculture, Forestry and
540 Fisheries, South Africa) for making available time series of biomass estimates of sardine and anchovy
541 off South Africa, ICES for use of similar data on Atlantic herring and a large number of people (none
542 mentioned, none forgotten) who assisted with data collection. The paper is an output of the “One-
543 third for the Birds Working Group”, which held meetings at Sète, France in 2010, Boulders, South
544 Africa in 2011, Kasitsna Bay, Alaska, USA in 2012 and Stora Karlsö, Sweden in 2013. Finally, we wish
545 to thank Dr Laura Koehn and an anonymous reviewer for their constructive comments on the
546 manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not
547 imply endorsement by the U.S. Government.

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>

551

552 **References**

- 553 Adams, N. J., Abrams, R. W., Siegfried, W. R., Nagy, K. A., & Kaplan, I. R. (1991). Energy expenditure
554 and food consumption by breeding Cape gannets *Morus capensis*. *Marine Ecology Progress*
555 *Series*. Inter-Research Science Center. <https://doi.org/10.2307/24816793>
- 556 Adams, N. J., & Klages, N. T. W. (2010). Foraging effort and prey choice in Cape gannets. *South*
557 *African Journal of Marine Science*, *21*(1), 157–163.
558 <https://doi.org/10.2989/025776199784126060>
- 559 Aebischer, N. J., Coulson, J. C., & Colebrook, J. M. (1990). Parallel long-term trends across four
560 marine trophic levels and weather. *Nature*, *347*(6295), 753–755.
561 <https://doi.org/10.1038/347753a0>
- 562 Ainley, D. G., Ballard, G., Barton, K. J., Karl, B. J., Rau, G. H., Ribic, C. a, & Wilson, P. R. (2003). Spatial
563 and temporal variation of diet within a presumed metapopulation of Adelie penguins. *Condor*,
564 *105*(1), 95–106.
- 565 Ainley, D. G., Ballard, G., & Dugger, K. M. (2006). Competition among penguins and cetaceans reveals
566 trophic cascades in the Western Ross Sea, Antarctica. *Ecology*, *87*(8), 2080–2093.
567 [https://doi.org/10.1890/0012-9658\(2006\)87\[2080:CAPACR\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2080:CAPACR]2.0.CO;2)
- 568 Andersen, T., Carstensen, J., Hernández-García, E., & Duarte, C. M. (2009). Ecological thresholds and
569 regime shifts: approaches to identification. *Trends in Ecology & Evolution*, *24*(1), 49–57.
570 <https://doi.org/10.1016/J.TREE.2008.07.014>
- 571 Anker-Nilssen, T., & Aarvak, T. (2006). *Long-term studies of seabirds in the municipality of Røst,*
572 *Nordland. Results with focus on 2004 and 2005*. Trondheim.
- 573 Anker-Nilssen, T., & Øyan, H. S. (1995). *Long-term studies of the breeding biology of puffins at Røst*.

574 Augustyn, J., Cockroft, A., Kerwath, S., Lamberth, S., Githaigi-Mwicigi, J., Pitcher, G., ... Auerswald, I.
575 (2018). South Africa. In B. F. Phillips & M. Perez-Ramirez (Eds.), *Climate change impacts in*
576 *fisheries and aquaculture: a global analysis* (pp. 479–522). John Wiley and Sons Inc.

577 Baird, P. H. (1990). Influence of Abiotic Factors and Prey Distribution on Diet and Reproductive
578 Success of Three Seabird Species in Alaska. *Ornis Scandinavica*, 21(3), 224.
579 <https://doi.org/10.2307/3676782>

580 Bakun, A. (2006). Wasp-waist populations and marine ecosystem dynamics: Navigating the “predator
581 pit” topographies. *Progress in Oceanography*, 68(2–4), 271–288.
582 <https://doi.org/10.1016/J.POCEAN.2006.02.004>

583 Barbeaux, S. J., Holsman, K., & Zador, S. (2020). Marine Heatwave Stress Test of Ecosystem-Based
584 Fisheries Management in the Gulf of Alaska Pacific Cod Fishery. *Frontiers in Marine Science*, 7,
585 703. <https://doi.org/10.3389/fmars.2020.00703>

586 Barbraud, C., Bertrand, A., Bouchón, M., Chaigneau, A., Delord, K., Demarcq, H., ... Bertrand, S.
587 (2017). Density dependence, prey accessibility and prey depletion by fisheries drive Peruvian
588 seabird population dynamics. *Ecography*. <https://doi.org/10.1111/ecog.02485>

589 Barrett, R. T., Gabrielsen, G. W., & Fauchald, P. (1995). Prolonged incubation in the Atlantic puffin
590 (*Fratercula arctica*) and evidence of mild hypothermia as an energy-saving mechanisms. In H. R.
591 Skojdal, C. Hopkins, K. E. Erikstad, & H. P. Leinaas (Eds.), *Ecology of fjords and coastal waters*
592 (pp. 479–488). Amsterdam: Elsevier Science.

593 Batchelor, A. L., & Ross, G. J. B. (1984). The diet and implications of dietary change of Cape Gannets
594 on Bird Island, Algoa Bay. *Ostrich*, 55(2), 45–63.
595 <https://doi.org/10.1080/00306525.1984.9634757>

596 Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator

597 abundances. *Journal of Animal Ecology*, 78(4), 699–714. <https://doi.org/10.1111/j.1365->
598 2656.2009.01531.x

599 Berruti, A., Underhill, L. G., Shelton, P. A., Moloney, C., & Crawford, R. J. M. (1993). Seasonal and
600 Interannual Variation in the Diet of Two Colonies of the Cape Gannet (*Morus capensis*) between
601 1977-78 and 1989. *Colonial Waterbirds*, 16(2), 158. <https://doi.org/10.2307/1521434>

602 Bertrand, A., Ballón, M., & Chaigneau, A. (2010). Acoustic Observation of Living Organisms Reveals
603 the Upper Limit of the Oxygen Minimum Zone. *PLoS ONE*, 5(4), e10330.
604 <https://doi.org/10.1371/journal.pone.0010330>

605 Birt, V., Birt, T., Goulet, D., Cairns, D. K., & Montevecchi, W. A. (1987). Ashmole's halo: direct
606 evidence for prey depletion by a seabird. *Marine Ecology Progress Series*. Retrieved from
607 <http://www.int-res.com/articles/meps/40/m040p205.pdf>

608 Botha, J. A., & Pistorius, P. A. (2018). Variability in the Foraging Distribution and Diet of Cape Gannets
609 between the Guard and Post-guard Phases of the Breeding Cycle. *Frontiers in Marine Science*, 5,
610 15. <https://doi.org/10.3389/fmars.2018.00015>

611 Boyd, C., Castillo, R., Hunt, G., Punt, A., VanBlaricom, G., Weimerskirch, H., & Bertrand, S. (2015).
612 Predictive modelling of habitat selection by marine predators with respect to the abundance
613 and depth distribution of pelagic prey. *Journal of Animal Ecology*, 84, 1575–1588. Retrieved
614 from <https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365->
615 2656.12409%4010.1111/%28ISSN%291365-2656.MovementEcology

616 Boyd, C., Grünbaum, D., Hunt, G. L., Punt, A. E., Weimerskirch, H., & Bertrand, S. (2016). Effectiveness
617 of social information used by seabirds searching for unpredictable and ephemeral prey.
618 *Behavioral Ecology*, 27(4), 1223–1234. Retrieved from
619 <https://academic.oup.com/beheco/article-abstract/27/4/1223/1744926>

620 Boyd, C., Grünbaum, D., Hunt, G. L., Punt, A. E., Weimerskirch, H., & Bertrand, S. (2017). Effects of
621 variation in the abundance and distribution of prey on the foraging success of central place
622 foragers. *Journal of Applied Ecology*, *54*(5), 1362–1372. <https://doi.org/10.1111/1365->
623 [2664.12832](https://doi.org/10.1111/1365-2664.12832)

624 Brekke, B., & Gabrielsen, G. (1994). Assimilation efficiency of adult Kittiwakes and Brunnich's
625 Guillemots fed Capelin and Arctic Cod. *Polar Biology*, *14*(4), 279–284.
626 <https://doi.org/10.1007/BF00239177>

627 Brown, B. E., Anthony, V. C., Anderson, E. D., Hennemuth, R., & Sherman, K. (1983). *The dynamics of*
628 *pelagic fishery resources off the northeastern coast of the United States under conditions of*
629 *extreme fishing perturbations (North Western Atlantic).*

630 Cairns, D. K. (1988). Seabirds as indicators of marine food supplies. *Biological Oceanography*, *5*, 261–
631 271.

632 Carpenter, S. R., Cole, J. J., Hodgson, J. R., Kitchell, J. F., Pace, M. L., Bade, D., ... Schindler, D. E.
633 (2001). Trophic cascades, nutrients, and lake productivity: whole-lake experiments. *Ecological*
634 *Monographs*, *71*(2), 163–186. <https://doi.org/10.1890/0012->
635 [9615\(2001\)071\[0163:TCNALP\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2001)071[0163:TCNALP]2.0.CO;2)

636 Casini, M., Eero, M., Carlshamre, S., & Lövgren, J. (2016). Using alternative biological information in
637 stock assessment: Condition-corrected natural mortality of Eastern Baltic cod. *ICES Journal of*
638 *Marine Science*. <https://doi.org/10.1093/icesjms/fsw117>

639 Casini, M., Hjelm, J., Molinero, J. C., Lövgren, J., Cardinale, M., Bartolino, V., ... Kornilovs, G. (2009).
640 Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proceedings of the*
641 *National Academy of Sciences of the United States of America*, *106*(1), 197–202.
642 <https://doi.org/10.1073/pnas.0806649105>

643 Coetzee, J., Merkle, D., de Moor, C., Twatwa, N., Barange, M., & Butterworth, D. (2008). Refined
644 estimates of South African pelagic fish biomass from hydro-acoustic surveys: quantifying the
645 effects of target strength, signal attenuation and receiver saturation. *African Journal of Marine
646 Science*, 30(2), 205–217. <https://doi.org/10.2989/AJMS.2008.30.2.1.551>

647 Cooper, J. (1978). Energetic Requirements for Growth and Maintenance of the Cape Gannet (Aves;
648 Sulidae). *Zoologica Africana*, 13(2), 305–317.
649 <https://doi.org/10.1080/00445096.1978.11447631>

650 Crawford, R. J. M. (2013). Long-term change in the population sizes and conservation status of South
651 Africa's seabirds. *Ostrich*, 84(2), v–ix. <https://doi.org/10.2989/00306525.2013.819661>

652 Crawford, R. J. M., Altwegg, R., Barham, B., Barham, P., Durant, J., Dyer, B., ... Whittington, P. (2011).
653 Collapse of South Africa's penguins in the early 21st century. *African Journal of Marine Science*,
654 33(1), 139–156. <https://doi.org/10.2989/1814232X.2011.572377>

655 Crawford, R. J. M., Dundee, B. L., Dyer, B. M., Klages, N. T. W., Meÿer, M. A., & Upfold, L. (2007).
656 Trends in numbers of Cape gannets (*Morus capensis*), 1956/1957–2005/2006, with a
657 consideration of the influence of food and other factors. *ICES Journal of Marine Science*, 64(1),
658 169–177. <https://doi.org/10.1093/icesjms/fsl011>

659 Crawford, R. J. M., Ryan, P. G., & Williams, A. J. (1991). Seabird consumption and production in the
660 Benguela and Western Agulhas ecosystems. *South African Journal of Marine Science*, 11(1),
661 357–375. <https://doi.org/10.2989/025776191784287709>

662 Crawford, R. J. M., Sydeman, W. J., Thompson, S. A., Sherley, R. B., & Makhado, A. B. (2019). Food
663 habits of an endangered seabird indicate recent poor forage fish availability off western South
664 Africa. *ICES Journal of Marine Science*, 76(5), 1344–1352.
665 <https://doi.org/10.1093/icesjms/fsz081>

666 Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J. M., Furness, R. W., ...
667 Sydemann, W. J. (2011). Global Seabird Response to Forage Fish Depletion--One-Third for the
668 Birds. *Science*, 334(6063), 1703–1706. <https://doi.org/10.1126/science.1212928>

669 Cury, P. M., Shin, Y., Planque, B., Durant, J., Fromentin, J., Kramerschadt, S., ... Grimm, V. (2008).
670 Ecosystem oceanography for global change in fisheries. *Trends in Ecology & Evolution*, 23(6),
671 338–346. <https://doi.org/10.1016/j.tree.2008.02.005>

672 Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., ... Croxall, J. P. (2019).
673 Threats to seabirds: A global assessment. *Biological Conservation*. Elsevier Ltd.
674 <https://doi.org/10.1016/j.biocon.2019.06.033>

675 Dickey-Collas, M., Engelhard, G. H., Rindorf, A., Raab, K., Smout, S., Aarts, G., ... Peck, M. A. (2014).
676 Ecosystem-based management objectives for the North Sea: riding the forage fish rollercoaster.
677 *ICES Journal of Marine Science*, 71(1), 128–142. <https://doi.org/10.1093/icesjms/fst075>

678 Dunn, E. H. (1975). Caloric Intake of Nestling Double-Crested Cormorants. *The Auk*, 92(3), 553–565.
679 <https://doi.org/10.2307/4084609>

680 Dutil, J.-D., & Lambert, Y. (2000). Natural mortality from poor condition in Atlantic cod (*Gadus*
681 *morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 57(4), 826–836.
682 <https://doi.org/10.1139/f00-023>

683 Eero, M. (2012). Reconstructing the population dynamics of sprat (*Sprattus sprattus balticus*) in the
684 Baltic Sea in the 20th century. *ICES Journal of Marine Science*, 69(6), 1010–1018.
685 <https://doi.org/10.1093/icesjms/fss051>

686 Ellis, H. I., & Gabrielsen, G. (2002). Energetics of free-ranging seabirds. In E. Schreiber & J. Burger
687 (Eds.), *Biology of marine birds* (pp. 359–407).

688 Enekvist, E. (2003). Energy intake of Common Guillemot, *Uria aalge*, chicks at Stora Karlsö, Sweden :

689 influence of changes in the Baltic Sea. Retrieved from [http://www.diva-](http://www.diva-portal.org/smash/record.jsf?pid=diva2%3A279689&dswid=page)
690 [portal.org/smash/record.jsf?pid=diva2%3A279689&dswid=page](http://www.diva-portal.org/smash/record.jsf?pid=diva2%3A279689&dswid=page)

691 Engelhard, G. H., Peck, M. A., Rindorf, A., C. Smout, S., Van Deurs, M., Raab, K., ... Dickey-Collas, M.
692 (2014). Forage fish, their fisheries, and their predators: Who drives whom? *ICES Journal of*
693 *Marine Science*, 71(1), 90–104. <https://doi.org/10.1093/icesjms/fst087>

694 Erikstad, K. E., Fauchald, P., Tveraa, T., & Steen, H. (1998). On the Cost of Reproduction in Long-Lived
695 Birds: The Influence of Environmental Variability. *Ecology*, 79(5), 1781.
696 <https://doi.org/10.2307/176796>

697 Essington, T. E., Moriarty, P. E., Froehlich, H. E., Hodgson, E. E., Koehn, L. E., Oken, K. L., ... Stawitz, C.
698 C. (2015). Fishing amplifies forage fish population collapses. *Proceedings of the National*
699 *Academy of Sciences of the United States of America*, 112(21), 6648–6652.
700 <https://doi.org/10.1073/pnas.1422020112>

701 Fauchald, P., Skov, H., Skern-Mauritzen, M., Johns, D., & Tveraa, T. (2011). Wasp-Waist Interactions
702 in the North Sea Ecosystem. *PLoS ONE*, 6(7), e22729.
703 <https://doi.org/10.1371/journal.pone.0022729>

704 Frank, K. T., Petrie, B., Choi, J. S., & Leggett, W. C. (2005). Trophic cascades in a formerly cod-
705 dominated ecosystem. *Science*, 308(5728), 1621–1623.
706 <https://doi.org/10.1126/science.1113075>

707 Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., & Wanless, S. (2006). From plankton
708 to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of*
709 *Animal Ecology*, 75(6), 1259–1268. <https://doi.org/10.1111/j.1365-2656.2006.01148.x>

710 Frederiksen, M., Furness, R., & Wanless, S. (2007). Regional variation in the role of bottom-up and
711 top-down processes in controlling sandeel abundance in the North Sea. *Marine Ecology*

712 *Progress Series*, 337, 279–286. <https://doi.org/10.3354/meps337279>

713 Fréon, P., Cury, P., Shannon, L., & Roy, C. (2005). Sustainable Exploitation of Small Pelagic Fish Stocks
714 Challenged by Environmental and Ecosystem Changes: A Review. *Bulletin of Marine Science*,
715 76(2), 385–462. Retrieved from
716 <https://www.ingentaconnect.com/content/umrsmas/bullmar/2005/00000076/00000002/art00>
717 013

718 Fromentin, J. M., Myers, R. A., Bjørnstad, O. N., Stenseth, N. C., Gjøsæter, J., & Christie, H. (2001).
719 Effects of density-dependent and stochastic processes on the regulation of cod populations.
720 *Ecology*, 82(2), 567–579. [https://doi.org/10.1890/0012-9658\(2001\)082\[0567:EODDAS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0567:EODDAS]2.0.CO;2)

721 Furness, R. (1978). Energy Requirements of Seabird Communities: A Bioenergetics Model. *The*
722 *Journal of Animal Ecology*, 47(1), 39. <https://doi.org/10.2307/3921>

723 Furness, R. (1990). A preliminary assessment of the quantities of Shetland sandeels taken by
724 seabirds, seals, predatory fish and the industrial fishery in 1981-83. *Ibis*, 132(2), 205–217.
725 <https://doi.org/10.1111/j.1474-919X.1990.tb01039.x>

726 Furness, R., & Tasker, M. (2000). Seabird-fishery interactions: quantifying the sensitivity of seabirds
727 to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the
728 North Sea. *Marine Ecology Progress Series*, 202, 253–264. <https://doi.org/10.3354/meps202253>

729 Gaichas, S., Skaret, G., Falk-Petersen, J., Link, J. S., Overholtz, W., Megrey, B. A., ... Aydin, K. (2009). A
730 comparison of community and trophic structure in five marine ecosystems based on energy
731 budgets and system metrics. *Progress in Oceanography*, 81(1–4), 47–62.
732 <https://doi.org/10.1016/j.pocean.2009.04.005>

733 Gaillard, J. M., & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: a case of
734 environmental canalization? *Ecology*, 84(12), 3294–3306. <https://doi.org/10.1890/02-0409>

735 Gislason, H., Daan, N., Rice, J. C., & Pope, J. G. (2010). Size, growth, temperature and the natural
736 mortality of marine fish. *Fish and Fisheries*. <https://doi.org/10.1111/j.1467-2979.2009.00350.x>

737 Goya, E. (2000). *Abundancia de aves guaneras y su relacion con la pesqueria de anchoveta peruana*
738 *de 1953 a 1999*.

739 Green, D. B., Klages, N. T. W., Crawford, R. J. M., Coetzee, J. C., Dyer, B. M., Rishworth, G. M., &
740 Pistorius, P. A. (2015). Dietary change in Cape gannets reflects distributional and demographic
741 shifts in two South African commercial fish stocks. *ICES Journal of Marine Science*, 72(3), 771–
742 781. <https://doi.org/10.1093/icesjms/fsu203>

743 Guinet, C., Jouventin, P., & Malacamp, J. (1995). Satellite remote sensing in monitoring change of
744 seabirds: use of Spot Image in king penguin population increase at Ile aux Cochons, Crozet
745 Archipelago. *Polar Biology*, 15(7), 511–515. <https://doi.org/10.1007/BF00237465>

746 Hedgren, S. (1975). The breeding population of Guillemot *Uria aalge* in the Baltic Sea. *Vår Fågelvärld*,
747 34, 43–52.

748 Hilborn, R., Amoroso, R. O., Bogazzi, E., Jensen, O. P., Parma, A. M., Szuwalski, C., & Walters, C. J.
749 (2017). When does fishing forage species affect their predators? *Fisheries Research*, 191, 211–
750 221. <https://doi.org/10.1016/J.FISHRES.2017.01.008>

751 Hilborn, R., & Walters, C. J. (1992). Quantitative fisheries stock assessment: Choice, dynamics and
752 uncertainty. *Reviews in Fish Biology and Fisheries*, 2(2), 177–178.
753 <https://doi.org/10.1007/BF00042883>

754 Hill, S. L., Hinke, J., Bertrand, S., Fritz, L., Furness, R. W., Ianelli, J. N., ... Ratcliffe, N. (2020). Reference
755 points for predators will progress ecosystem-based management of fisheries. *Fish and Fisheries*,
756 faf.12434. <https://doi.org/10.1111/faf.12434>

757 Hilton, G. M., Furness, R. W., & Houston, D. C. (2000). A comparative study of digestion in North

758 Atlantic seabirds. *Journal of Avian Biology*, 31(1), 36–46. <https://doi.org/10.1034/j.1600->
759 048X.2000.310106.x

760 Holsman, K. K., & Aydin, K. (2015). Comparative methods for evaluating climate change impacts on
761 the foraging ecology of Alaskan groundfish. *Marine Ecology Progress Series*, 521, 217–235.
762 <https://doi.org/10.3354/MEPS11102>

763 Hunt, G. L., Furness, R. W., & Kerr Building, G. (1996). ICES Cooperative research report.
764 <https://doi.org/10.17895/ices.pub.4624>

765 Hunt, G. L., & McKinnell, S. (2006). Interplay between top-down, bottom-up, and wasp-waist control
766 in marine ecosystems. *Progress in Oceanography*, 68(2–4), 115–124.
767 <https://doi.org/10.1016/j.pocean.2006.02.008>

768 ICES-HAWG. (2020). *Herring Assessment Working Group Report*.

769 ICES-WKSand. (2016). *Report of the benchmark workshop on sandeel*. Begren, Norway.

770 ICES. (2012). *Report of the Working Group on Widely Distributed Stocks (WGWIDE)*. Lowestoft.

771 ICES. (2018). *ICES Advice on fishing opportunities, catch, and effort. Sprat (Sprattus sprattus) in*
772 *subdivisions 22-32 (Baltic Sea)*.

773 IUCN. (2019). Red List of Threatened Species. Retrieved November 7, 2019, from www.iucnredlist.org

774 Jahncke, J., Checkley, D. M., & Hunt, G. L. (2004). Trends in carbon flux to seabirds in the Peruvian
775 upwelling system: effects of wind and fisheries on population regulation. *Fisheries*
776 *Oceanography*, 13(3), 208–223. <https://doi.org/10.1111/j.1365-2419.2004.00283.x>

777 Jarvis, M. J. F. (1974). The Ecological Significance of Clutch Size in the South African Gannet (*Sula*
778 *capensis* (Lichtenstein)). *The Journal of Animal Ecology*, 43(1), 1. <https://doi.org/10.2307/3154>

779 Jones, T., Parrish, J. K., Peterson, W. T., Bjorkstedt, E. P., Bond, N. A., Ballance, L. T., ... Harvey, J.

780 (2018). Massive Mortality of a Planktivorous Seabird in Response to a Marine Heatwave.
781 *Geophysical Research Letters*, 45(7), 3193–3202.
782 [https://doi.org/10.1002/2017GL076164@10.1002/\(ISSN\)2169-9291.MMH1](https://doi.org/10.1002/2017GL076164@10.1002/(ISSN)2169-9291.MMH1)

783 Kadin, M., Olsson, O., Hentati-Sundberg, J., Ehrning, E. W., & Blenckner, T. (2016). Common
784 Guillemot *Uria aalge* parents adjust provisioning rates to compensate for low food quality. *Ibis*,
785 158(1), 167–178. <https://doi.org/10.1111/ibi.12335>

786 Kadin, M., Österblom, H., Hentati-Sundberg, J., & Olsson, O. (2012). Contrasting effects of food
787 quality and quantity on a marine top predator. *Marine Ecology Progress Series*, 444, 239–249.
788 <https://doi.org/10.3354/meps09417>

789 Koehn, L. E., Essington, T. E., Marshall, K. N., Sydeman, W. J., Szoboszlai, A. I., & Thayer, J. A. (2017).
790 Trade-offs between forage fish fisheries and their predators in the California Current. *ICES*
791 *Journal of Marine Science*, 74(9), 2448–2458. <https://doi.org/10.1093/icesjms/fsx072>

792 Laugksch, R. C., & Duffy, D. C. (1984). Energetics equations and food consumption of seabirds in two
793 marine upwelling areas: comparisons and the need for standardization. *South African Journal of*
794 *Marine Science*, 2(1), 145–148. <https://doi.org/10.2989/02577618409504365>

795 Lewis, S., Sherratt, T. N., Hamer, K. C., & Wanless, S. (2001). Evidence of intra-specific competition for
796 food in a pelagic seabird. *Nature*, 412(6849), 816–819. <https://doi.org/10.1038/35090566>

797 Litzow, M. A., & Ciannelli, L. (2007). Oscillating trophic control induces community reorganization in a
798 marine ecosystem. *Ecology Letters*, 10(12), 1124–1134. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2007.01111.x)
799 [0248.2007.01111.x](https://doi.org/10.1111/j.1461-0248.2007.01111.x)

800 Lluch-Belda, D., Schwartzlose, R. A., Serra, R., Parrish, R., Kawasaki, T., Hedgecock, D., & Crawford, R.
801 J. M. (1992). Sardine and anchovy regime fluctuations of abundance in four regions of the world
802 oceans: a workshop report. *Fisheries Oceanography*, 1(4), 339–347.

803 <https://doi.org/10.1111/j.1365-2419.1992.tb00006.x>

804 MacCall, A. D. (1990). *Dynamic geography of marine fish populations*. Seattle: University of
805 Washington.

806 Martin, A. R. (1989). The diet of Atlantic Puffin *Fratercula arctica* and Northern Gannet *Sula bassana*
807 chicks at a Shetland colony during a period of changing prey availability. *Bird Study*, 36(3), 170–
808 180. <https://doi.org/10.1080/00063658909477022>

809 Mitchell, P. I., Newton, S. F., Ratcliffe, N., & Dunn, T. E. (2004). *Seabird Populations of Britain and*
810 *Ireland: results of the seabird 2000 census (1998-2002)*. London. Retrieved from
811 <http://www.jncc.defra.gov.uk/page-1530>.

812 Nur, N., & Sydeman, W. J. (1999). Survival, breeding probability and reproductive success in relation
813 to population dynamics of brandt's cormorants phalacrocorax penicillatus. *Bird Study*, 46, S92–
814 S103. <https://doi.org/10.1080/00063659909477236>

815 Oken, K. L., & Essington, T. E. (2015). How detectable is predation in stage-structured populations?
816 Insights from a simulation-testing analysis. *Journal of Animal Ecology*, 84(1), 60–70.
817 <https://doi.org/10.1111/1365-2656.12274>

818 Oliveros-Ramos, R., & Peña, C. (2011). Modeling and analysis of the recruitment of peruvian anchovy
819 (*Engraulis ringens*) between 1961 and 2009. *Ciencias Marinas*, 37(4B), 659–674. Retrieved from
820 <http://www.redalyc.org/articulo.oa?id=48021256010>

821 Olsson, O., & Hentati-Sundberg, J. (2017). Population trends and status of four seabird species (*Uria*
822 *aalge*, *Alca torda*, *Larus fuscus*, *Larus argentatus*) at Stora Karlsö in the Baltic Sea. *Ornis Svecica*,
823 27(2–4), 64–93. <https://doi.org/10.34080/os.v27.19558>

824 Österblom, H., Casini, M., Olsson, O., & Bignert, A. (2006). Fish, seabirds and trophic cascades in the
825 Baltic Sea. *Marine Ecology Progress Series*, 323, 233–238. <https://doi.org/10.3354/meps323233>

- 826 Øyan, H. S., & Anker-Nilssen, T. (1996). Allocation of Growth in Food-Stressed Atlantic Puffin Chicks.
827 *The Auk*, 113(4), 830–841. <https://doi.org/10.2307/4088861>
- 828 Passuni, G., Barbraud, C., Chaigneau, A., Bertrand, A., Oliveros-Ramos, R., Ledesma, J., ... Bertrand, S.
829 (2018). Long-term changes in the breeding seasonality of Peruvian seabirds and regime shifts in
830 the Northern Humboldt Current System. *Marine Ecology Progress Series*, 597, 231–242.
831 <https://doi.org/10.3354/meps12590>
- 832 Passuni, G., Barbraud, C., Chaigneau, A., Demarcq, H., Ledesma, J., Bertrand, A., ... Bertrand, S.
833 (2015). Seasonality in marine ecosystems: Peruvian seabirds, anchovy and oceanographic
834 conditions. *Ecology*, 97(1), 150708023447006. <https://doi.org/10.1890/14-1134.1>
- 835 Peck, M. A., Neuenfeldt, S., Essington, T. E., Trenkel, V. M., Takasuka, A., Gislason, H., ... Rice, J. C.
836 (2014). Forage Fish Interactions: a symposium on “Creating the tools for ecosystem-based
837 management of marine resources.” *ICES Journal of Marine Science*, 71(1), 1–4.
838 <https://doi.org/10.1093/icesjms/fst174>
- 839 Pedersen, J., & Hislop, J. R. G. (2001). Seasonal variations in the energy density of fishes in the North
840 Sea. *Journal of Fish Biology*, 59(2), 380–389. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8649.2001.tb00137.x)
841 [8649.2001.tb00137.x](https://doi.org/10.1111/j.1095-8649.2001.tb00137.x)
- 842 Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., ... Thomas, A. C.
843 (2015). Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod
844 fishery. *Science*, 350(6262), 809–812. <https://doi.org/10.1126/science.aac9819>
- 845 Piatt, J. F., Harding, A., Shultz, M., Speckman, S., van Pelt, T., Drew, G., & Kettle, A. (2007). Seabirds as
846 indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series*, 352, 221–
847 234. <https://doi.org/10.3354/meps07078>
- 848 Piatt, J. F., Parrish, J. K., Renner, H. M., Schoen, S. K., Jones, T. T., Arimitsu, M. L., ... Sydeman, W. J.

849 (2020). Extreme mortality and reproductive failure of common murrelets resulting from the
850 northeast Pacific marine heatwave of 2014-2016. *PLOS ONE*, 15(1), e0226087.
851 <https://doi.org/10.1371/journal.pone.0226087>

852 Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., ... Sainsbury, K. J.
853 (2004). Ecosystem-Based Fishery Management. *Science*, 305(5682), 346.
854 <https://doi.org/10.1126/science.1098222>

855 Queiros, Q., Fromentin, J., Astruc, G., Bauer, R. R. K., & Saraux, C. (2018). Dolphin predation pressure
856 on pelagic and demersal fish in the Northwestern Mediterranean Sea. *Marine Ecology Progress
857 Series*, 603, 13–27. <https://doi.org/10.3354/meps12672>

858 Robinson, W. M. L., Butterworth, D. S., & Plagányi, É. E. (2015). Quantifying the projected impact of
859 the South African sardine fishery on the Robben Island penguin colony. *ICES Journal of Marine
860 Science: Journal Du Conseil*, 72(6), 1822–1833. <https://doi.org/10.1093/icesjms/fsv035>

861 Roth, J. E., Nur, N., Warzybok, P., & Sydeman, W. J. (2008). Annual prey consumption of a dominant
862 seabird, the common murre, in the California Current system. *ICES Journal of Marine Science*,
863 65(6), 1046–1056. <https://doi.org/10.1093/icesjms/fsn077>

864 Ruggerone, G., Springer, A., Shaul, L., & van Vliet, G. (2019). Unprecedented biennial pattern of birth
865 and mortality in an endangered apex predator, the southern resident killer whale, in the
866 eastern North Pacific Ocean. *Marine Ecology Progress Series*, 608, 291–296.
867 <https://doi.org/10.3354/meps12835>

868 Sætre, R., Toresen, R., & Anker-Nilssen, T. (2002). Factors affecting the recruitment variability of the
869 Norwegian spring-spawning herring (*Clupea harengus* L.). *ICES Journal of Marine Science*, 59(4),
870 725–736. <https://doi.org/10.1006/jmsc.2002.1180>

871 Sandvik, H., Erikstad, K. E., Fauchald, P., & Tveraa, T. (2008). High survival of immatures in a long-

872 lived seabird: insights from a long-term study of the Atlantic Puffin (*Fratercula arctica*). *The Auk*,
873 125(3), 723–730. <https://doi.org/10.1525/auk.2008.07059>

874 Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., ...
875 Zuzunaga, J. Z. (1999). Worldwide large-scale fluctuations of sardine and anchovy populations.
876 *South African Journal of Marine Science*, 21(1), 289–347.
877 <https://doi.org/10.2989/025776199784125962>

878 Shannon, L. J., Christensen, V., & Walters, C. J. (2004). Modelling stock dynamics in the southern
879 Benguela ecosystem for the period 1978–2002. *African Journal of Marine Science*, 26(1), 179–
880 196. <https://doi.org/10.2989/18142320409504056>

881 Shealer, D. A. (2002). Foraging behaviour and food of seabirds. In E. A. Schreiber & J. Burger (Eds.),
882 *Biology of marine birds* (pp. 137–177). CRC Press.

883 Smout, S., Rindorf, A., Hammond, P. S., Harwood, J., & Matthiopoulos, J. (2014). Modelling prey
884 consumption and switching by UK grey seals. *ICES Journal of Marine Science*, 71(1), 81–89.
885 <https://doi.org/10.1093/icesjms/fst109>

886 Speckman, S. G., Piatt, J. F., Minte-Vera, C. V., & Parrish, J. K. (2005). Parallel structure among
887 environmental gradients and three trophic levels in a subarctic estuary. *Progress in*
888 *Oceanography*, 66(1), 25–65. <https://doi.org/10.1016/j.pocean.2005.04.001>

889 Springer, A. M., & Van Vliet, G. B. (2014). Climate change, pink salmon, and the nexus between
890 bottom-up and top-down forcing in the subarctic Pacific Ocean and Bering Sea. *Proceedings of*
891 *the National Academy of Sciences of the United States of America*, 111(18).
892 <https://doi.org/10.1073/pnas.1319089111>

893 Sydeman, W. J., Thompson, S. A., Anker-Nilssen, T., Arimitsu, M., Bennison, A., Bertrand, S., ... Zador,
894 S. (2017). Best practices for assessing forage fish fisheries-seabird resource competition.

895 *Fisheries Research*, 194, 209–221. <https://doi.org/10.1016/j.fishres.2017.05.018>

896 Toresen, R., & Østvedt, O. J. (2000). Variation in abundance of Norwegian spring-spawning herring
897 (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic
898 fluctuations. *Fish and Fisheries*, 1(3), 231–256. <https://doi.org/10.1111/j.1467->
899 2979.2000.00022.x

900 Van Beveren, E., Fromentin, J.-M., Bonhommeau, S., Nieblas, A.-E., Metral, L., Brisset, B., ... Saraux, C.
901 (2017). Predator–prey interactions in the face of management regulations: changes in
902 Mediterranean small pelagic species are not due to increased tuna predation. *Canadian Journal*
903 *of Fisheries and Aquatic Sciences*, 74(9), 1422–1430. <https://doi.org/10.1139/cjfas-2016-0152>

904 von Biela, V., Arimitsu, M., Piatt, J. F., Heflin, B., Schoen SK Trowbridge, J., & Clawson, C. (2019).
905 Extreme reduction in nutritional value of a key forage fish during the Pacific marine heatwave
906 of 2014-2016. *Marine Ecology Progress Series*, 613, 171–182.
907 <https://doi.org/10.3354/meps12891>

908 Walsh, P., Halley, D., Harris, M., del Nevo, A., Sim, L., & Tasker, M. (1995). *Seabird monitoring*
909 *handbook*. Retrieved from <http://nora.nerc.ac.uk/id/eprint/8798/1/Bird1.pdf>

910 Weimerskirch, H., Bertrand, S., Silva, J., Bost, C., & Peraltilla, S. (2012). Foraging in Guanay cormorant
911 and Peruvian booby, the major guano-producing seabirds in the Humboldt Current System.
912 *Marine Ecology Progress Series*, 458, 231–245. <https://doi.org/10.3354/meps09752>

913 Worm, B., & Myers, R. A. (2003). Meta-analysis of cod-shrimp interactions reveals top-down control
914 in oceanic food webs. *Ecology*, 84(1), 162–173. <https://doi.org/10.1890/0012->
915 9658(2003)084[0162:MAOCSI]2.0.CO;2

916

917

	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>
--	---	--	--	--	--	--	--	--

<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 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>
--	---	---	--	---	--	---	---	---

<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 $M_{\text{chick}} = 0.5 M_{\text{adult}}$</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>
--------------------------------	--	-----------------------------------	---	---	--	---	--	--

<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>
---------------------------------	--	--	--	---	--	---	--	--

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

Variables	Ecosystem/Species	Model type	AICc	Δ AICc	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			

		Power	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	
	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	14
		Exponential	-21.6	1.1	
		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 ($\Delta AICc \leq 2$) 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.

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 ($108 \text{ g.chick}^{-1}.\text{day}^{-1}$; 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. 150 days 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 murre 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 murrelets 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 murrelets 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 ($C_t = 7021 \pm 891$ vs. Catches = 326,200 \pm 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 procellariiform (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 procellariiforms and $DEE = 3.9 * m^{0.871}$ for pelecyaniforms). 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 procellariiforms and $BMR = 1.392 * m^{0.823}$ for pelecyaniforms).

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 murre 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 pelecyaniforms ($DEE = 3.9 * m^{0.871}$). 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 pelecyaniforms (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 ($M=0.7 \text{ yr}^{-1}$) 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 ($C_t = 472,489 \pm 390,792$ vs. Catches = 5,199,381 $\pm 342,858$, *i.e.* 11 times less consumption than catches).

References

- Adams, N. J., Abrams, R. W., Siegfried, W. R., Nagy, K. A., & Kaplan, I. R. (1991). Energy expenditure and food consumption by breeding Cape gannets *Morus capensis*. *Marine Ecology Progress Series*, Vol. 70, pp. 1–9. doi: 10.2307/24816793
- Albertsen, J. (1996). *Food choice of breeding Puffins Fratercula arctica revealed by stable isotope analysis*. University of Trondheim, Norway.
- Anker-Nilssen, T. (1992). *Food supply as a determinant of reproduction and population development in Norwegian Puffins Fratercula arctica*. Trondheim.
- Anker-Nilssen, T., & Aarvak, T. (2006). *Anker-Nilssen, T., & Aarvak, T. (2006). Long-term studies of seabirds in the municipality of Røst, Nordland. Results with focus on 2004 and 2005*. Trondheim.
- Anker-Nilssen, T., & Aarvak, T. (2009). Satellite telemetry reveals post-breeding movements of Atlantic puffins *Fratercula arctica* from Røst, North Norway. *Polar Biology*, 32(11), 1657–1664. doi: 10.1007/s00300-009-0665-7
- Anker-Nilssen, T., & Øyan, H. S. (1995). *Long-term studies of the breeding biology of puffins at Røst*.
- Anker-Nilssen, T., & Røstad, O. W. (1993). Census and Monitoring of Puffins *Fratercula arctica* on Røst, N Norway, 1979-1988. *Ornis Scandinavica*, 24(1), 1. doi: 10.2307/3676402
- Augustyn, J., Cockroft, A., Kerwath, S., Lamberth, S., Githaigi-Mwicigi, J., Pitcher, G., ... Auerswald, I. (2018). South Africa. In B. F. Phillips & M. Perez-Ramirez (Eds.), *Climate change impacts in fisheries and aquaculture: a global analysis* (pp. 479–522). John Wiley and Sons Inc.
- Barrett, R. T., Anker-Nilssen, T., Gabrielsen, G. W., & Chapdelaine, G. (2002). Food consumption by seabirds in Norwegian waters. *ICES Journal of Marine Science*, 59(1), 43–57. doi: 10.1006/jmsc.2001.1145
- Barrett, R. T., Gabrielsen, G. W., & Fauchald, P. (1995). Prolonged incubation in the Atlantic puffin (*Fratercula arctica*) and evidence of mild hypothermia as an energy-saving mechanisms. In H. R. Skooldal, C. Hopkins, K. E. Erikstad, & H. P. Leinaas (Eds.), *Ecology of fjords and coastal waters* (pp. 479–488). Amsterdam: Elsevier Science.
- Barrett, R. T., Nilsen, E., & Anker-Nilssen, T. (2012). Long-term decline in egg size of Atlantic

- puffins *Fratercula arctica* is related to changes in forage fish stocks and climate conditions. *Marine Ecology Progress Series*, 457, 1–10. doi: 10.3354/meps09813
- Batchelor, A. L., & Ross, G. J. B. (1984). The diet and implications of dietary change of Cape Gannets on Bird Island, Algoa Bay. *Ostrich*, 55(2), 45–63. doi: 10.1080/00306525.1984.9634757
- Berruti, A., Underhill, L. G., Shelton, P. A., Moloney, C., & Crawford, R. J. M. (1993). Seasonal and Interannual Variation in the Diet of Two Colonies of the Cape Gannet (*Morus capensis*) between 1977–78 and 1989. *Colonial Waterbirds*, 16(2), 158. doi: 10.2307/1521434
- Bertrand, S., Joo, R., Arbulu Smet, C., Tremblay, Y., Barbraud, C., & Weimerskirch, H. (2012). Local depletion by a fishery can affect seabird foraging. *Journal of Applied Ecology*, 49(5), 1168–1177. doi: 10.1111/j.1365-2664.2012.02190.x
- Brekke, B., & Gabrielsen, G. (1994). Assimilation efficiency of adult Kittiwakes and Brunnich's Guillemots fed Capelin and Arctic Cod. *Polar Biology*, 14(4), 279–284. doi: 10.1007/BF00239177
- Coetzee, J., Merkle, D., de Moor, C., Twatwa, N., Barange, M., & Butterworth, D. (2008). Refined estimates of South African pelagic fish biomass from hydro-acoustic surveys: quantifying the effects of target strength, signal attenuation and receiver saturation. *African Journal of Marine Science*, 30(2), 205–217. doi: 10.2989/AJMS.2008.30.2.1.551
- Cooper, J. (1978). Energetic Requirements for Growth and Maintenance of the Cape Gannet (Aves; Sulidae). *Zoologica Africana*, 13(2), 305–317. doi: 10.1080/00445096.1978.11447631
- Crawford, R. J. M. (1999). Seabird responses to long-term changes of prey resources off southern Africa. In N. Adams & R. Slotow (Eds.), *Proceedings of 22nd International Ornithological Congress* (pp. 688–705). Durban: BirdLife South Africa.
- Crawford, R. J. M., Dundee, B. L., Dyer, B. M., Klages, N. T. W., Meyer, M. A., & Upfold, L. (2007). Trends in numbers of Cape gannets (*Morus capensis*), 1956/1957–2005/2006, with a consideration of the influence of food and other factors. *ICES Journal of Marine Science*, 64(1), 169–177. doi: 10.1093/icesjms/fsl011
- Crawford, R. J. M., Ryan, P. G., & Williams, A. J. (1991). Seabird consumption and production in the Benguela and Western Agulhas ecosystems. *South African Journal of Marine Science*, 11(1), 357–375. doi: 10.2989/025776191784287709
- Crawford, R. J. M., Sydeman, W. J., Thompson, S. A., Sherley, R. B., & Makhado, A. B. (2019). Food habits of an endangered seabird indicate recent poor forage fish availability off western South Africa. *ICES Journal of Marine Science*, 76(5), 1344–1352. doi: 10.1093/icesjms/fsz081
- Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J. M., Furness, R. W., ... Sydeman, W. J. (2011). Global Seabird Response to Forage Fish Depletion--One-Third for the Birds. *Science*, 334(6063), 1703–1706. doi: 10.1126/science.1212928
- Distiller, G., Altwegg, R., Crawford, R., Klages, N., & Barham, B. (2012). Factors affecting adult survival and inter-colony movement at the three South African colonies of Cape gannet. *Marine Ecology Progress Series*, 461, 245–255. doi: 10.3354/meps09807
- Dunn, E. H. (1975). Caloric Intake of Nestling Double-Crested Cormorants. *The Auk*, 92(3), 553–565. doi: 10.2307/4084609
- Ellis, H. I., & Gabrielsen, G. (2002). Energetics of free-ranging seabirds. In E. Schreiber & J. Burger (Eds.), *Biology of marine birds* (pp. 359–407).
- Enekvist, E. (2003). *Energy intake of Common Guillemot, Uria aalge, chicks at Stora Karlsö*,

- Sweden : influence of changes in the Baltic Sea. Retrieved from <http://www.diva-portal.org/smash/record.jsf?pid=diva2%3A279689&dswid=page>
- Fayet, A. L., Freeman, R., Anker-Nilssen, T., Diamond, A., Erikstad, K. E., Fifield, D., ... Guilford, T. (2017). Ocean-wide Drivers of Migration Strategies and Their Influence on Population Breeding Performance in a Declining Seabird. *Current Biology*, 27(24), 3871-3878.e3. doi: 10.1016/J.CUB.2017.11.009
- Furness, R. (1990). A preliminary assessment of the quantities of Shetland sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1981-83. *Ibis*, 132(2), 205–217. doi: 10.1111/j.1474-919X.1990.tb01039.x
- Furness, R., & Tasker, M. (2000). Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series*, 202, 253–264. doi: 10.3354/meps202253
- Gimenez, O., Anker-Nilssen, T., & Grosbois, V. (2012). Exploring causal pathways in demographic parameter variation: path analysis of mark-recapture data. *Methods in Ecology and Evolution*, 3(2), 427–432. doi: 10.1111/j.2041-210X.2011.00150.x
- Goya, E. (2000). *Abundancia de aves guaneras y su relacion con la pesqueria de anchoveta peruana de 1953 a 1999*.
- Hedgren, S. (1975). The breeding population of Guillemot *Uria aalge* in the Baltic Sea. *Vår Fågelvärld*, 34, 43–52.
- Hedgren, S. (1976). *On the food of the common guillemot Uria aalge at the island of Stora Karlsö, the Baltic Sea*.
- Hilton, G. M., Furness, R. W., & Houston, D. C. (2000). A comparative study of digestion in North Atlantic seabirds. *Journal of Avian Biology*, 31(1), 36–46. doi: 10.1034/j.1600-048X.2000.310106.x
- ICES. (2012). *Report of the Working Group on Widely Distributed Stocks (WGWIDE)*. Lowestoft.
- ICES. (2018). *ICES Advice on fishing opportunities, catch, and effort. Sprat (Sprattus sprattus) in subdivisions 22-32 (Baltic Sea)*.
- Jahncke, J., Checkley, D. M., & Hunt, G. L. (2004). Trends in carbon flux to seabirds in the Peruvian upwelling system: effects of wind and fisheries on population regulation. *Fisheries Oceanography*, 13(3), 208–223. doi: 10.1111/j.1365-2419.2004.00283.x
- Jarvis, M. J. F. (1974). The Ecological Significance of Clutch Size in the South African Gannet (*Sula capensis* (Lichtenstein)). *The Journal of Animal Ecology*, 43(1), 1. doi: 10.2307/3154
- Kadin, M., Olsson, O., Hentati-Sundberg, J., Ehrning, E. W., & Blenckner, T. (2016). Common Guillemot *Uria aalge* parents adjust provisioning rates to compensate for low food quality. *Ibis*, 158(1), 167–178. doi: 10.1111/ibi.12335
- Kadin, M., Österblom, H., Hentati-Sundberg, J., & Olsson, O. (2012). Contrasting effects of food quality and quantity on a marine top predator. *Marine Ecology Progress Series*, 444, 239–249. doi: 10.3354/meps09417
- Klages, N. T. W. (1994). Dispersal and site fidelity of Cap Gannets *Morus Capensis*. *Ostrich*, 65(2), 218–224. doi: 10.1080/00306525.1994.9639685
- Laugksch, R. C., & Duffy, D. C. (1984). Energetics equations and food consumption of seabirds in two marine upwelling areas: comparisons and the need for standardization. *South African Journal of Marine Science*, 2(1), 145–148. doi: 10.2989/02577618409504365
- Lockerbie, E. M., & Shannon, L. (2019). Toward Exploring Possible Future States of the

- Southern Benguela. *Frontiers in Marine Science*, 6. doi: 10.3389/fmars.2019.00380
- Lyngs, P., & Durinck, J. (1998). *Diet of Guillemots in the central Baltic Sea Diet of Guillemots Uria aalge in the central Baltic Sea*. Retrieved from <https://www.researchgate.net/publication/296665974>
- Martin, A. R. (1989). The diet of Atlantic Puffin *Fratercula arctica* and Northern Gannet *Sula bassana* chicks at a Shetland colony during a period of changing prey availability. *Bird Study*, 36(3), 170–180. doi: 10.1080/00063658909477022
- Mitchell, P. I., Newton, S. F., Ratcliffe, N., & Dunn, T. E. (2004). *Seabird Populations of Britain and Ireland: results of the seabird 2000 census (1998-2002)*. Retrieved from <http://www.jncc.defra.gov.uk/page-1530>. To find out more about JNCC visit <http://www.jncc.defra.gov.uk/page-1729>.
- Nelson, J. B. (2005). *Pelicans, Cormorants and their relatives Pelecanidae, Sulidae, Phalacrocoracidae, Anhingidae, Fregatidae, Phaethontidae*. Oxford: Oxford University Press.
- Oliveros-Ramos, R., & Peña, C. (2011). Modeling and analysis of the recruitment of peruvian anchovy (*Engraulis ringens*) between 1961 and 2009. *Ciencias Marinas*, 37(4B), 659–674. Retrieved from <http://www.redalyc.org/articulo.oa?id=48021256010>
- Olsson, O., & Hentati-Sundberg, J. (2017). Population trends and status of four seabird species (*Uria aalge*, *Alca torda*, *Larus fuscus*, *Larus argentatus*) at Stora Karlsö in the Baltic Sea. *Ornis Svecica*, 27(2–4), 64–93. doi: 10.34080/os.v27.19558
- Österblom, H., & Olsson, O. (2002). Changes in feeding behaviour and reproductive success in the Common Guillemot *Uria aalge* on the island of Stora Karlsö. *Ornis Svecica*, 12, 53–62.
- Øyan, H. S., & Anker-Nilssen, T. (1996). Allocation of Growth in Food-Stressed Atlantic Puffin Chicks. *The Auk*, 113(4), 830–841. doi: 10.2307/4088861
- Passuni, G., Barbraud, C., Chaigneau, A., Bertrand, A., Oliveros-Ramos, R., Ledesma, J., ... Bertrand, S. (2018). Long-term changes in the breeding seasonality of Peruvian seabirds and regime shifts in the Northern Humboldt Current System. *Marine Ecology Progress Series*, 597, 231–242. doi: 10.3354/meps12590
- Passuni, G., Barbraud, C., Chaigneau, A., Demarcq, H., Ledesma, J., Bertrand, A., ... Bertrand, S. (2015). Seasonality in marine ecosystems: Peruvian seabirds, anchovy and oceanographic conditions. *Ecology*, 97(1), 150708023447006. doi: 10.1890/14-1134.1
- Pedersen, J., & Hislop, J. R. G. (2001). Seasonal variations in the energy density of fishes in the North Sea. *Journal of Fish Biology*, 59(2), 380–389. doi: 10.1111/j.1095-8649.2001.tb00137.x
- Pichegru, L., Ryan, P., van der Lingen, C., Coetzee, J., Ropert-Coudert, Y., & Grémillet, D. (2007). Foraging behaviour and energetics of Cape gannets *Morus capensis* feeding on live prey and fishery discards in the Benguela upwelling system. *Marine Ecology Progress Series*, 350, 127–136. doi: 10.3354/meps07128
- Roth, J. E., Nur, N., Warzybok, P., & Sydeman, W. J. (2008). Annual prey consumption of a dominant seabird, the common murre, in the California Current system. *ICES Journal of Marine Science*, 65(6), 1046–1056. doi: 10.1093/icesjms/fsn077
- Sandvik, H., Erikstad, K. E., Fauchald, P., & Tveraa, T. (2008). High survival of immatures in a long-lived seabird: insights from a long-term study of the Atlantic Puffin (*Fratercula arctica*). *The Auk*, 125(3), 723–730. doi: 10.1525/auk.2008.07059
- Shannon, L. J., Ortego Cisneros, K., Lamont, T., H., W., Crawford, R. J. M., Jarre, A., & Coll, M. (2020). Exploring temporal variability in the Southern Benguela ecosystem over the past

four decades using a time-dynamic ecosystem model. *Frontiers in Marine Science*. doi: 10.3389/fmars.2020.00540

Toresen, R., & Østvedt, O. J. (2000). Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. *Fish and Fisheries*, 1(3), 231–256. doi: 10.1111/j.1467-2979.2000.00022.x

Walsh, P., Halley, D., Harris, M., del Nevo, A., Sim, L., & Tasker, M. (1995). *Seabird monitoring handbook*. Retrieved from <http://nora.nerc.ac.uk/id/eprint/8798/1/Bird1.pdf>

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 <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%