

1 Precautionary catch limits on forage fish would rarely 2 advance marine predator conservation

3 Christopher M. Free^{1,2*}, Olaf P. Jensen², Ray Hilborn³

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5 ¹ *Bren School of Environmental Science and Management, University of California, Santa Barbara, Santa*
6 *Barbara, CA; cfree14@gmail.com*

7 ² *Department of Marine and Coastal Sciences, Rutgers University, New Brunswick, NJ, USA;*
8 *olaf.p.jensen@gmail.com*

9 ³ *School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA;*
10 *hilbornr@gmail.com*

11
12 * **Corresponding author:** Bren School of Environmental Science and Management, University of
13 California, Santa Barbara, 2400 Bren Hall, Santa Barbara, CA 93106, USA; cfree14@gmail.com; +1 (610)
14 999-4732

15 Abstract

16 Forage fish — small, low-trophic level fish such as herrings, sardines, and anchovies — are
17 critical prey species in marine ecosystems and also support large commercial fisheries. There
18 are increasing calls for precautionary catch limits on forage fish to protect valuable fish
19 predators and protected seabirds and marine mammals. However, the effectiveness of these
20 regulations, which assume that increasing prey abundance increases predator productivity, are
21 under debate. We used prey-linked population models to measure the influence of forage fish
22 abundance on the productivity of 45 marine predator populations of 32 species from five
23 regions. Our results indicate that predator productivity is rarely influenced by the abundance of
24 their prey. Only six predator populations were positively influenced by prey abundance; more
25 populations were negatively influenced. Thus, precautionary regulations that limit forage fish
26 harvest to less than the maximum sustainable yield are unlikely to have measurable benefits for
27 most of their predators.

28
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30 models, marine mammals, seabirds, precautionary management, predator-prey dynamics

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39 1. Introduction

40 Forage fish are small pelagic fish (e.g. herrings, sardines, anchovies) that provide
41 benefits to both people and marine ecosystems. They represent the largest species group
42 landed in marine capture fisheries (21 million mt or 25.5% of reported landings in 2015; (FAO
43 2018)) and are under increasing demand as a source of fish meal for livestock and aquaculture
44 and food for humans (Tacon & Metian 2015). Seabirds, marine mammals, and large piscivorous
45 fish also rely on forage fish for food (Cury 2000), and may therefore be in direct competition with
46 fisheries (Smith et al. 2011; Pikitch et al. 2014; Rountos et al. 2015). As a result, there have
47 been increasing calls for precautionary catch limits on forage fish to protect populations of
48 valuable fish predators (e.g., tuna, salmon) and protected seabird and marine mammal species
49 (Pikitch et al. 2012). For example, the Forage Fish Conservation Act (H.R. 2236), introduced to
50 the United States Congress in April 2019 and undergoing hearings currently, would require
51 reducing catch limits for forage fish in consideration of predator needs and prohibit the
52 development of new forage fisheries until their importance to predators is assessed.

53
54 However, the effectiveness of precautionary regulations is under debate (Pikitch et al.
55 2012, 2018; Hilborn et al. 2017a, 2017b). On one hand, forage fish represent a large portion of
56 marine predator diets and reductions in prey availability below the thresholds necessary for
57 successful foraging, offspring provisioning, or survival could impact predator population growth.
58 Indeed, field studies show that fishing forage fish can reduce seabird breeding success
59 (Frederiksen et al. 2008) and ecosystem models predict that marine predator populations
60 should be sensitive to prey depletion (Smith et al. 2011; Pikitch et al. 2014). On the other hand,
61 marine predators often exhibit high mobility and diet flexibility, and species with location-based
62 breeding tend to locate breeding sites where prey abundance is stable. Together, these
63 behaviors can make them resilient to changes in prey abundance. Correlations between time
64 series of predator productivity and prey abundance indicate that predator population growth is
65 seldom correlated with the abundance of their primary prey (Hilborn et al. 2017a).

66
67 The lack of consensus regarding management of forage fish is likely due to the
68 complexity of predator-prey systems and common pitfalls in the way these systems are studied
69 (Sydeman et al. 2017). Although field studies offer the opportunity to establish a causal
70 understanding of the impact of fishing and subsequent prey depletion on marine predators, they
71 are difficult to design given natural variability in forage fish and the movements of both predators

72 and prey (Sherley et al. 2018). Ecosystem models can reveal direct and indirect effects
73 stemming from predator-prey relationships but these models are sensitive to (often implicit)
74 assumptions about prey switching, top-down vs. bottom-up control, and other poorly understood
75 processes. Furthermore, ecosystem models seldom include sufficient taxonomic resolution to
76 capture predator-specific sensitivities to prey depletion ((Essington & Plagányi 2014) but see
77 (Koehn et al. 2017)) and their conclusions can be sensitive to model choice (Kaplan et al. 2013).
78 Finally, correlational studies present the opportunity to use historical data to evaluate observed
79 predator-prey relationships but cannot demonstrate causal relationships and often fail to
80 account for spatial and temporal mismatches between predator and prey data as well as the
81 lagged effects of prey depletion on predator dynamics (Sydeman et al. 2017).

82

83 Ecosystem models of intermediate complexity ('MICE' models; (Plagányi et al. 2014b))
84 attempt to balance the advantages of single-species and whole-of-ecosystem models and may
85 have greater potential to evaluate the impact of fishing on forage fish and their predators. By
86 representing the minimum number of ecosystem components required to address the question
87 under consideration, these models are generally more focused and resolved than typical whole-
88 of-ecosystem models. MICE have been used to show that fisheries targeting different forage
89 species can influence predator populations differently (Plagányi et al. 2014a), that the effect of
90 changing prey spatial distributions can be larger than the effect of changing abundance
91 (Robinson et al. 2015), and that the effect of changing prey abundance can be unpredictable
92 when predator populations are already reduced (Watters et al. 2013).

93

94 While each of these models was tailored to a specific predator-prey system, simpler
95 MICE could be used to assess predator-prey systems across many regions in a single analysis.
96 This represents a crucial next step in understanding the frequency with which forage fish
97 abundance drives predator abundance and thus the extent to which precautionary regulations
98 on forage fish are likely to have the desired benefits for their predators. Here, we use a MICE
99 approach to measure the influence of forage fish abundance on the productivity (i.e., ability of a
100 predator population to grow in the absence of fishing) of 45 marine predator populations of 32
101 species (28/20 fish, 10/9 seabird, 7/3 mammal populations/species). The populations come from
102 five regions (US West Coast, US East Coast, Europe, Humboldt Current, South Africa) where
103 forage fish support large fisheries and are critical to the ecosystem.

104 2. Methods

105 2.1 Data collection

106 We identified 45 marine predator populations (28 fish, 10 seabird, and 7 mammal
107 populations; **Figure 1**) meeting the following criteria: (1) they rely on forage fish for $\geq 20\%$ of
108 their diet; (2) they spatially overlap with an assessed population (i.e., has an abundance index
109 or biomass estimate) of a critical prey species (i.e., $\geq 10\%$ of their diet); (3) they share ≥ 20 years
110 of overlapping abundance data with a critical prey species if they are fish predators or ≥ 15 years
111 of overlapping data if they are seabird or marine mammal predators (see **supplemental**
112 **methods** for more details). The data requirements for seabirds and marine mammals were
113 relaxed because they generally have shorter and less complete time series than fish. The
114 majority of fish abundance time series were sourced from the RAM Legacy Stock Assessment
115 Database (v4.4; (Ricard et al. 2012)). Fourteen came from government or academic stock
116 assessments not included in the database. All fish predator time series were reported as total
117 biomass in metric tons. Most prey time series were reported as absolute biomass, but some
118 were reported as indices of relative abundance. Marine mammal abundance time series came
119 primarily from NOAA Marine Mammal Stock Assessments (Carretta et al. 2017; Hayes et al.
120 2017) and were reported largely in total abundance or pup abundance. Seabird abundance time
121 series were sourced from a mixture of peer-reviewed journal publications, technical reports,
122 books, theses, and government websites. They were reported in a mixture of units including
123 total abundance, adult abundance, and number of nests or breeding pairs.

124 2.2 Population models

125 We modeled marine predator productivity in three stages. First, we modeled productivity
126 without environmental covariates and used this “base” model as a benchmark for evaluating
127 models with additional environmental covariates. Second, we extended the base model to
128 evaluate whether abundance of either the primary prey species or sum of all available critical
129 prey species influences predator productivity. Finally, we used the extended model to measure
130 the influence of sea surface temperature on predator productivity and evaluate the importance
131 of temperature relative to the importance of prey abundance.

132 2.2.1 Base model

133 We modeled predator productivity using a Pella-Tomlinson surplus production model
 134 (Pella & Tomlinson 1969) because it contains a shape parameter (p) that allows it to replicate
 135 either the Fox ($p \rightarrow 0$) or Schaefer ($p=1$) production models (Schaefer 1954; Fox Jr. 1970):

$$136$$

$$137 \quad SP_{i,t} = \frac{r_i}{p} B_{i,t} \left(1 - \left(\frac{B_{i,t}}{K_i}\right)^p\right) + \varepsilon_{i,t} \quad \text{Eq. 1}$$

138

139 where $SP_{i,t}$ is the surplus production for population i in year t , $B_{i,t}$ is the biomass, r_i is the intrinsic
 140 rate of growth, K_i is the carrying capacity, and $\varepsilon_{i,t}$ is independent identically distributed lognormal
 141 residual process variability. Surplus production was calculated for each predator population as
 142 the net change in total biomass in the absence of harvest:

$$143$$

$$144 \quad SP_{i,t} = B_{i,t+1} - B_{i,t} + C_{i,t} \quad \text{Eq. 2}$$

145

146 where $SP_{i,t}$ is the surplus production for population i over year t , $B_{i,t}$ and $B_{i,t+1}$ are the biomasses
 147 of population i in years t and $t+1$, respectively, and $C_{i,t}$ is the catch for population i removed
 148 between years t and $t+1$ ($C_{i,t}$ is zero for seabirds and marine mammals, which are not subject to
 149 harvest). We used Akaike Information Criterion (AIC; (Akaike 1974)) to compare models with
 150 shape parameters (p) that maximize productivity at 50% ($p=1.00$), 45% ($p=0.55$), 40% ($p=0.20$),
 151 and 37% ($p=0.01$) of carrying capacity and selected the model with the lowest AIC score as the
 152 “base” model. We evaluated these shape parameter values because 50% produces the
 153 symmetric Schaefer model, 40% is the meta-analytic mean for fish (Thorson et al. 2012), and
 154 37% is the asymptotic limit of this parameterization of the Pella-Tomlinson model.

155

156 In this model and its extensions below, we: (1) scaled predator abundance and
 157 production to each population's maximum abundance to ease model fitting; (2) placed a
 158 likelihood penalty on carrying capacities greater than five times the maximum abundance to
 159 constrain unrealistically large carrying capacities; and (3) fit the models using maximum
 160 likelihood estimation in the *TMB* package (Kristensen et al. 2016) in R (R Core Team 2019).

161 2.2.2 Prey-linked models

162 To evaluate the influence of prey abundance on predator productivity, we extended the
 163 base model to include a multiplicative influence term:

164

$$SP_{i,t} = \frac{r_i}{p} B_{i,t} \left(1 - \left(\frac{B_{i,t}}{K_i}\right)^p\right) * \exp(Prey_{i,t} * \theta_i) + \varepsilon_i \quad \text{Eq. 3}$$

166

167 where $Prey_{i,t}$ is the abundance of prey and θ_i is the influence of prey abundance on productivity.

168 We evaluated two measures of prey abundance: (1) the abundance of the primary prey species

169 (i.e., species representing the highest percentage of a predator's diet) and (2) the sum

170 abundance of all available critical prey species (i.e., species comprising $\geq 10\%$ of a predator's

171 diet). A composite abundance could only be calculated for the 18 predator populations

172 overlapping with critical prey populations described in the same units (i.e., all metric tons) and

173 was only calculated for years with data for all critical species. We used data for only the primary

174 prey species for the remaining 27 populations.

175

176 There are compelling arguments for estimating the prey influences as either fixed or

177 random effects. On one hand, estimating prey influence as fixed effects imposes no constraints

178 on the magnitude and distribution of the influences and could more accurately identify

179 influences that deviate from the patterns exhibited by other populations. On the other hand,

180 estimating prey influence as random effects constrains poorly informed and unrealistically large

181 influences. Thus, we also evaluated models with prey influences estimated as random effects:

182

$$\theta_i \sim N(\mu_{prey}, \sigma_{prey}^2) \quad \text{Eq.4}$$

184

185 where μ_{prey} and σ_{prey} are the mean and standard deviation of the global distribution of prey

186 influences (θ_i), respectively. In both models, $\theta_i > 0$ means that increasing prey abundance

187 magnifies productivity and $\theta_i < 0$ means that increasing prey abundance reduces productivity.

188

189 To ease model fitting, we centered and scaled the prey abundance metrics as a z-

190 scores. To evaluate the hypothesis that prey abundance influences predator productivity, we

191 compared the prey-linked production models to the base model using AIC.

192 2.2.3 Temperature-linked models

193 We compared the importance of prey abundance on predator productivity relative to that

194 of sea surface temperature, a widely available ecosystem indicator and established driver of

195 marine fisheries productivity (Free et al. 2019). The temperature-linked models were structurally

196 identical to the fixed and random effects prey-linked models but used mean annual sea surface
197 temperature (SST) as a covariate instead of prey abundance. We calculated the mean annual
198 SST experienced by each population using the population centroid and the COBE SST dataset
199 (COBE v2), which provides monthly SST on a globally complete 1°x1° grid from 1850-present
200 based on an interpolation of in-situ and satellite-derived SST observations (Ishii et al. 2005). We
201 centered SST data around each population's mean SST to ease model fitting. We used AIC to
202 compare support for the prey-linked and temperature-linked production models.

203 2.3 Power analysis

204 We measured the ability of the prey-linked fixed effects model to detect an influence of
205 prey abundance on predator productivity by applying the model to simulated predator
206 populations representing the 45 populations in our dataset (see **supplemental methods** for
207 more details). We simulated each predator population in scenarios combining each of four prey
208 influence strengths (0.25 to 1.00 by 0.25) and four levels of process variability (0.1 to 0.4 by
209 0.1). These levels were selected because they span the range of prey influence and process
210 variability values estimated by the prey-linked fixed effects models. Each simulation began at
211 the observed initial biomass and progressed with catch determined by the observed exploitation
212 rate and population growth rate determined by the carrying capacity and time-varying intrinsic
213 growth rate estimated by the composite prey-linked fixed effects model (the “best” prey model;
214 **Table 1**). Population growth rates were influenced by the observed composite prey densities
215 and the evaluated combination of prey influence and process variability parameters following
216 Eq. 3. We performed 100 iterations of each scenario, fit the fixed effects model to each scenario
217 iteration (45 per scenario iteration), recorded the percentage of populations estimated to be
218 significantly positively influenced by prey abundance, and calculated the mean percentage
219 across the 100 iterations performed for each scenario.

220 3. Results

221 Significant influences of prey abundance on predator productivity were only detected
222 when estimating prey influences as fixed effects (**Figure 2**). Neither of the prey-linked random
223 effects models identified significant influences of prey abundance on predator productivity and
224 both failed to garner more support than the base model based on AIC (**Table 1**). By
225 comparison, both the random and fixed effects temperature-linked models identified significant
226 influences of ocean warming on predator productivity (**Figure 2**) and both garnered more

227 support than the base model based on AIC (**Table 1**). The fixed effect temperature-linked model
228 was the best overall descriptor of predator population dynamics (**Figure 2; Table 1**).

229

230 The fixed effects prey-linked models identified the same thirteen predator populations
231 (28.8% of evaluated populations) as being significantly influenced by prey abundance. They
232 identified significant positive influences for only six populations (4 fish, 2 seabirds) and
233 significant negative influences for seven populations (3 fish, 2 seabirds, 2 mammals) (**Figure 2**).
234 The influence of prey abundance on predator productivity when estimated as a fixed effect was
235 weakly structured by the importance of forage fish to predator diets (**Figure 3**). Populations of
236 species with higher dependence on forage fish were somewhat more likely to experience
237 increasing productivity with increasing prey abundance.

238

239 The prey-linked fixed effects model has high power to detect significant influences of
240 prey abundance on predator productivity (**Figure 4**). Even with weak prey influences ($\theta=0.25$)
241 and high process variability ($\sigma_P=0.4$), the model successfully detected 77% of positive prey
242 influences. With stronger prey influences and lower process variabilities, the model successfully
243 detected 85-99% of positive prey influences (**Figure 4**).

244 4. Discussion

245 Our results indicate that precautionary catch limits on forage fish are unlikely to be an
246 effective tool for advancing the protection of marine predators. We were only able to detect
247 significant influences of prey abundance on predator productivity when estimating these
248 influences as fixed effects, which are anti-conservative (i.e., more likely to overestimate
249 magnitude and significance of an effect), especially for small and noisy datasets (Bell et al.
250 2019). Even in the fixed effects models, only 13.3% of predator populations exhibited a positive
251 response to increasing prey abundance. In fact, more exhibited a negative response (15.5%). In
252 comparison, the influence of sea surface temperature, a known driver of marine population
253 dynamics (Free et al. 2019), was strong enough to detect in both random and fixed effects
254 modeling frameworks, with the fixed effects temperature-linked model garnering the most
255 statistical support among all models.

256

257 The resilience of predator populations to changing prey conditions is supported by a
258 large number of field studies documenting behavioral plasticity in diet composition, foraging

259 sites, and breeding site selection across taxa and geographies (Brakes & Dall 2016; Gilmour et
260 al. 2018). For example, Great skuas in the North Sea switch prey in response to fisheries-driven
261 declines in sandeel abundance, allowing them to maintain healthy population status (Church et
262 al. 2019). Little penguin in southeast Australia adaptively change forage locations based on
263 catch rates in prior visits and social cues (Carroll et al. 2018). Humpback whales in the Gulf of
264 Maine exhibit high behavioral plasticity based on the movement and structure of prey fields
265 (Kirchner et al. 2018). Furthermore, seabirds and marine mammals with location-based
266 breeding have evolved to select breeding sites that are adjacent to areas with high, stable, and
267 diverse prey availability, which buffers them against changing prey conditions (Hilborn et al.
268 2017a). Finally, diet specialization (i.e., diet dominated by a single prey species) was rare
269 except in seabirds and generalist diet strategies are more robust to fluctuations in prey (Schoen
270 et al. 2018). Furthermore, instances of apparent specialization in highly mobile predators based
271 on stomach contents are often an artifact of prey patchiness in space and time and may not
272 accurately reflect the dietary flexibility of an individual or population (Young et al. 2018).

273

274 The counterintuitive finding that predator population productivity can be negatively
275 impacted by increasing prey abundance could arise through several mechanisms. For fish
276 predators, this could occur through the cultivation-dependensation hypothesis or through intense
277 overfishing. The cultivation-dependensation hypothesis (Walters & Kitchell 2001) suggests that
278 adult prey species often consume or compete with juvenile predator species and that the
279 depletion of adult predators from fishing can result in the release of prey from predation. This
280 results in an increase in prey abundance while predator productivity declines. Although
281 empirical studies testing this hypothesis are limited, strong evidence for cultivation-dependensation
282 effects has been found for North Atlantic cod and herring populations (Minto & Worm 2012).
283 Alternatively, the continuation of excessive fishing for predators could reduce predator
284 productivity while reforms in forage fisheries simultaneously rebuild prey abundance (Hilborn &
285 Litzinger 2009). For all taxa, predators and prey may respond differently to environmental
286 change and favorable conditions for prey may be unfavorable to predators. Finally, the recovery
287 of predators can result in reduced prey abundance (i.e., through top-down control), resulting in
288 increasing predator productivity with decreasing prey abundance (van Gemert et al. 2018).

289

290 Although seabird and marine mammal populations rarely benefitted from increases in
291 population-wide prey abundance, they could see greater benefits from increases in local
292 abundance, which can be achieved by restricting fishing near breeding locations. For example,

293 the Cape Gannet population on the Western Cape of South Africa, one of two seabird
294 populations identified as having been positively influenced by prey abundance, has declined
295 since the 1950s partially due to declines in local prey abundance (Sherley et al. 2019). Declines
296 in the local abundance of sardine and anchovy resulted in increased adult foraging effort, which
297 reduced adult body condition, increased chick predation risk via reduced nest attendance, and
298 slowed chick growth (Cohen et al. 2014). A number of other studies confirm that predator
299 reproductive success is linked to local prey abundance (Cury et al. 2011), suggesting that
300 spatial-temporal restrictions in fishing around breeding sites could be more effective than
301 precautionary population-wide regulations, which likely fail because local abundance is not
302 necessarily correlated with total abundance (Robinson et al. 2015).

303

304 The impact of prey on predator productivity is inherently difficult to detect (Sydeman et
305 al. 2017; Sherley et al. 2018) and our study is subject to several analytical constraints. First, we
306 were unable to evaluate the influence of a predator's entire prey field on its productivity because
307 (1) its prey species were not assessed in all or part of its range and/or (2) it preys on juvenile
308 predator species not being considered for precautionary regulations. Second, the strength of the
309 prey influence could be muddled because we do not consider the size-selectivity of predation,
310 i.e., changes in abundance within particular size classes could show a stronger signal than
311 changes in total or spawning stock biomass. Third, the predator populations evaluated here
312 come from regions with strong fisheries management (Hilborn et al. 2020) and forage fish
313 populations in these areas have been relatively well-managed over the past 35 years (**Figure**
314 **S1**). Although precautionary catch limits for forage fish may not be effective conservation tools
315 in these regions, they may be more effective in regions where ineffective fisheries management
316 has allowed depletion of forage fish populations well below target abundance.

317

318 Our results suggest that the expected benefits of precautionary management of forage
319 fish for the conservation of their predators are unlikely to be detectable in most cases. At the
320 same time, forgoing sustainable harvest of forage fish places greater pressure on other protein
321 sources -- a trade-off with important conservation implications that will vary depending on the
322 protein source that replaces forage fish (Hilborn et al. 2018). Thus, conservation actions that
323 effectively enhance the resilience of marine predators populations while minimizing impacts on
324 fisheries that provide food, support livelihoods, and offset terrestrial impacts are central to
325 advancing holistic sustainability. These measures could include efforts to (1) reduce bycatch
326 and incidental mortality, a serious threat to both seabirds and marine mammals, through

327 modifications to fishing gear or dynamic ocean management (Hazen et al. 2018); (2) protect
328 breeding sites by restoring habitat, removing invasives, and reducing human disturbance
329 (Croxall et al. 2012); or (3) restrict fishing close to breeding sites. Seabirds and marine
330 mammals are among the most highly threatened marine animals (Dias et al. 2019) and
331 preserving these critical members of marine ecosystems (Heithaus et al. 2008; Ritchie &
332 Johnson 2009) will depend on implementing measures that are empirically demonstrated to be
333 effective.

For Peer Review

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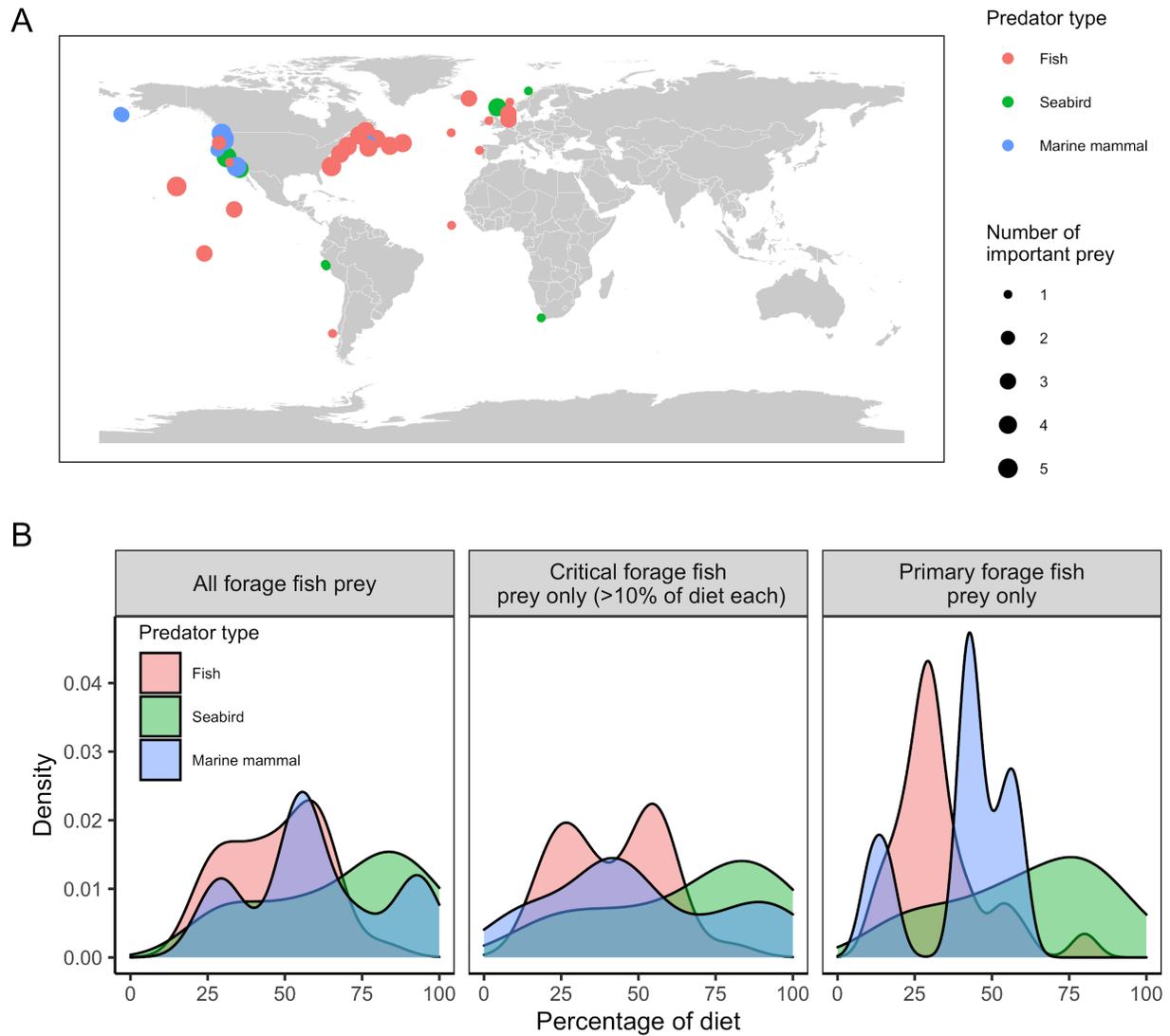
483 Tables & Figures

484 **Table 1.** AIC comparison of candidate surplus production models (PT=Pella-Tomlinson;
 485 SST=sea surface temperature).

486

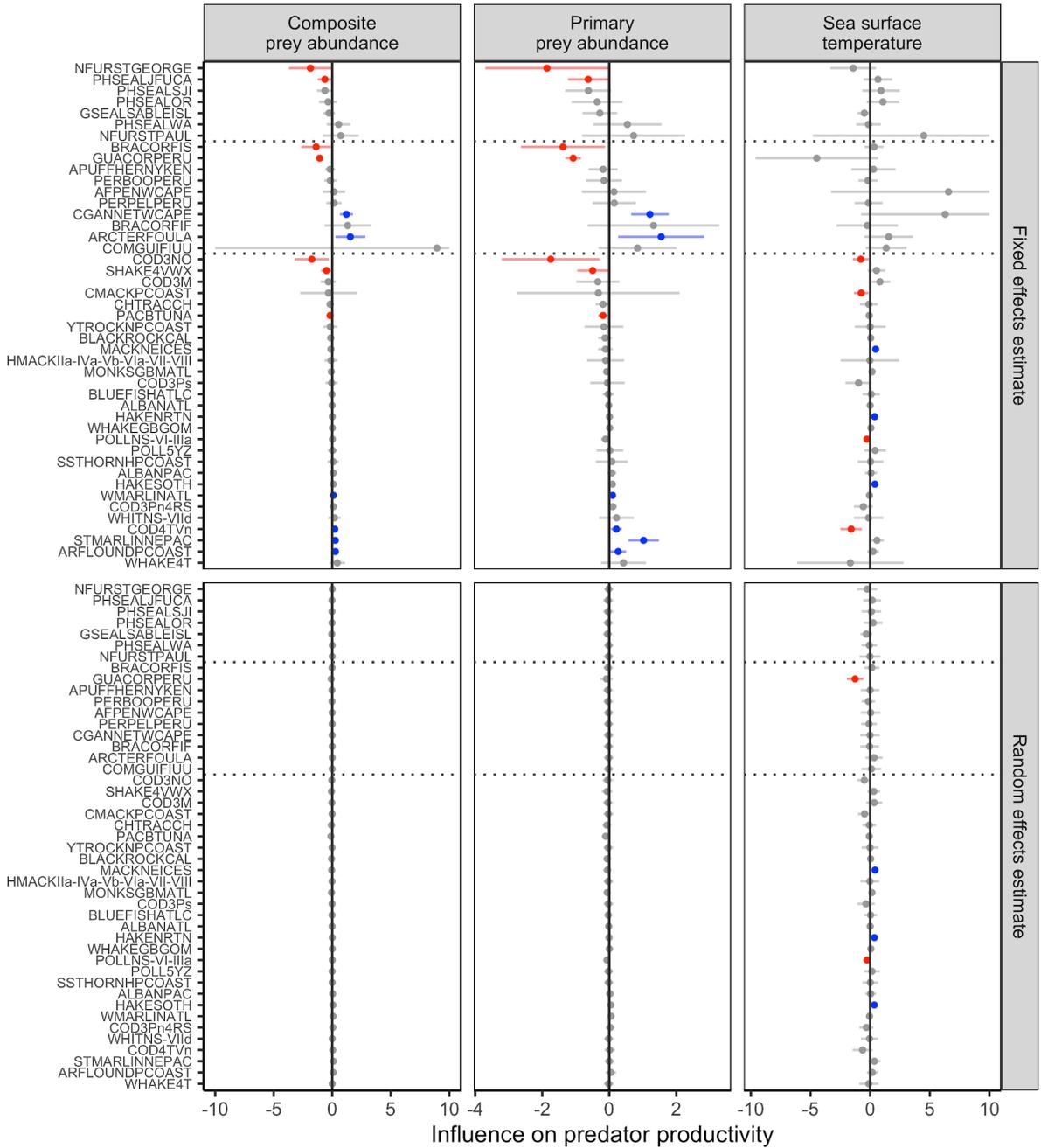
Model	K	Likelihood	AIC	Δ AIC
<i>Question 1: Is productivity symmetric?</i>				
PT model (MSY@45%K) (base model)	135	-1938.3	-3606.6	0.0
PT model (MSY@40%K)	135	-1937.6	-3605.2	1.4
PT model (MSY@37%K)	135	-1935.3	-3600.5	6.0
PT model (MSY@50%K)	135	-1934.8	-3599.5	7.1
<i>Question 2: Does prey abundance influence productivity?</i>				
Primary prey (fixed effects) (best prey model)	180	-2000.3	-3640.6	0.0
Composite prey (fixed effects)	180	-1997.7	-3635.4	5.2
Primary prey (random effects)	137	-1940.6	-3607.2	33.4
PT model (MSY@45%K) (base model)	135	-1938.3	-3606.6	34.0
Composite prey (random effects)	137	-1940.2	-3606.5	34.2
<i>Question 3: Does primary prey influence productivity as much as SST?</i>				
SST (fixed effects) (best SST model)	180	-2012.0	-3664.1	0.0
Primary prey (fixed effects) (best prey model)	180	-2000.3	-3640.6	23.5
Composite prey (fixed effects)	180	-1997.7	-3635.4	28.7
SST (random effects)	137	-1953.6	-3633.1	30.9
Primary prey (random effects)	137	-1940.6	-3607.2	56.9
PT model (MSY@45%K) (base model)	135	-1938.3	-3606.6	57.5
Composite prey (random effects)	137	-1940.2	-3606.5	57.6

487

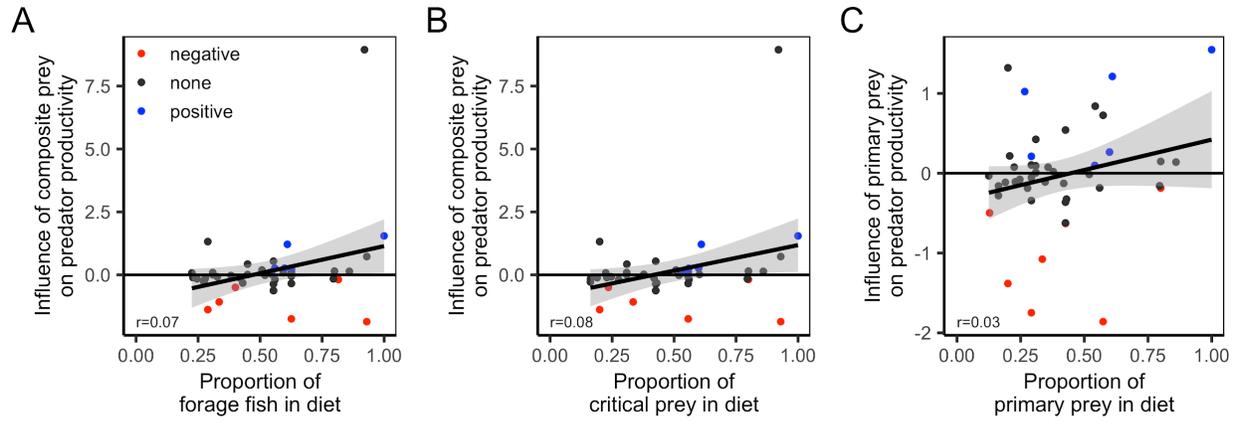


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490 **Figure 1.** The **(A)** location of the evaluated marine predator populations and **(B)** their
491 dependence on forage fish as a source of prey. In Panel B, density distributions show the
492 percent of predator diets comprised of all forage fish prey, critical forage fish prey (i.e., all
493 species individually representing >10% of the diet), and the primary forage fish prey (i.e., the
494 species representing the largest percentage of the diet).



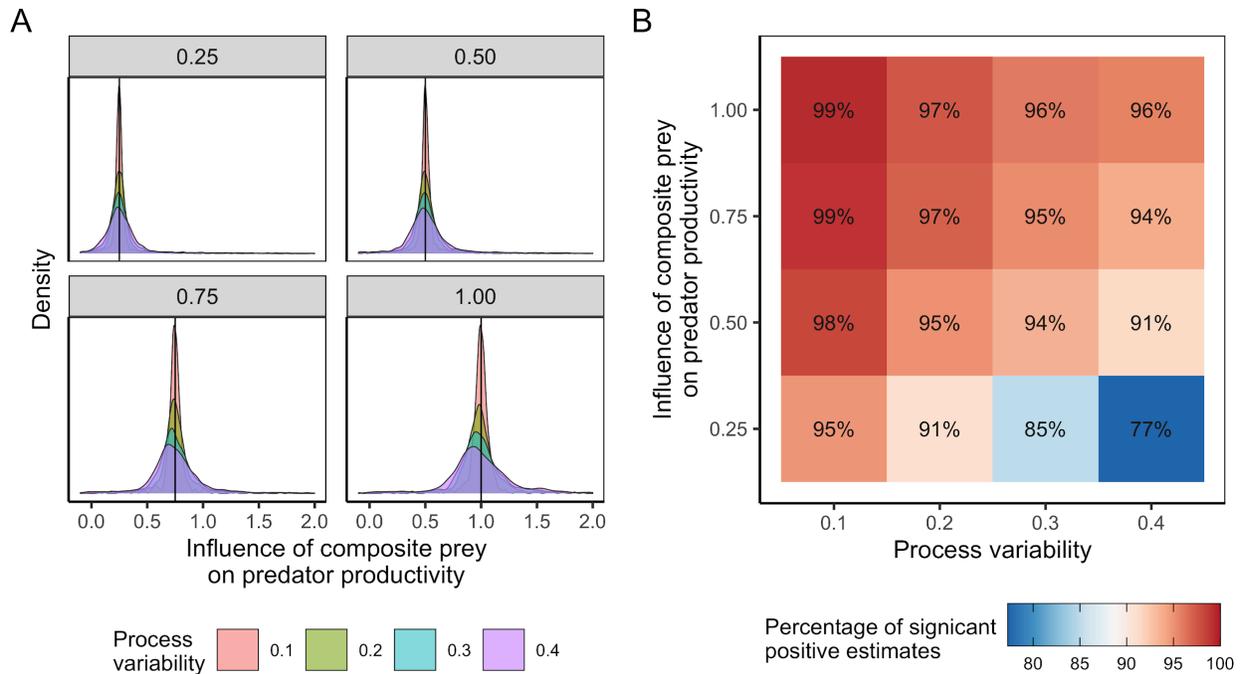
495
 496 **Figure 2.** Influence of (a) composite prey abundance, (b) primary prey abundance, and (c) sea
 497 surface temperature on predator productivity when estimated as either random or fixed effects.
 498 Points show mean estimates and error bars show 95% confidence intervals. Significant positive
 499 and negative influences are shown in blue and red, respectively. Horizontal lines divide
 500 estimates for fish, seabird, and marine mammal predators. See **Table S5** for more information
 501 on each predator population.



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503

504 **Figure 3.** Impact of the contribution of forage fish to predator diets in determining the influence
505 of prey abundance on predator productivity as measured in the fixed effects framework. Point
506 color indicates the statistical significance of the prey influence estimate.



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Figure 4. The ability of the prey-linked fixed effects model to estimate the influence of prey abundance on predator productivity when applied to simulated predator populations with specified prey influences and process variabilities. Panel A shows the distribution of prey influence estimates relative to the specified prey influence strength (dark vertical line) in simulations with varying levels of process variability. Panel B shows the percentage of statistically significant positive prey influence estimates at specified levels of prey influence and process variability.

515 Supporting Information

516 1. Supplemental Methods

517 2.1 Prey data

518 We identified 17 prey species important in the five study regions. We identified 46 prey
519 populations with time series of total biomass or spawning stock biomass (total biomass
520 preferred) longer than 20 years after trimming years poorly informed by catch and survey data
521 (**Tables S1-S3**). All but five prey populations were sourced from the RAM Legacy Stock
522 Assessment Database (RAMLDB v4.4; (Ricard et al. 2012)). The others came from government
523 or academic stock assessments not included in the database. Biomass estimates are reported
524 in metric tons for all populations except the northern shortfin squid and ICES 31 Atlantic herring
525 populations, which are reported as abundance indices.

526 1.2 Predator data

527 We conducted a literature review to identify marine predators (fish, birds, and mammals)
528 that eat these species and quantify the importance of these species to each predator. We
529 calculated the importance of a prey species to a predator as the mean proportion of the prey
530 species in the diet of a predator by region. We calculated mean diet proportions using the
531 following composition metrics, listed in order of preference: (1) by weight; (2) by count; (3) by
532 energetic contribution; (4) by frequency of occurrence; (5) by ecosystem model; and (6)
533 unknown. In some cases, diet proportions sum to values greater than one since they are
534 averaged across studies. We only considered predator populations whose diets are comprised
535 of greater than 20% of the prey species identified here. Overall, we found >150 studies
536 describing the diet composition of 138 predator species and 155 region-predator couples.
537

538 We identified 38 fish predator populations whose diets are more than 20% forage fish
539 and with time series of total biomass (metric tons) and catch or landings (metric tons; catch
540 preferred) longer than 20 years after trimming years poorly informed by catch and survey data
541 (**Tables S1, S4, S5**). All fish predator populations were sourced from the RAM Legacy Stock
542 Assessment Database (Ricard et al. 2012). We identified 33 seabird and marine mammal
543 populations whose diets are more than 20% forage fish and with time series of abundance
544 longer than 15 years (**Tables S1, S6**). We relaxed the data requirements for seabirds and
545 mammals given their tendency to have shorter and less complete time series. Marine mammal
546 abundance time series came primarily from NOAA Marine Mammal Stock Assessments
547 (Carretta et al. 2017; Hayes et al. 2017) and are reported largely in total abundance or pup
548 abundance. Seabird abundance time series were sourced from a mixture of peer-reviewed
549 journal publications, technical reports, books, theses, and government websites. They are
550 reported in a mixture of units including total abundance, adult abundance, and number of nests
551 or breeding pairs.

552 1.3 Linking predator and prey data

553 Overall, we identified 45 marine predator populations (28 fish, 10 seabirds, 7 marine
554 mammals) that spatially overlapped with populations of their primary prey. We evaluated the
555 spatial overlap of fish/prey populations using the RAM Legacy Stock Boundary Database (Free
556 2017), which delineates the spatial boundaries assumed by the underlying stock assessment.
557 We evaluated the spatial overlap of seabird/prey populations and mammal/prey populations by
558 mapping the locations of the evaluated seabird colonies and marine mammal distributions.
559 When a predator population was overlapped by multiple populations of its primary prey, we
560 summed the abundance time series of the overlapping prey populations. For example, the North
561 Sea whiting population overlaps sandeel populations in Sandeel Areas 1, 2, and 3 and was
562 assigned a composite prey abundance time series that sums abundance across these three
563 populations. In all instances ($n=3$), the component prey population biomasses were in identical
564 units.

565 1.4 Power analysis

566 We used simulation testing to measure the power of the composite prey-linked fixed
567 effects model to detect an influence of prey abundance on predator productivity under various
568 combinations of prey influence (4 levels; 0.25 to 1.00 by 0.25) and process variability (4 levels;
569 0.1 to 0.4 by 0.1). Each predator population was simulated for the number of years in its
570 observed time series (**Figure S5**). Simulations began with observed initial biomasses, catch
571 was determined by the observed exploitation rate, and time-varying population growth rates
572 were determined by the model estimated carrying capacities and intrinsic growth rates. The
573 population growth rate was influenced by the observed composite prey abundance and the
574 evaluated combination of prey influence (θ) and process variability (σ_P) parameters (**Table S7**).
575

576 Thus, biomass in time t for predator population i was calculated as:

$$577 \quad B_{i,t} = B_{i,t-1} + SP_{i,t-1} - C_{i,t-1} \quad \text{Eq. 5}$$

578 where $B_{i,t}$ and $B_{i,t+1}$ are the biomasses of population i in years t and $t+1$, respectively, $SP_{i,t}$ is the
581 surplus production for population i over year t , and $C_{i,t}$ is the catch for population i removed
582 between years t and $t+1$ ($C_{i,t}$ is zero for seabirds and marine mammals, which are not subject to
583 harvest). The surplus production between times t and $t-1$ was calculated as:

$$584 \quad SP_{i,t-1} = \frac{r_i}{p} B_{i,t} \left(1 - \left(\frac{B_{i,t}}{K_i}\right)^p\right) * \exp(\text{Prey}_{i,t} * \theta_i) + \varepsilon_{i,t} \quad \text{Eq. 6}$$

586 where the shape parameter, p , is fixed at 0.55, r_i is the intrinsic rate of growth, K_i is the carrying
588 capacity, $\text{Prey}_{i,t}$ is the observed composite prey abundance, θ is the influence of prey abundance
589 on productivity, and $\varepsilon_{i,t}$ is independent identically distributed lognormal residual process
590 variability with standard deviation, σ_P . Catch in time $t-1$ was calculated as:

$$591 \quad C_{i,t-1} = ER_{Obs,i,t-1} * B_{i,t-1} \quad \text{Eq. 7}$$

593
594 where $ER_{obs,i,t-1}$ is the observed exploitation rate (observed catch divided by observed biomass).
595

596 We performed 100 iterations of each scenario, fit the fixed effects model to each
597 scenario iteration (45 per scenario iteration), recorded the percentage of populations estimated
598 to be significantly positively influenced by prey abundance, and calculated the mean percentage
599 across the 100 iterations performed for each scenario.

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600 2. Supplemental Tables & Figures

601

602 **Table S1.** Predator and prey population selection criteria and sample sizes.

603

Criteria	# of populations
<i>Prey populations</i>	
All RAM Legacy Populations	1252
Populations of prey species	63
Populations in 4 study regions	54
Populations with ≥ 20 years of TB or SSB data	42
Plus 5 populations not in the RAMLDB	47
Populations with ≥ 20 years of data after trimming	47
<i>Fish predator populations</i>	
All RAM Legacy populations	1252
Populations of predator species	171
Populations in 4 study regions	147
Populations with TB and catch in metric tons	93
Populations with TB and catch time series ≥ 20 years	88
Populations with regional diet information	73
Populations with $\geq 20\%$ of diet composed of forage fish	45
Populations with ≥ 20 years of data after trimming	38
Populations with overlapping primary prey populations	28
<i>Bird/mammal predator populations</i>	
Populations with ≥ 15 years of data	37
Populations with regional diet information	34
Populations with $\geq 20\%$ of diet composed of forage fish	33
Populations with overlapping primary prey populations	29
Populations with ≥ 15 years of data after merging	23
Removed 3 highly correlated Peruvian bird populations	20
Removed 2 population with wild dynamics	18

604

605 **Table S2.** Number of prey populations by region and species.

606

Region / prey species	# of stocks
<i>Europe (n=28)</i>	
Atlantic herring (<i>Clupea harengus</i>)	12
Atlantic herring (<i>Clupea harengus</i>)	1
Atlantic mackerel (<i>Scomber scombrus</i>)	1
Blue whiting (<i>Micromesistius poutassou</i>)	1
Capelin (<i>Mallotus villosus</i>)	2
European sprat (<i>Sprattus sprattus</i>)	2
Lesser sand-eel (<i>Ammodytes marinus</i>)	3
Lesser sand-eel (<i>Ammodytes</i> spp.)	2
Norway pout (<i>Trisopterus esmarkii</i>)	1
Whiting (<i>Merlangius merlangus</i>)	3
<i>Humboldt Current (n=4)</i>	
Peruvian anchoveta (<i>Engraulis ringens</i>)	4
<i>South Africa (n=5)</i>	
European anchovy (<i>Engraulis encrasicolus</i>)	2
Pacific sardine (<i>Sardinops sagax</i>)	2
Pacific sardine (<i>Sardinops sagax</i>)	1
<i>US/Canada East Coast (n=13)</i>	
Atlantic herring (<i>Clupea harengus</i>)	6
Atlantic mackerel (<i>Scomber scombrus</i>)	2
Atlantic menhaden (<i>Brevoortia tyrannus</i>)	1
Gulf menhaden (<i>Brevoortia patronus</i>)	1
Longfin inshore squid (<i>Doryteuthis pealeii</i>)	1
Northern shortfin squid (<i>Illex illecebrosus</i>)	2
<i>US/Canada West Coast (n=11)</i>	
Northern anchovy (<i>Engraulis mordax</i>)	1
Pacific chub mackerel (<i>Scomber japonicus</i>)	1
Pacific hake (<i>Merluccius productus</i>)	1
Pacific sardine (<i>Sardinops sagax</i>)	1
Rockfish spp. (<i>Sebastes</i> spp.)	3
Walleye pollock (<i>Theragra chalcogramma</i>)	4

607

608 **Table S3.** Prey population details.
609

Stock id	Species	Area	Biomass type	Years	# of years
<i>Europe (n=28)</i>					
ATLHERRROST	Atlantic herring (<i>Clupea harengus</i>)	Rost	Index	1975-2004	29
HERR2224IIIa	Atlantic herring (<i>Clupea harengus</i>)	22-24-IIIa	SSB	1991-2016	26
HERR2529-32	Atlantic herring (<i>Clupea harengus</i>)	Subdivisions 25-29 and 32	SSB	1974-2016	43
HERR30	Atlantic herring (<i>Clupea harengus</i>)	Bothnian Sea	SSB	1973-2016	44
HERR31	Atlantic herring (<i>Clupea harengus</i>)	Bothnian Bay	SSB	1980-2015	36
HERRIsum	Atlantic herring (<i>Clupea harengus</i>)	Iceland Grounds	TB	1987-2015	29
HERRNIRS	Atlantic herring (<i>Clupea harengus</i>)	Irish Sea	SSB	1961-2016	56
HERRNORSS	Atlantic herring (<i>Clupea harengus</i>)	I-II-IVa-V-XIVa	TB	1988-2015	28
HERRNS-IIIa-VIId	Atlantic herring (<i>Clupea harengus</i>)	IIIa, VIId and North Sea	SSB	1947-2016	70
HERRRIGA	Atlantic herring (<i>Clupea harengus</i>)	Gulf of Riga East of Gotland	SSB	1977-2016	40
HERRSIRS	Atlantic herring (<i>Clupea harengus</i>)	ICES VIIa-g-h-j	SSB	1958-2016	59
HERRVIa	Atlantic herring (<i>Clupea harengus</i>)	West of Scotland	TB	1957-2013	57
HERRVIaVIIbc	Atlantic herring (<i>Clupea harengus</i>)	VIa, VIIb and VIIC	SSB	1957-2016	60
MACKNEICES	Atlantic mackerel (<i>Scomber scombrus</i>)	IIa-IIIabd-IV-Vb-VI-VII-VIIIabcde-XII-XIV-Ixa	SSB	1980-2014	35
BWHITNEA	Blue whiting (<i>Micromesistius poutassou</i>)	Northeast Atlantic	SSB	1981-2015	35
CAPEIIa-V-XIV	Capelin (<i>Mallotus villosus</i>)	IIa-V-XIV	SSB	1979-2016	38
CAPENOR	Capelin (<i>Mallotus villosus</i>)	Barents Sea	TB	1972-2006	35
SPRAT22-32	European sprat (<i>Sprattus sprattus</i>)	Baltic Areas 22-32	TB	1974-2016	43
SPRATNS	European sprat (<i>Sprattus sprattus</i>)	North Sea	SSB	1974-2016	43
SEELNSSA1	Lesser sand-eel (<i>Ammodytes marinus</i>)	Sandeel Area 1	SSB	1983-2016	34
SEELNSSA2	Lesser sand-eel (<i>Ammodytes marinus</i>)	Sandeel Area 2	SSB	1983-2016	34
SEELNSSA3	Lesser sand-eel (<i>Ammodytes marinus</i>)	Sandeel Area 3	SSB	1983-2016	34
SANDEELSA4	Lesser sand-eel (<i>Ammodytes</i> spp.)	Sandeel Area 4	TB	1993-2015	23
SANDEELSA7	Lesser sand-eel (<i>Ammodytes</i> spp.)	Sandeel Area 7	TB	1976-2004	29
NPOUTIIIa-IV	Norway pout (<i>Trisopterus esmarkii</i>)	IIIa and North Sea	SSB	1983-2014	32

WHITNS-VIId	Whiting (Merlangius merlangus)	IV and VIId	TB	1990-2016	27
WHITVIa	Whiting (Merlangius merlangus)	West of Scotland	TB	1981-2016	36
WHITVIIek	Whiting (Merlangius merlangus)	Celtic Sea	SSB	1999-2016	18
<i>Humboldt Current (n=4)</i>					
PANCHCCH	Peruvian anchoveta (Engraulis ringens)	Central Chile	TB	1985-2016	32
PANCHCSCH	Peruvian anchoveta (Engraulis ringens)	Central-Southern Chile	TB	1990-2016	27
PANCHNCHSP	Peruvian anchoveta (Engraulis ringens)	Northern Chile Southern Peru	TB	1984-2015	32
PANCHPERUNC	Peruvian anchoveta (Engraulis ringens)	North-Central Peruvian coast	TB	1963-2015	53
<i>South Africa (n=5)</i>					
EANCHOROBHEN_SPWN	European anchovy (Engraulis encrasicolus)	Robben Island	Index	1989-2004	16
EANCHOROBHEN_YOY	European anchovy (Engraulis encrasicolus)	Robben Island	Index	1989-2004	16
PSARDROBBEN_SPWN	Pacific sardine (Sardinops sagax)	Robben Island	Index	1989-2005	17
PSARDROBBEN_YOY	Pacific sardine (Sardinops sagax)	Robben Island	Index	1989-2005	17
SARDSA	Pacific sardine (Sardinops sagax)	South Africa	SSB	1983-2015	33
<i>US/Canada East Coast (n=13)</i>					
HERR4RFA	Atlantic herring (Clupea harengus)	NAFO division 4R	SSB	1973-2003	31
HERR4RSP	Atlantic herring (Clupea harengus)	NAFO division 4R	TB	1965-2004	40
HERR4TFA	Atlantic herring (Clupea harengus)	Southern Gulf of St. Lawrence	SSB	1978-2014	37
HERR4TSP	Atlantic herring (Clupea harengus)	Southern Gulf of St. Lawrence	SSB	1978-2014	37
HERR4VWX	Atlantic herring (Clupea harengus)	Scotian Shelf and Bay of Fundy	TB	1965-2006	42
HERRNWATLC	Atlantic herring (Clupea harengus)	Northwestern Atlantic Coast	SSB	1965-2014	50
ATLMACKUSEAST	Atlantic mackerel (Scomber scombrus)	Northwest Atlantic	SSB	1968-2016	49
MACKNWATLSA3-4	Atlantic mackerel (Scomber scombrus)	Northwest Atlantic (NAFO Subareas 3 and 4)	TB	1968-2013	46
MENATLAN	Atlantic menhaden (Brevoortia tyrannus)	Atlantic	TB	1955-2016	62
MENATGM	Gulf menhaden (Brevoortia patronus)	Gulf of Mexico	TB	1977-2011	35
LISQUIDATLC	Longfin inshore squid (Doryteuthis pealeii)	Atlantic Coast	TB	1976-2009	34
ILLEXNAFO3-4	Northern shortfin squid (Illex illecebrosus)	Subareas 3+4	TB	1970-2015	46
ILLEXNWATLC	Northern shortfin squid (Illex illecebrosus)	Northwestern Atlantic Coast	TB	1967-2005	39
<i>US/Canada West Coast (n=11)</i>					

NANCHSCAL	Northern anchovy (<i>Engraulis mordax</i>)	Southern California	SSB	1951-2011	61
CMACKPCOAST	Pacific chub mackerel (<i>Scomber japonicus</i>)	Pacific Coast	TB	1983-2015	33
PHAKEPCOAST	Pacific hake (<i>Merluccius productus</i>)	Pacific Coast	SSB	1966-2016	51
SARDPCOAST	Pacific sardine (<i>Sardinops sagax</i>)	Pacific Coast	TB	1994-2016	23
ROCKSEFI1	Rockfish spp. (<i>Sebastes</i> spp.)	SE Farallon Island	Index	1980-1997	18
ROCKSEFI2	Rockfish spp. (<i>Sebastes</i> spp.)	SE Farallon Island	Index	1983-1997	15
ROCKSEFI3	Rockfish spp. (<i>Sebastes</i> spp.)	SE Farallon Island	Index	1987-2002	16
WPOLLAI	Walleye pollock (<i>Theragra chalcogramma</i>)	Aleutian Islands	TB	1978-2015	38
WPOLLBOGO	Walleye pollock (<i>Theragra chalcogramma</i>)	Bogoslof	TB	1990-2015	26
WPOLLEBS	Walleye pollock (<i>Theragra chalcogramma</i>)	Eastern Bering Sea	TB	1964-2015	52
WPOLLGA	Walleye pollock (<i>Theragra chalcogramma</i>)	Gulf of Alaska	TB	1970-2015	46

611 **Table S4.** Number of fish predator populations by region and species.
 612

Region / predator species	# of stocks
<i>Europe (n=12)</i>	
Atlantic mackerel (<i>Scomber scombrus</i>)	1
European hake (<i>Merluccius merluccius</i>)	2
Horse mackerel (<i>Trachurus trachurus</i>)	1
Megrim (<i>Lepidorhombus whiffiagonis</i>)	2
Pollock (<i>Pollachius virens</i>)	4
Whiting (<i>Merlangius merlangus</i>)	2
<i>Humboldt Current (n=1)</i>	
Chilean jack mackerel (<i>Trachurus murphyi</i>)	1
<i>USA/Canada East Coast (n=13)</i>	
Albacore tuna (<i>Thunnus alalunga</i>)	1
Atlantic cod (<i>Gadus morhua</i>)	5
Bluefish (<i>Pomatomus saltatrix</i>)	1
Goosefish (<i>Lophius americanus</i>)	1
Pollock (<i>Pollachius virens</i>)	1
Silver hake (<i>Merluccius bilinearis</i>)	1
White hake (<i>Urophycis tenuis</i>)	2
White marlin (<i>Kajikia albida</i>)	1
<i>USA/Canada West Coast (n=12)</i>	
Albacore tuna (<i>Thunnus alalunga</i>)	1
Arrowtooth flounder (<i>Atheresthes stomias</i>)	3
Black rockfish (<i>Sebastes melanops</i>)	2
Pacific bluefin tuna (<i>Thunnus orientalis</i>)	1
Pacific chub mackerel (<i>Scomber japonicus</i>)	1
Shortspine thornyhead (<i>Sebastes alascanus</i>)	2
Striped marlin (<i>Kajikia audax</i>)	1
Yellowtail rockfish (<i>Sebastes flavidus</i>)	1

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614 **Table S5.** Fish predator population details.
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Predator stock	Common name (scientific name)	Area	Primary prey	Primary prey stocks	% of diet	Additional important prey	Add. important prey stocks	% of diet
Atlantic Ocean								
ALBANATL	Albacore tuna (<i>Thunnus alalunga</i>)	Northern Atlantic	Northern shortfin squid	NANCHSCAL	52%	-----	-----	52%
WMARLINATL	White marlin (<i>Kajikia albigata</i>)	Atlantic Ocean	Northern shortfin squid	NANCHSCAL	54%	-----	-----	54%
Europe								
MACKNEICES	Atlantic mackerel (<i>Scomber scombrus</i>)	Ila-IIlabd-IV-Vb-VI-VII-VIIIabcde-XII-XIV-IXa	Sandeel spp.	SEELNSSA1, SEELNSSA2, SEELNSSA3	19%	-----	-----	19%
HAKENRTN	European hake (<i>Merluccius merluccius</i>)	Illa-IV-VI-VII-VIIIabd	Blue whiting	BWHITNEA	31%	-----	-----	31%
HAKESOTH	European hake (<i>Merluccius merluccius</i>)	VIIIc-IXa	Blue whiting	BWHITNEA	31%	-----	-----	31%
HMAKIIa-IVa-Vb-VIa-VII-VIII	Horse mackerel (<i>Trachurus trachurus</i>)	Ila-IVa-Vb-VIa-VII-VIII	Norway pout	NPOUTIIla-IV	23%	-----	-----	23%
MEG8c9a	Megrim (<i>Lepidorhombus whiffiagonis</i>)	VIIIc-IXa	European sprat	no overlap	34%	Norway pout	no overlap	58%
MEGVII-VIIIabd	Megrim (<i>Lepidorhombus whiffiagonis</i>)	VII and VIIIabd	European sprat	no overlap	34%	Norway pout	no overlap	58%
POLLFAPL	Pollock (<i>Pollachius virens</i>)	Faeroe Plateau	Norway pout	no overlap	35%	Sandeel spp.	no overlap	60%
POLLIEG	Pollock (<i>Pollachius virens</i>)	Iceland Grounds	Norway pout	no overlap	35%	Sandeel spp.	no overlap	60%
POLLNEAR	Pollock (<i>Pollachius virens</i>)	North-East Arctic	Norway pout	no overlap	35%	Sandeel spp.	no overlap	60%
POLLNS-VI-Illa	Pollock (<i>Pollachius virens</i>)	Illa, VI and North Sea	Norway pout	NPOUTIIla-IV	35%	Sandeel spp.	SEELNSSA1, SEELNSSA2, SEELNSSA3	60%
WHITNS-VIId	Whiting (<i>Merlangius merlangus</i>)	IV and VIId	Sandeel spp.	SEELNSSA1, SEELNSSA2, SEELNSSA3	21%	European sprat, Norway pout	NPOUTIIla-IV	51%
WHITVIa	Whiting (<i>Merlangius merlangus</i>)	West of Scotland	Sandeel spp.	no overlap	21%	European sprat, Norway pout	no overlap	51%
Humboldt Current								
CHTRACCH	Chilean jack mackerel (<i>Trachurus murphyi</i>)	Chilean EEZ and offshore	Peruvian anchoveta	PANCHNCHSP, PANCHCCH, PANCHCSCH	28%	-----	-----	28%
Pacific Ocean								
ALBANPAC	Albacore tuna (<i>Thunnus alalunga</i>)	North Pacific Ocean	Northern anchovy	NANCHSCAL	36%	Pacific hake	PHAKEPCOAST	54%
PACBTUNA	Pacific bluefin tuna (<i>Thunnus orientalis</i>)	Pacific Ocean	Northern anchovy	NANCHSCAL	80%	-----	-----	80%
STMARLINNEPAC	Striped marlin (<i>Kajikia audax</i>)	Northeast Pacific	Pacific chub mackerel	CMACKPCOAST	27%	Pacific hake, Pacific sardine	PHAKEPCOAST, SARDPCOAST	56%
USA/Canada East								
COD3M	Atlantic cod (<i>Gadus morhua</i>)	Flemish Cap	Northern shortfin squid	ILLEXNAFO3-4	29%	Atlantic herring, Atlantic mackerel	MACKNWATLSA3-4	56%
COD3NO	Atlantic cod (<i>Gadus morhua</i>)	Southern Grand Banks	Northern shortfin squid	ILLEXNAFO3-4	29%	Atlantic herring, Atlantic mackerel	MACKNWATLSA3-4, HERR4RFA,	56%
COD3Ph4RS	Atlantic cod (<i>Gadus morhua</i>)	Northern Gulf of St. Lawrence	Northern shortfin squid	ILLEXNAFO3-4	29%	Atlantic herring, Atlantic mackerel	HERR4RSP	56%
COD3Ps	Atlantic cod (<i>Gadus morhua</i>)	St. Pierre Bank	Northern shortfin squid	ILLEXNAFO3-4	29%	Atlantic herring, Atlantic mackerel	MACKNWATLSA3-4, HERR4TFA,	56%
COD4TVn	Atlantic cod (<i>Gadus morhua</i>)	Southern Gulf of St. Lawrence	Northern shortfin squid	ILLEXNAFO3-4	29%	Atlantic herring, Atlantic mackerel	HERR4TSP	56%
BLUEFISHATLC	Bluefish (<i>Pomatomus saltatrix</i>)	Atlantic Coast	Atlantic menhaden	MENATLAN	13%	Longfin inshore squid	LISQUIDATLC	23%
MONKSGBMATL	Goosefish (<i>Lophius americanus</i>)	Southern Georges Bank / Mid-Atlantic	Northern shortfin squid	ILLEXNWATLC	25%	-----	-----	25%
POLL5YZ	Pollock (<i>Pollachius virens</i>)	Gulf of Maine / Georges Bank	Longfin inshore squid	LISQUIDATLC	38%	-----	-----	38%
SHAKE4VWX	Silver hake (<i>Merluccius bilinearis</i>)	Scotian Shelf and Bay of Fundy	Atlantic mackerel	MACKNWATLSA3-4	13%	Northern shortfin squid	ILLEXNAFO3-4	24%
WHAKE4T	White hake (<i>Urophycis tenuis</i>)	Southern Gulf of St. Lawrence	Northern shortfin squid	ILLEXNAFO3-4	31%	-----	-----	31%
WHAKEGBGOM	White hake (<i>Urophycis tenuis</i>)	Gulf of Maine / Georges Bank	Northern shortfin squid	ILLEXNWATLC	31%	-----	-----	31%
USA/Canada West								
ARFLOUNDBSAI	Arrowtooth flounder (<i>Atheresthes stomias</i>)	Bering Sea and Aleutian Islands	Pacific hake	no overlap	60%	-----	-----	60%
ARFLOUNDDGA	Arrowtooth flounder (<i>Atheresthes stomias</i>)	Gulf of Alaska	Pacific hake	no overlap	60%	-----	-----	60%
ARFLOUNDPACOAST	Arrowtooth flounder (<i>Atheresthes stomias</i>)	Pacific Coast	Pacific hake	PHAKEPCOAST	60%	-----	-----	60%
BLACKROCKCAL	Black rockfish (<i>Sebastes melanops</i>)	California	Northern anchovy	NANCHSCAL	42%	-----	-----	42%
BLACKROCKWASH	Black rockfish (<i>Sebastes melanops</i>)	Washington	Northern anchovy	no overlap	42%	-----	-----	42%
CMACKPCOAST	Pacific chub mackerel (<i>Scomber japonicus</i>)	Pacific Coast	Northern anchovy	NANCHSCAL	43%	-----	-----	43%
SSTHORNHGA	Shortspine thornyhead (<i>Sebastes alascanus</i>)	Gulf of Alaska	Pacific hake	no overlap	22%	-----	-----	22%
SSTHORHPACOAST	Shortspine thornyhead (<i>Sebastes alascanus</i>)	Pacific Coast	Pacific hake	PHAKEPCOAST	22%	-----	-----	22%
YTROCKNPACOAST	Yellowtail rockfish (<i>Sebastes flavidus</i>)	Northern Pacific Coast	Pacific hake	PHAKEPCOAST	16%	-----	-----	16%

617 **Table S6.** Seabird and marine mammal population details.

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Predator stock	Common name (scientific name)	Area	Primary prey	Primary prey stocks	% of diet	Additional important prey	Add. important prey stocks	% of diet
Europe								
ARCTERFOULA	Arctic tern (<i>Sterna paradisaea</i>)	Shetland Islands	Lesser sand-eel	SANDELSA7	100%			100%
APUFFHERNYKEN	Atlantic puffin (<i>Fratercula arctica</i>)	Norwegian Sea	Herring	ATLHERRROST	56%			56%
COMGUISHETALL	Common guillemot (<i>Uria aalge</i>)	Shetland Islands	European sprat	SPRATNS	69%	Lesser sand-eel, Sandeel spp.	SANDELSA7	159%
Humboldt Current								
GUACORPERU	Guanay cormorant (<i>Phalacrocorax bougainvillii</i>)	Peru	Peruvian anchoveta	PANCHPERUNC	34%			34%
PERBOOPERU614S	Peruvian booby (<i>Sula variegata</i>)	Peru	Peruvian anchoveta	PANCHPERUNC	80%			80%
PERBOOPERU	Peruvian booby (<i>Sula variegata</i>)	Peru	Peruvian anchoveta	PANCHPERUNC	80%			80%
PERPELPERU614S	Peruvian pelican (<i>Pelecanus thagus</i>)	Peru	Peruvian anchoveta	PANCHPERUNC	80%			80%
PERPELPERU	Peruvian pelican (<i>Pelecanus thagus</i>)	Peru	Peruvian anchoveta	PANCHPERUNC	80%			80%
South Africa								
AFPENWCAPE	African penguin (<i>Spheniscus demersus</i>)	Benguela Current	Sardine/anchovy	SARDSA	86%			86%
CGANNETWCAPE	Cape gannet (<i>Morus capensis</i>)	Benguela Current	Sardine/anchovy	SARDSA	61%			61%
US/Canada East Coast								
GSEALSABLEISL	Grey seal (<i>Halichoerus grypus</i>)	NW Atlantic	Atlantic mackerel	MACKNWATLSA3-4	16%			16%
US/Canada West Coast								
BRACORFIF	Brandt cormorant (<i>Phalacrocorax penicillatus</i>)	California	Northern anchovy	NANCHSCAL	20%			20%
BRACORFIS	Brandt cormorant (<i>Phalacrocorax penicillatus</i>)	California	Northern anchovy	NANCHSCAL	20%			20%
SEALIONSCBpup	California sea lion (<i>Zalophus californianus</i>)	California	Northern anchovy	NANCHSCAL	11%			11%
COMGUJFIUJ	Common guillemot (<i>Uria aalge</i>)	California	Pacific hake	PHAKEPCOAST	54%	California market squid, Northern anchovy	NANCHSCAL	92%
ELETERSDB	Elegant tern (<i>Thalasseus elegans</i>)	California	Northern anchovy	NANCHSCAL	43%			43%
HUMPBACCAOR	Humpback whale (<i>Megaptera novaeangliae</i>)	CA/OR	Pacific sardine	SARDPCOAST	51%	Northern anchovy	NANCHSCAL	73%
NFURSTGEORGE	Northern fur seal (<i>Callorhinus ursinus</i>)	Pribolof Islands	Walleye pollock	WPOLLEBS	57%	Armhook squid		93%
NFURSTPAUL	Northern fur seal (<i>Callorhinus ursinus</i>)	Pribolof Islands	Walleye pollock	WPOLLEBS	57%	Armhook squid		93%
PHSEALWA	Pacific harbor seal (<i>Phoca vitulina richardsi</i>)	Washington	Pacific hake	PHAKEPCOAST	43%			43%
PHSEALFUCA	Pacific harbor seal (<i>Phoca vitulina richardsi</i>)	Washington	Pacific hake	PHAKEPCOAST	43%			43%
PHSEALOR	Pacific harbor seal (<i>Phoca vitulina richardsi</i>)	Oregon	Pacific hake	PHAKEPCOAST	43%			43%
PHSEALSJ	Pacific harbor seal (<i>Phoca vitulina richardsi</i>)	Washington	Pacific hake	PHAKEPCOAST	43%			43%

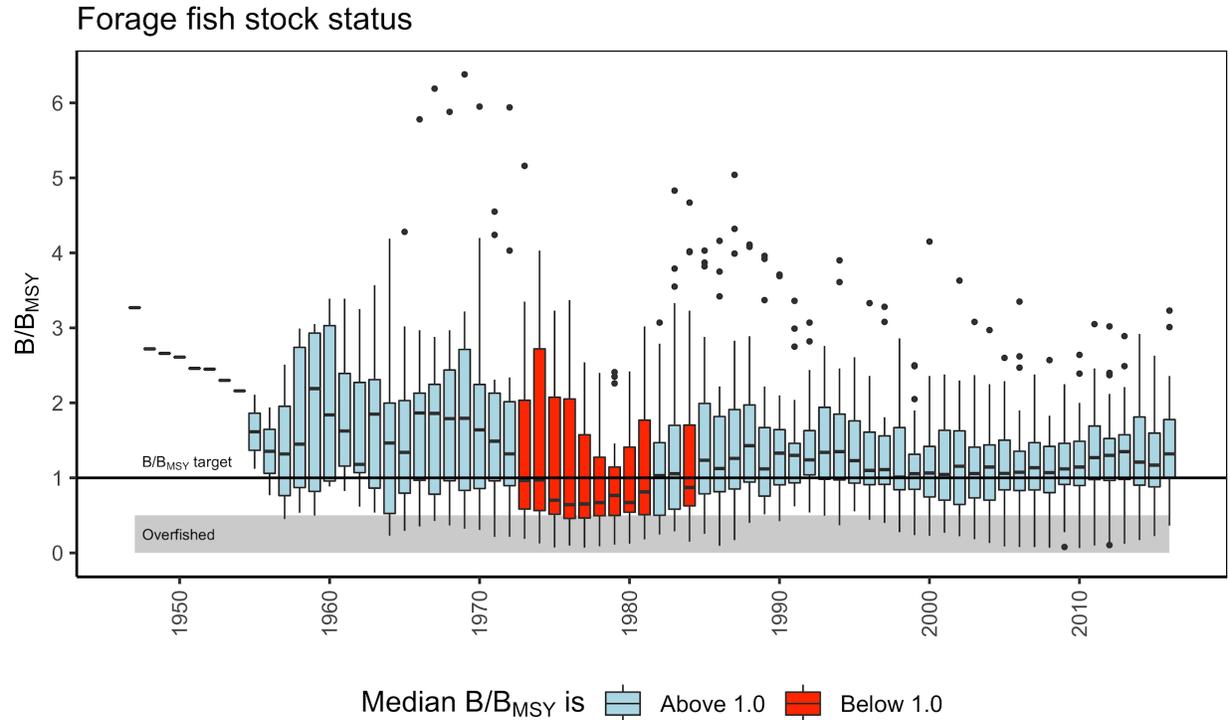
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621 **Table S7.** Source of simulation parameters for the power analysis (FE=fixed effects).
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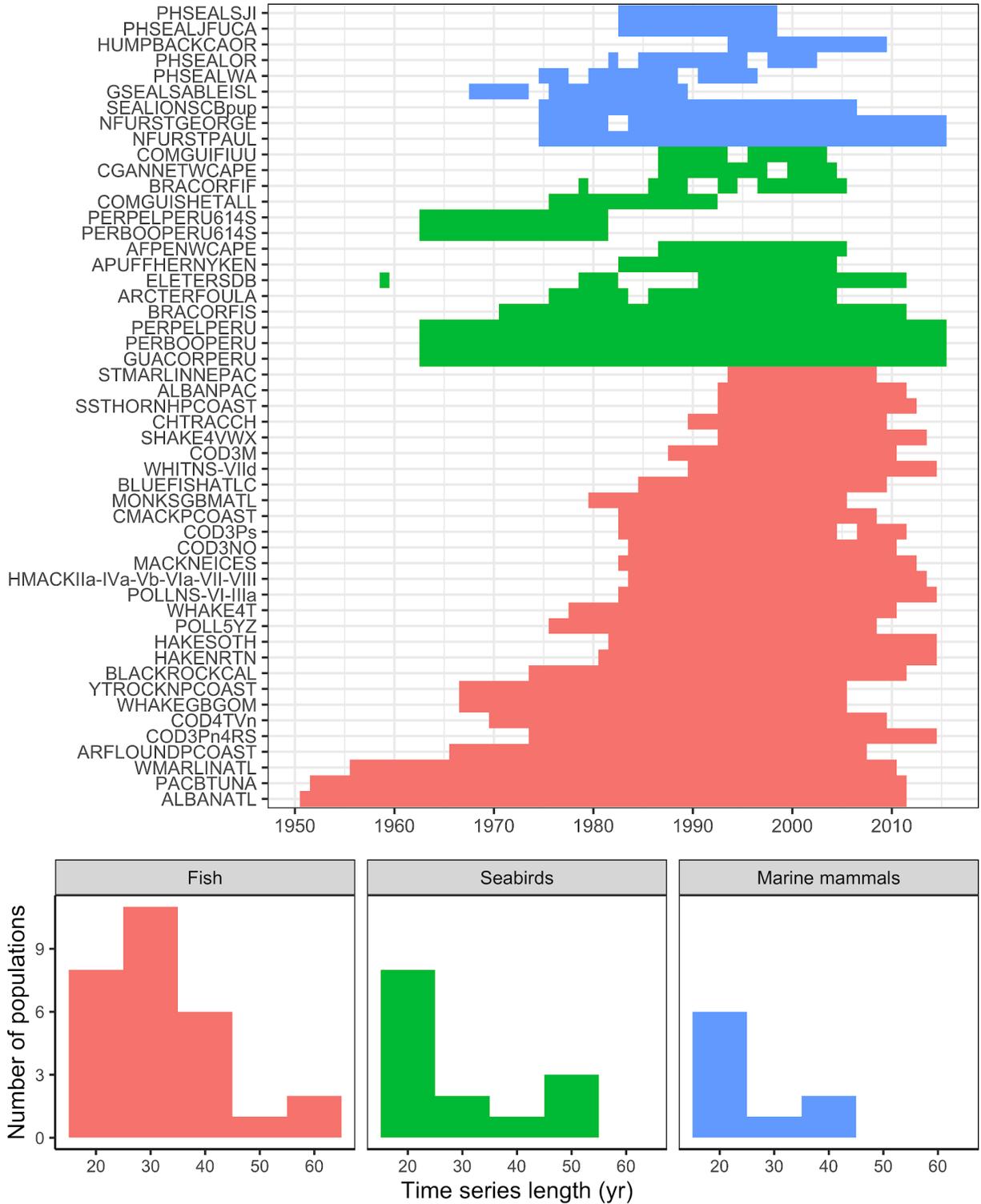
Type	Parameter	Source
Input	r_i , intrinsic rate of growth	Estimated by the FE composite prey model
Input	K_i , carrying capacity	Estimated by the FE composite prey model
Input	$SST_{i,t}$, SST time series	Observed
Input	$B_{0,i}$, biomass in initial year	Observed
Input	$U_{i,t}$, exploitation rate time series	Observed (observed catch / observed biomass)
Input	θ , influence of prey on productivity	Varied (n=4): 0.25 to 1.00 by 0.25
Input	σ_p , s.d. of the productivity process error	Varied (n=4): 0.1 to 0.4 by 0.1
Output	$B_{i,t}$, biomass time series	Simulated
Output	$C_{i,t}$, catch time series	Simulated
Output	$P_{i,t}$, productivity time series	Simulated

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625 **Figure S1.** Boxplots showing status (B/B_{MSY}) of forage fish populations over time. The solid
 626 horizontal line shows the B/B_{MSY} target and the grey shading indicates overfished stocks (B/B_{MSY}
 627 < 0.5). In boxplots, the solid line indicates median, box indicates interquartile range (IQR),
 628 whiskers indicate 1.5 times the IQR, and points indicate outliers.

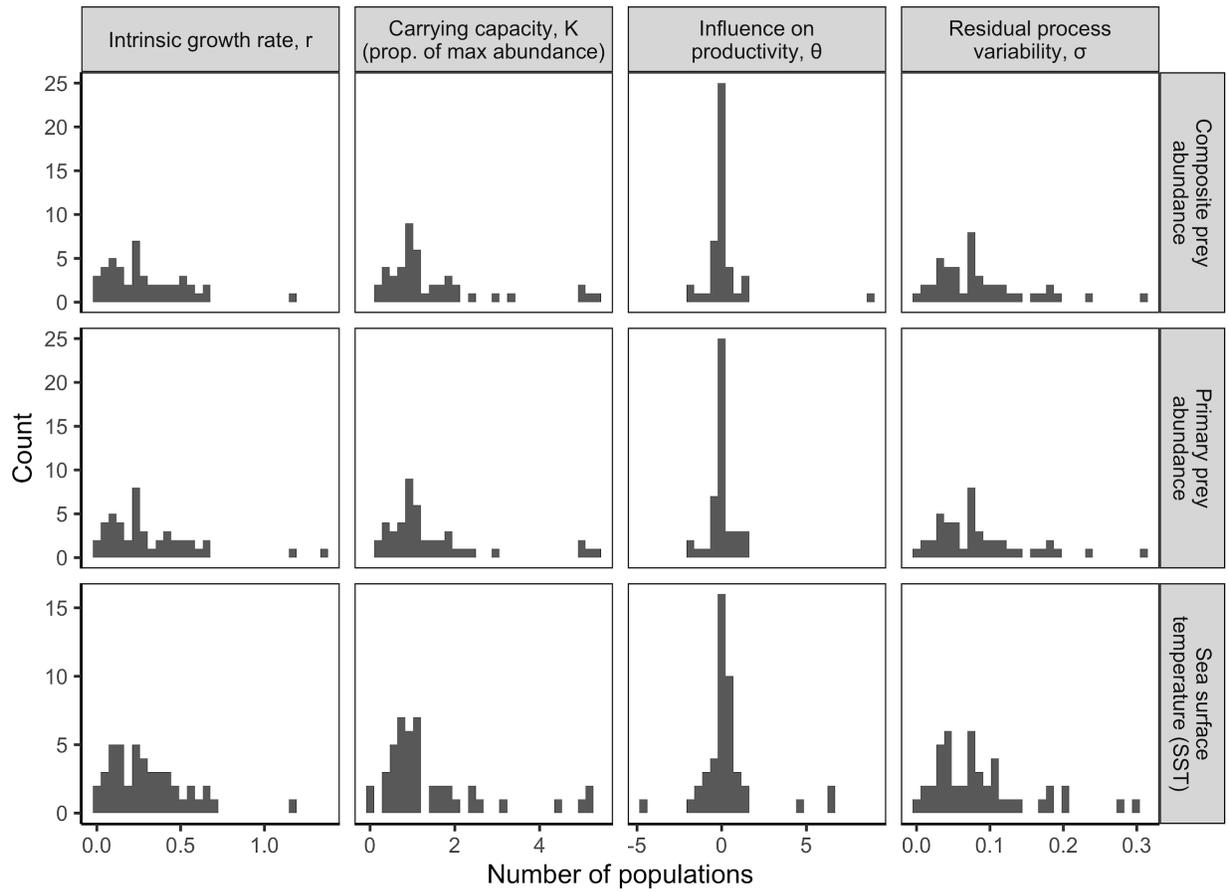


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Figure S2. Length of prey-linked predator time series by predator type. See **Table S5** for more information on each predator population.

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Fixed effects models

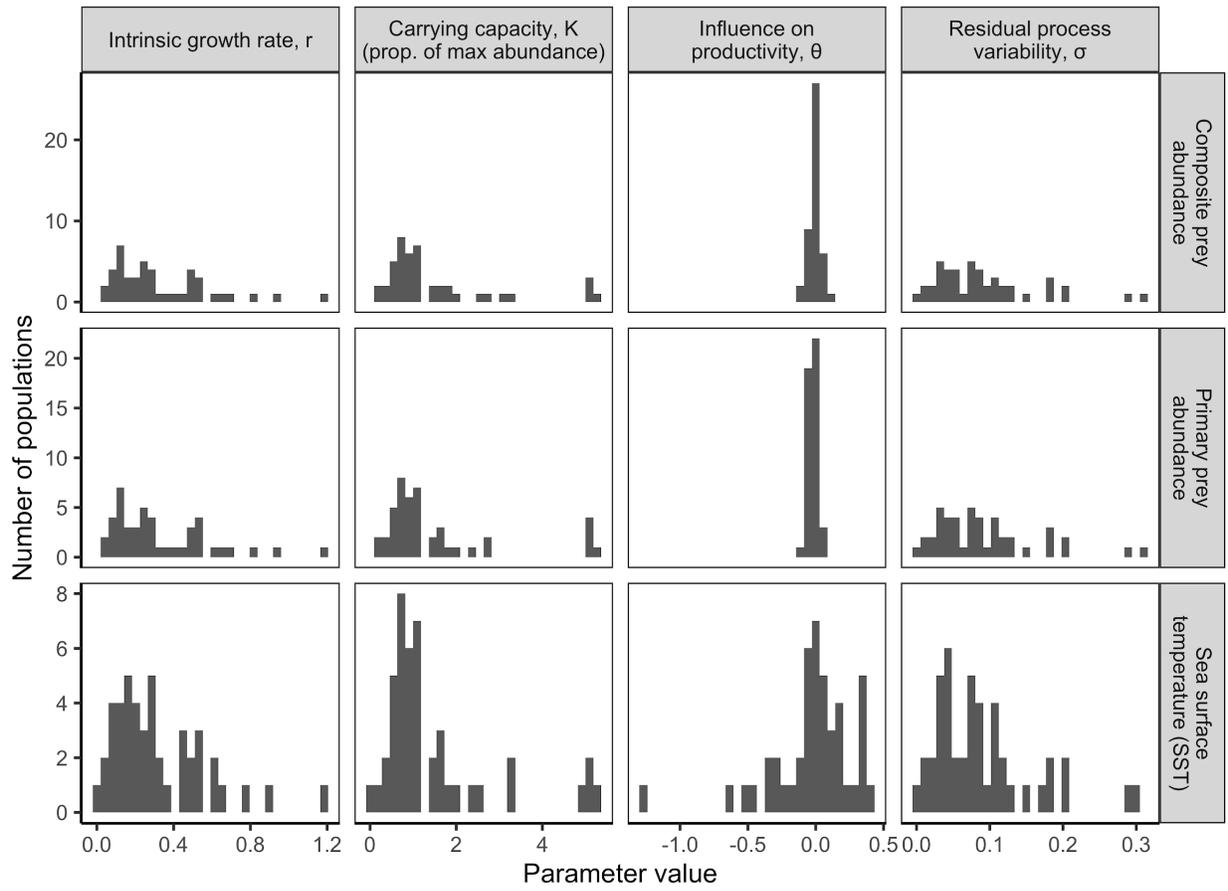


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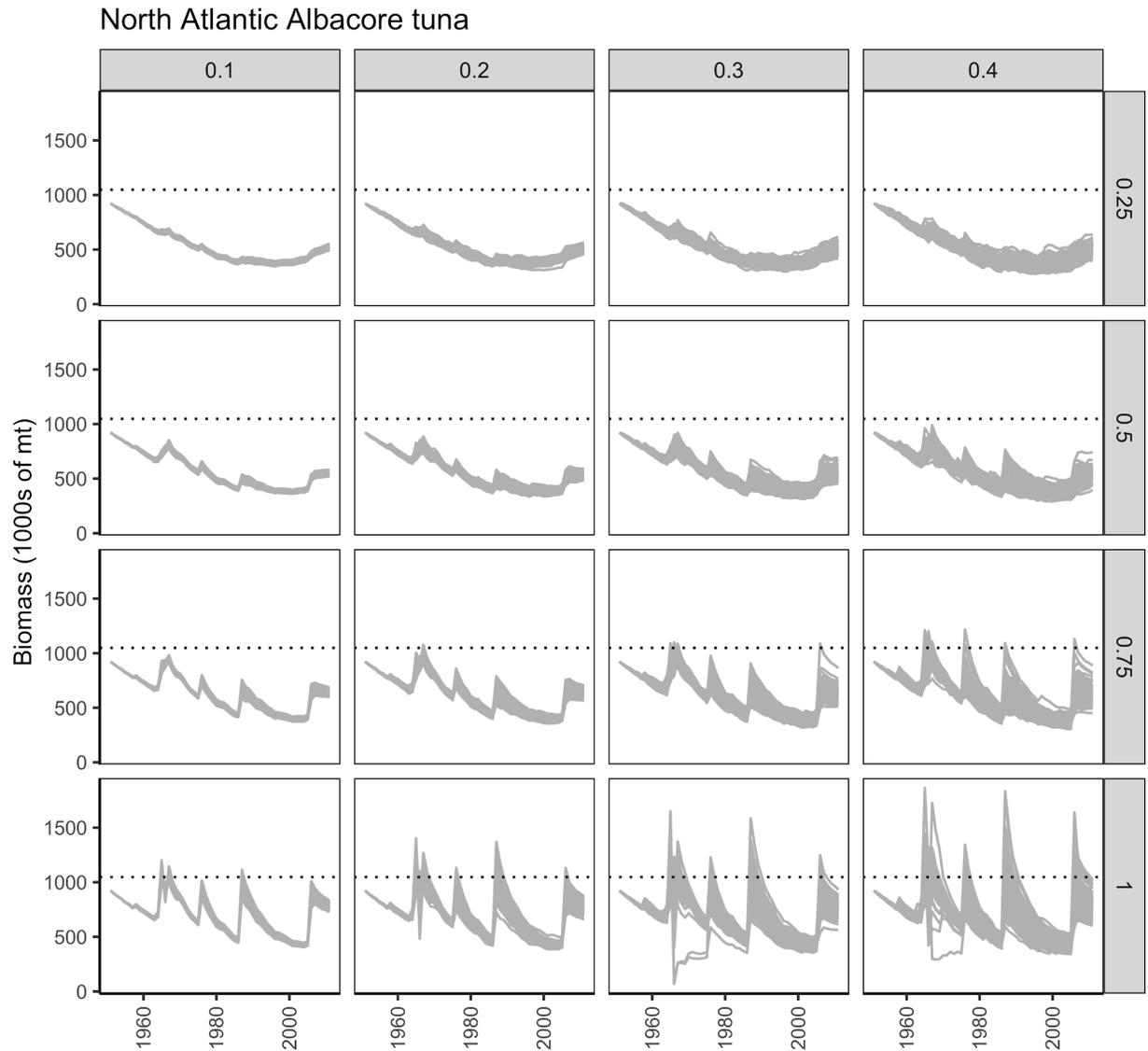
Figure S3. Distribution of parameter estimates from the three fixed effects models.

Random effects models



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Figure S4. Distribution of parameter estimates from the three random effects models.



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Figure S5. Examples simulations for the power analysis. Rows represent varied strengths of prey influence and columns represent varied levels of process variability. Dotted horizontal lines show the carrying capacity estimated by the composite prey-linked fixed effects model.