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1 **Global patterns in marine predatory fish**

2

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11

12 **Large teleost (bony) fish are a dominant group of predators in the oceans constituting a major**
13 **source of food and livelihood for humans. These species differ markedly in morphology and**
14 **feeding habits across oceanic regions; large pelagic species such as tunas and billfish typically**
15 **occur in the tropics, whereas demersal species of gadoids and flatfish dominate boreal and**
16 **temperate regions. Despite their importance for fisheries and the structuring of marine**
17 **ecosystems, the underlying factors determining the global distribution and productivity of these**
18 **two groups of teleost predators are poorly known. Here we show how latitudinal differences in**
19 **predatory fish can essentially be explained by the inflow of energy at the base of the pelagic and**
20 **benthic food chain. A low productive benthic energy pathway favours large pelagic species,**
21 **whereas equal productivities support large demersal generalists that outcompete the pelagic**
22 **specialists. Our findings demonstrate the vulnerability of large teleost predators to ecosystem-**
23 **wide changes in energy flows and hence provide key insight to predict responses of these**
24 **important marine resources under global change.**

25 Marine top predators influence the structure and dynamics of food webs by imposing mortality and
26 behavioural changes on prey and by feeding on parallel pathways of energy from both the pelagic
27 (open water) and the benthic (bottom) zone of the ocean¹⁻³. Many of these predator species have
28 declined in population sizes and distribution ranges, which in several cases has resulted in large-scale
29 changes in ecosystems, involving trophic cascades²⁻⁴.

30 Large teleost fish are a dominant group of predators in the global oceans, support lucrative commercial
31 and recreational fisheries and provide food for human populations worldwide⁵⁻⁷. These predators
32 clearly differ in morphology and feeding habits across the world. In tropical and subtropical regions,
33 teleost predators are often fast, mobile species that feed within the pelagic zone^{8,9}, while in boreal and

34 temperate regions the largest teleost species are typically slower growing, demersal (bottom-living)¹⁰
35 and adapted to feeding on both pelagic and benthic organisms^{6,11-14}. Despite their importance for
36 structuring marine ecosystems and their significant socio-economic value, the underlying factors
37 determining the global distribution and productivity of these two groups of marine predatory fish are
38 poorly known. Here we test the specific hypothesis that spatial patterns in the distribution and
39 productivity of these groups are primarily driven by pronounced global differences in the productivity
40 of a pelagic and a benthic energy pathway in marine food webs worldwide (Fig. 1).

41 We examine this hypothesis by assessing the relative productivity of large marine teleost fishes using
42 global fisheries landings data¹⁵ across 232 marine ecoregions¹⁶. For each ecoregion, we calculate the
43 average proportion of large pelagic vs demersal fish landings between 1970 and 2014. We show that in
44 this case, the proportion of landings represents a good estimate of the dominant predatory feeding
45 strategy in the sea. We develop a food-web model with two energy channels, one pelagic and one
46 benthic, to formally test our hypothesis and to predict the biomass fraction of pelagic vs demersal
47 predatory fish worldwide.

48 **Results**

49 The proportion of large pelagic and demersal teleost predators varied strongly in fisheries landings
50 across the globe (Fig. 2). As expected, large pelagic fish dominate in the tropics and subtropics, while
51 large demersal fish prevail in temperate and polar regions in both hemispheres. Despite the pronounced
52 latitudinal gradients, some areas in the tropics have a relatively low proportion of large pelagic fish
53 (e.g. Gulf of Mexico, Brazilian shelf), primarily due to high landings of demersal fish species; e.g. the
54 highly abundant largehead hairtail (*Trichiurus lepturus*).

55 Whether landings data can predict biomass (and as such the dominant predatory fish feeding strategy in
56 the sea) has been disputed¹⁷. Here, we use weight fractions in landings and do not predict absolute
57 biomass. Nevertheless, average landings and biomass¹⁸ are highly correlated for 71 pelagic and
58 demersal predatory fish stocks (Supplementary Fig. 1, p-value <0.001, $r^2 = 0.78$). The weight fraction
59 in landings also corresponds well to the fraction in biomass over time, based on assessed pelagic and
60 demersal fish stocks¹⁸ from nine different large marine ecosystems (LMEs) (Supplementary Fig. 2, p-
61 value < 0.001, $r^2 = 0.91$). Proportions of pelagic and demersal fish landings weighted with the
62 economic value of species¹⁹ (i.e. a crude measure of potential fisheries preferences) demonstrate a
63 similar global pattern (Supplementary Fig. 3, p-value < 0.001, $r^2 = 0.97$), highlighting that price
64 differences between both groups are overshadowed by the considerably larger differences in the weight
65 of the landings of the two groups. Further robustness checks show that the global patterns remain
66 highly similar if large elasmobranches are included in the analysis (Supplementary Fig. 4, p-value <
67 0.001, $r^2 = 0.98$) or illegal, unregulated and unreported (IUU) catches and discards (p-value < 0.001, r^2
68 = 0.99). The robustness of our result to the potential biases described above provide strong support for
69 using the weight fraction of pelagic vs demersal fish based on global landings as our response variable
70 to estimate the dominant predatory fish feeding strategy in the sea.

71 We hypothesize that the relative production of pelagic and demersal predatory fish is dependent on the
72 differences in inflow of energy at the base of the pelagic and benthic pathway (Fig. 1). Most of the
73 ocean net primary production (NPP) occurs in the pelagic layer. Yet, in some regions, sufficient carbon
74 reaches the bottom via sinking and other active transport processes to support high production of
75 benthic organisms. There are multiple environmental conditions that can influence the downward flux
76 of carbon to the seafloor. First, there is a clear relation with bathymetry, as in deeper oceans only a

77 fraction of the production from the pelagic zone may reach the seabed²⁰. The proportion of NPP which
78 reaches the bottom also varies with latitude. This happens because low water temperatures decelerate
79 remineralization processes and subsequently increase the proportion of NPP available for export^{21,22},
80 but also because seasonal variability in NPP may result in a temporal mismatch between phytoplankton
81 and zooplankton production leading to a larger fraction of (ungrazed) NPP sinking to the bottom during
82 the spring bloom in seasonal environments²³. Finally, it has been suggested that the proportion of NPP
83 sinking to the seabed is dependent on the depth of the photic zone and either total NPP or chlorophyll
84 concentration²⁴.

85 We approximated the difference in pelagic and benthic production by calculating the ratio between the
86 fraction of NPP that remains in the photic zone (F_{photic})²⁴ versus the fraction of NPP that reaches the
87 seabed (F_{seabed}) (see Supplementary Fig. 5). Using non-linear regression models, we found that the ratio
88 between F_{photic} and F_{seabed} explains a substantial part of the global variability in the proportion of large
89 pelagic vs demersal fish landings (Fig. 3, deviance explained = 68%, p-value < 0.001; see other
90 environmental predictors in Supplementary Table 1). The results show how in most tropical and
91 subtropical areas a highly productive pelagic energy pathway favours large pelagic fish, while in many
92 temperate and polar regions more equal productivities of the two pathways favour large demersal fish
93 (feeding as a generalist on both pelagic and demersal resources).

94 In order to further test our hypothesis, we developed a food-web model with two energy channels to
95 predict the biomass fraction of large pelagic species across ecoregions (Fig. 1 and Supplementary Table
96 2-3). The pelagic and benthic energy pathways are modelled as two separate channels that have their
97 own resource carrying capacity. The carrying capacity of the pelagic resource is calculated by
98 multiplying a total resource carrying capacity constant (R_{max}) with F_{photic} , the carrying capacity of the

99 demersal resource was $R_{\max} \cdot F_{\text{seabed}}$. The resources are both preyed upon by an intermediate trophic
100 level, representing smaller fishes and invertebrates, while two groups of predators are included at the
101 top of the energy pathways; a pelagic specialist feeding exclusively on a pelagic diet, and a demersal
102 generalist feeding on both energy pathways.

103 The food-web model predicted global patterns in pelagic vs demersal predators largely corresponding
104 to the proportions of large pelagic fish derived from landings (Fig. 4a-b, $r^2 = 0.58$). However, some
105 areas showed a strong mismatch between model predictions and landings data (Fig. 4b-c). Interestingly,
106 the largest differences can be observed at high latitudes in the Southern Ocean and the temperate North
107 Pacific where the model predicts a higher production of pelagic specialists compared to the proportions
108 derived from landings. We expect that the model predictions are realistic because large pelagic
109 predators are indeed present and highly abundant in many of these areas. However, not as predatory
110 fish but as fast, pelagic-feeding endotherms that maintain a high body temperature and activity despite
111 the cold waters. For example, the Aleutian Islands, Kamchatka shelf, Antarctica and South Georgia
112 (Fig. 4c, red areas) harbour high biodiversity and densities of penguins and pinnipeds²⁵⁻²⁷. While this
113 lends support to our model predictions, we stress the need for further research on the complementary
114 roles of marine endo- and ectotherm predators. There is also a mismatch in ecoregions in the tropics
115 where the model predicts higher production of demersal generalists compared to the proportions in
116 landings (Fig. 4c, blue areas). In these regions, the energy fluxes to the seabed are predicted to be
117 relatively high (Supplementary Fig. 5), thereby potentially supporting a high production of demersal
118 generalists. The high fraction of NPP predicted to reach the seabed is consistent with other studies,
119 using alternative methods, to predict the carbon flux to the seabed on a global scale²³. In many of these
120 areas, relatively high catch rates of sharks and rays can be observed¹⁵, species that are often demersal

121 generalists and as such similar to demersal teleost predators. Although the contribution of large sharks
122 and rays to overall fisheries landings is marginal (Supplementary Fig. 4), potentially the result of long-
123 term overfishing²⁸, including elasmobranch predators in the analysis increases the amount of demersal
124 generalists substantially near Australia, Peru and Chile in areas where the model predicts higher
125 production of demersal generalists compared to the proportions in landings (Fig. 4c, Supplementary
126 Fig. 4). An alternative explanation for the lower proportion of demersal generalists in the landings can
127 be due to the ability of pelagic predators to disperse widely⁹ and as such dampen local differences in
128 fish abundances of the two predatory groups that have originated from variation in the energy flux to
129 the seabed.

130 **Discussion**

131 Our study supports the hypothesis that the inflow of energy at the base of the pelagic and benthic
132 channel determines the dominant feeding strategy of large teleost predatory fishes. Pelagic specialists
133 dominate when energy is primarily channelled through the pelagic pathway, while demersal generalists
134 outcompete the specialists when both pelagic and benthic resources are available. This explanation
135 assumes that demersal generalists' niches and diets overlap with pelagic specialists because they
136 exploit both benthic and pelagic resources. Overlapping diets have indeed been observed in areas
137 where both groups of species co-occur^{11,29,30}. Further, overlapping diets may occur even in the absence
138 of direct spatial overlap between the predator groups, due to pronounced habitat shifts of pelagic prey
139 species through daily (vertical) and seasonal (onshore-offshore) migrations (e.g.^{31,32}). Since both large
140 pelagic and demersal predators may access and feed on these highly mobile prey, but at different times,
141 in different areas and even on different life stages, they engage in exploitative competition. Niche
142 overlap will be lower in deep sea environments where demersal species are less able to exploit pelagic

143 resources. Even though reduced niche overlap in deep sea environments is not explicitly represented in
144 our model or data analysis, it is implicitly captured because the fluxes are typically low in deep sea
145 areas and consequently pelagic specialists are dominating. Although the degree of dietary overlap and
146 the strength of competition between pelagic and demersal predators at a global scale are poorly known,
147 our results suggest that competition between pelagic and demersal feeding strategies exists.
148 Consequently, a decline in the productivity of the benthic energy pathway will shift dominance towards
149 pelagic specialists (and vice versa).

150 We assumed that large pelagic teleost fish are superior in exploiting the pelagic resource compared to
151 large demersal species. Large pelagic fish are highly adapted to feeding on fast-moving pelagic
152 resources (such as forage fish) and have developed specific morphological features (e.g. high muscle
153 protein, large gill surface area and the warming of muscles) to support an active pelagic lifestyle^{33,34}.
154 Such physiological and morphological adaptations can explain the superiority of pelagic specialists to
155 feed on pelagic prey compared to the more “sluggish” demersal generalists. Yet, we lack knowledge to
156 explicitly account for the energetic costs associated with these physiological and morphological
157 adaptations³³ in a food-web model, and also, to account for the costs of finding, capturing and digesting
158 prey for both groups of species. Quantifying these energetic costs will allow for a further refinement of
159 the food-web model and support estimates of fish production of both species groups across oceanic
160 regions.

161 Our global analysis of predatory fish largely ignored the role of non-teleost fish and marine endotherm
162 predators. The contribution of non-teleost predators in global fisheries landings is low (Supplementary
163 Fig. 4). Yet, non-teleost predators are typically overfished²⁸ and abundances were likely much higher in
164 the past and may increase again in the future. The potential increase in abundance highlights the need to

165 understand the interplay between teleost and non-teleost predatory fish for future predictions of the
166 global occurrence and productivity of fish predators. Additionally, it is unclear from our study under
167 which environmental conditions endotherm predators are a highly abundant and dominant predatory
168 species group. Following the results of our food-web analysis (Fig. 4), we hypothesized that pelagic-
169 feeding endotherms are the dominant predatory group at high latitudes in the Southern Ocean and the
170 temperate North Pacific. Yet, the complementary roles of marine endo- and ectotherm predators in
171 relation to temperature and the productivity of the pelagic and benthic energy pathways needs further
172 study.

173 When top predators feed on both pelagic and benthic prey resources, they act as couplers of these
174 energy pathways. This coupling may infer stability to the food web if the predators balance the strength
175 of their feeding interactions on pelagic and benthic prey with the relative difference in productivity
176 (and turnover rates) of the pathways¹. We argue that not all predatory fish act as such “balanced”
177 couplers, as species can be specialized on exploiting pelagic resources. The specialization implies that
178 ecosystem-level variations in the productivity of the pelagic and benthic energy pathways will not only
179 affect the occurrence and productivity of large predatory fishes, but also the stability of the ecosystem.

180 There is large uncertainty related to current predictions of future fish and fisheries production,
181 primarily since it is unclear how climate change will affect ocean primary production and how energy
182 will be transferred to the upper trophic levels of marine ecosystems^{35,36}. Our findings suggest that
183 changes in the global occurrence and productivity of large predatory fishes can be anticipated by
184 understanding how climate change will affect the base of pelagic and benthic food chains. Changes in
185 the productivity of these energy pathways in response to climate change are expected^{37,38} and, in some
186 instances, already observed, e.g. large-scale changes in phytoplankton abundance and ocean primary

187 production^{39,40}. For most continental shelf areas, climate change has been predicted to decrease detritus
188 fluxes to the seafloor³⁵, thereby potentially limiting large demersal fish abundances and fisheries
189 production. Accounting for the changes in the pelagic and demersal energy pathways is therefore key to
190 reliably predict the effects of climate change on the upper trophic levels of marine ecosystems, and the
191 impact on supported fisheries.

192 **Method**

193 Global fisheries data

194 We used global fisheries landings data¹⁵ to determine general patterns in feeding strategies of marine
195 predatory fish between 1970 and 2014. The spatial fisheries landings data is predominately from global
196 fisheries catch statistics assembled by the Food and Agriculture Organization of the United Nations
197 (FAO) and complemented by statistics from various international and national agencies. These datasets,
198 with higher spatial resolution, were nested into the broader FAO regions, replacing the data reported at
199 the coarser spatial resolution. The global fisheries landings data was mapped to 30-min spatial cells
200 using information on the distribution of reported taxa and fishing fleets¹⁵. For the purpose of this study,
201 we aggregated the data and examined fisheries landings data on a marine ecoregion scale¹⁶.

202 Feeding strategies of marine fish

203 To examine the productivity of marine teleost fish along the pelagic and benthic energy pathways, we
204 classified fish into two general feeding strategies, either feeding exclusively on the pelagic pathway
205 (pelagic fish) or (partly) relying on the benthic pathway for feeding (demersal fish). This was done
206 using the functional group classification system developed in the Sea Around Us (SAU) project⁴¹. Data
207 classified using the SAU project as shark, ray, any type of invertebrate or bathydemersal and
208 bathypelagic fish (these groups include the mesopelagic fish) were removed (see Supplementary Table
209 4). This limited our analysis to teleost fish and the two dominant feeding strategies. The two feeding
210 strategies were further divided on the basis of fish maximum size⁴². Large predatory species were
211 classified as fish with a maximum size ≥ 90 cm. The choice of this maximum size limit did not affect
212 our analysis as it can range from 70 – 150 cm without changing the results (Supplementary Fig. 6). Part
213 of the fisheries landings has not been identified (e.g. marine animals, marine fishes not identified) and

214 these observations were excluded. Other data are identified at too general a taxonomic grouping to
215 derive the correct size-class (e.g. Gadiformes, Gadidae) and these landings data were assumed to
216 represent species with smaller maximum sizes than 70 cm.

217 For each of the ecoregions, we calculated the average weight fraction of pelagic fish compared to
218 demersal fish in the fisheries landings data between 1970 and 2014. This was only done for ecoregions
219 where at least 60% of the landings data (in tonnes) could be classified into one of the functional groups
220 from the SAU project (but note that the main findings are unaffected when more or less strict criteria
221 for ecoregion selection are chosen). All fractions were averaged over at least 24 years of data (for 219
222 ecoregions fractions were averaged over 45 years of data).

223 Besides the large predatory teleost fish, we also determined whether there were general patterns in
224 feeding strategies of teleost fish species with a maximum size < 90 cm (Supplementary Fig. 7). The
225 results show there is no clear latitudinal pattern and no relationship between the small pelagic fish
226 fraction and $F_{\text{photic}}/F_{\text{seabed}}$. The pattern is not improved when pelagic and benthic invertebrate landings
227 are included in the analysis (Supplementary Fig. 7).

228 Potential bias due to the use of fisheries landings

229 Our assessment of the global variation in the large predatory fish may be biased by our use of global
230 fisheries landings data instead of biomass data. We included a variety of analyses to examine this
231 potential bias. We first examined with available stock assessments from the RAM Legacy Stock
232 Assessment database¹⁸, the relationship between catch and biomass of large teleost fish. For this
233 analysis, data was available for 71 different large predatory fish stocks (38 pelagic and 33 demersal,
234 Supplementary Table 5). For each stock, we averaged both total biomass and total catch for all years
235 with assessment data and examined across stocks the relationship between average biomass and catch

236 and whether this differs between both feeding groups (model comparison using AIC scores).
237 Afterwards, we tested the relationship between the weight fraction of pelagic fish versus demersal fish
238 in catch and biomass over time. This was done by selecting pelagic and demersal fish in all size groups
239 from the RAM stock assessment database¹⁸ for nine different Large Marine Ecosystems (LMEs) over
240 multiple years. The LMEs and years are selected since they have data available on assessed fish stocks
241 in both feeding strategies (see Supplementary Table 6). To further check robustness of our findings, we
242 examined how much the fraction large pelagic and demersal fish varied when the fraction is corrected
243 for the economic value of the species (assuming that species are preferred by fisheries when they have
244 higher economic value). Nominal economic value, standardized per unit weight, were derived for each
245 species and year from Sumaila et al.¹⁹, and were used to estimate the economic value of both feeding
246 groups (standardized per unit weight) per ecoregion and year. When multiple species from the same
247 feeding group were present in the landings in a particular ecoregion and year, the economic value of
248 that feeding group was averaged by weighting all species with the landings. Afterwards, we calculated
249 the price difference between pelagic and demersal fish for each year and ecoregion and averaged this
250 across all years per ecoregion. A price-corrected weight fraction large pelagic fish was then calculated
251 by: $wf \cdot (1-pf) / (wf \cdot (1-pf) + (1-wf) \cdot pf)$, where wf is the weight fraction large pelagic fish from
252 fisheries landings and pf is the price fraction (a fraction of 0.9 means that pelagic fish are 9 times more
253 valuable than demersal fish at similar tonnes of landings) (Supplementary Fig. 3). We also examined
254 how the inclusion of large sharks and rays (taken from the fisheries landings database¹⁵) affected the
255 global patterns in predatory fish. Classification of pelagic (oceanic) sharks and rays followed⁴³, all
256 other taxa were classified as demersal generalists (maximum body size is based on⁴²). Finally, we
257 examined how estimates of illegal, unregulated and unreported (IUU) catches and discarded fish
258 affected our calculation of the weight fraction of large pelagic vs demersal fish. Estimates of IUU

259 catches and discarded fish were taken from the spatial fisheries landings database¹⁵ per ecoregion and
260 year.

261 Pelagic and benthic energy production

262 We hypothesized that the relative production of pelagic and demersal fish in fisheries landings across
263 ecoregions is dependent on the differences in pelagic and benthic production. We approximated the
264 difference in production by calculating the ratio between the fraction of NPP that remains in the photic
265 zone (F_{photic}) versus the fraction of NPP that sinks to the seabed (F_{seabed}). This was done by first
266 calculating the fraction of NPP that sinks out of the photic zone (*pe*-ratio) and secondly by accounting
267 for energy loss between the depth of the photic zone and the seabed.

268 We used an empirical relationship introduced by Dunne et al.²⁴ to calculate the *pe*-ratio. This
269 relationship captures ~60% of observed global variation in *pe*-ratio using field-derived estimates of sea
270 surface temperature (SST), primary production (NPP) and the photic zone depth (Z_{eu}). In this
271 calculation, increased temperature reduces the *pe*-ratio, while it is increased with increasing primary
272 production and a smaller photic zone depth: $\text{pe-ratio} = -0.0101\text{SST} + 0.0582\ln\left(\frac{\text{NPP}}{Z_{\text{eu}}}\right) + 0.419$. To
273 estimate the *pe*-ratio on a global scale with the empirical model, we used average annual sea surface
274 temperature (degrees Celsius) between 1998 and 2008
275 (<http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html>), average daily net primary
276 production ($\text{mg C} / \text{m}^2 / \text{day}$) from the Vertically Generalized Production Model (VGPM) using
277 MODIS data between 2003 and 2008 (<http://www.science.oregonstate.edu/ocean.productivity>)⁴⁴ and
278 we approximated the photic zone depth from average daily surface chlorophyll-a concentrations (mg
279 $\text{Chl} / \text{m}^3 / \text{day}$) from the Sea-viewing Wide Field of view Sensor (SeaWiFS) between 1998 and 2008
280 (<http://oceancolor.gsfc.nasa.gov/cms>) (following⁴⁵, see for original description⁴⁶). The sea surface

281 temperature data was resampled to a 1/12 degrees grid to be able to use more detailed information on
282 spatial variation in bathymetry. The derived *pe*-ratios varied across the globe between 0.04 and 0.74
283 and were used to calculate F_{photic} (Supplementary Fig. 5), the predicted fraction of NPP that remains in
284 the photic zone:

$$285 \quad F_{\text{photic}} = 1 - r,$$

286 where r is the *pe*-ratio.

287 The fraction of NPP that sinks out of the photic zone is reduced in energetic content before it reaches
288 the seabed, especially in deeper oceans where only a fraction of the production from the pelagic zone
289 may reach the seabed. To account for this effect, we accounted for energy loss, adjusting a function
290 described in⁴⁷:

291 For all grid cells where the seabed depth is equal or shallower than depth of the photic zone:

$$292 \quad F_{\text{seabed}} = \textit{pe}\text{-ratio},$$

293 all other grid cells:

$$294 \quad F_{\text{seabed}} = \textit{pe}\text{-ratio} (\text{seabed depth} / \text{depth photic zone})^{-0.86}$$

295 Bathymetric data (m) was extracted per 1/12 degrees grid from the ETOPO1 Global Relief Model with
296 sea ice cover⁴⁸.

297 The calculated fluxes in the pelagic and benthic zone only provide a first-approximation of the relative
298 productivity of the pathways. The estimates ignore different aspects well-known to influence pelagic
299 and benthic energy pathways, such as the role of benthic primary producers, which especially in

300 coastal waters contribute to a large part of the overall production⁴⁹, areas with high subsurface
301 productivity, where NPP is underestimated when using satellite-derived NPP products^{50,51}, and any
302 active transport processes to the seafloor^{52,53}. Despite these limitations, the predicted large-scale spatial
303 variation in F_{photic} and F_{seabed} (Supplementary Fig. 5) seems to be consistent with other studies, using
304 alternative methods^{23,54}.

305 Data aggregation per ecoregion and data analysis

306 Both F_{photic} and F_{seabed} were averaged per ecoregion. To account for latitudinal differences in grid size
307 all F_{photic} and F_{seabed} values per ecoregion were weighted with respect to latitude (weighting factor =
308 $\cos(\pi/180 \cdot \text{degrees latitude})$) following⁵⁵. Besides, as fish production is expected to be highest in areas
309 with high primary production⁵⁶, we also weighted F_{photic} and F_{seabed} per ecoregion with respect to grid
310 cell differences in NPP.

311 Relationships between the fraction of pelagic fish and the ratio between F_{photic} and F_{seabed} were
312 examined using generalized additive models with a beta distribution (continuous probability
313 distribution between 0 and 1) and (after model fit inspection) with a cauchit link function. The ratio
314 between F_{photic} and F_{seabed} was \log_{10} transformed, while the pelagic fish fraction was transformed to
315 avoid zeros and ones following⁵⁷; $y = (y(n-1)+0.5)/n$, where y is the pelagic fish fraction and n the
316 number of ecoregions. Maps were produced using `rworldmap`⁵⁸.

317 Food-web model

318 Following the results of the fisheries data analyses, a food-web model was developed to study the
319 competitive interactions between large pelagic specialists and demersal generalists across marine
320 ecoregions. The benthic and pelagic energy pathways were modelled as two separate channels that

321 have their own resource carrying capacities with semi-chemostat dynamics. The carrying capacity of
322 the pelagic resource (K_p) was calculated by multiplying the total resource carrying capacity (R_{\max}) with
323 F_{photic} , the carrying capacity of the demersal resource (K_B) was $R_{\max} \cdot F_{\text{seabed}}$ (see for model formulation
324 Supplementary Table 2). The resources were both preyed upon by an intermediate trophic level, while
325 two predatory species were included at the top of the energy pathways (following Fig. 1).

326 We hypothesized that large pelagic teleost fish are superior in exploiting the pelagic resource compared
327 to large demersal species (see for arguments the second paragraph in the discussion section). To
328 incorporate this in the model, feeding as a generalist comes at a cost and this cost was implemented
329 with a lower attack rate of the generalist, meaning that the specialist is superior in exploiting the
330 pelagic resource. The value of the attack rate parameter was selected to obtain (approximately) an equal
331 amount of ecoregions that either overestimated the amount of pelagic or demersal fish compared to
332 fisheries landings. It resulted in an attack rate of the generalist that is 0.8 of the attack rate of the
333 specialist. This value can be varied between 0.65 and 0.95 without changing the r^2 of the statistical
334 relationship between landings data and model output with 4% (r^2 is 58% when a value of 0.8 is used,
335 see Fig. 4).

336 **Data availability:**

337 A table is available as supplementary data with information per ecoregion on the fraction pelagic fish in
338 landings, environmental variables and the food-web model outcome. Detailed global fisheries landings
339 data is available from Watson¹⁵.

340

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476 **Author contributions:**

477 PDvD, ML, BRMK, KHA conceived the study. RAW contributed with fisheries landings data. PDvD
478 performed the research with support of ML and KHA. PDvD, ML and KHA wrote the manuscript. All
479 authors contributed to interpretation of the results and commented on the manuscript.

480 **Author information:**

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483 **Figure legends**

484 **Figure 1. Conceptual figure illustrating the competitive interactions between large pelagic**
485 **specialists and large demersal generalists that feed on smaller pelagic and/or demersal fish and**
486 **invertebrates.** The smaller pelagic and demersal fish feed on zooplankton or zoobenthos. Illustration
487 by H. van Someren Gréve.

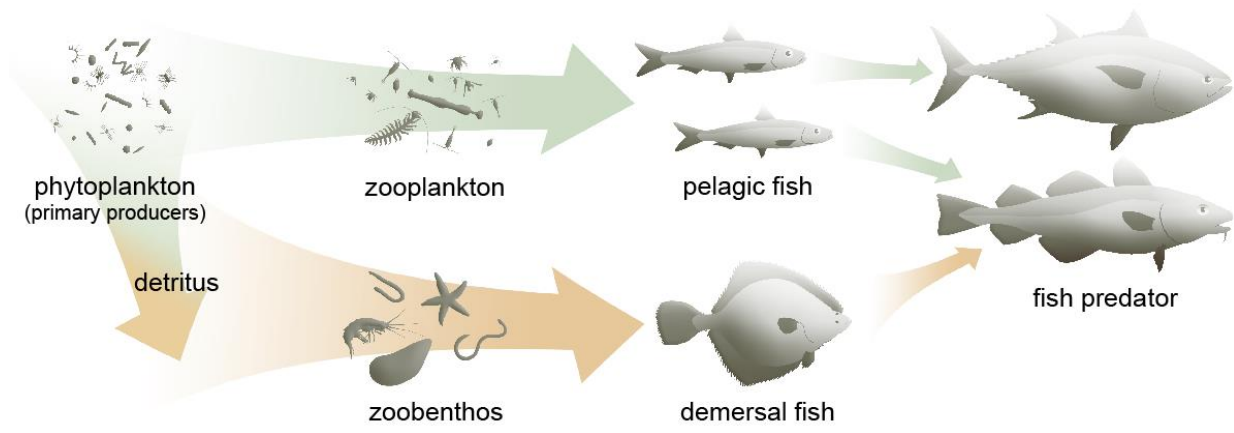
488 **Figure 2. Average weight fraction of large pelagic fish compared to large demersal fish in**
489 **fisheries landings between 1970 and 2014.** Large pelagic fish are the dominant group of fish in most
490 tropical and subtropical areas, whereas large demersal fish are dominant in temperate regions and the
491 exclusive group at the poles. Grey ecoregions in the map are excluded from the analysis due to limited
492 data availability (see method section). The boxplots show the ecoregions (n=217) in bins of 5 degrees
493 latitude, the midline of the box shows the median of the data, the limits of the box show the first and
494 third quartile and the whiskers extend to a maximum of 1.5 times the interquartile range. The line is
495 derived with a loess smoother.

496 **Figure 3. Relationships between the fraction of large pelagic fishes in fisheries landings and the**
497 **ratio between the fraction of net primary production (NPP) that remains in the photic zone**
498 **(F_{photic}) versus the fraction that reaches the seabed (F_{seabed}) for all ecoregions with available data**
499 **(n=217).** Large demersal fish are dominant at approximately equal pelagic – benthic NPP ratios, while
500 pelagic fish are dominant in areas where a high fraction of NPP remains in the photic zone (and/or
501 where a low fraction of NPP reaches the seabed) (generalized additive model, p-value < 0.001,
502 deviance explained = 68%). The fit is indicated by the solid line, the grey area shows the 95%
503 confidence interval. Fish illustrations by H. van Someren Gréve.

504 **Figure 4. Predictions of the dominance of large pelagic specialists or demersal generalists across**
505 **marine ecoregions using a food-web model. a,** Map of the predicted weight fraction large pelagic
506 specialists compared to demersal generalists in the food-web model based on region-specific energy
507 fluxes. **b,** Relationship between the fraction large pelagic fish in fisheries landings data and food-web
508 model for each ecoregion ($y = 0.04 + 0.92x_1$, $r^2 = 0.58$, p-value < 0.001), coloured points correspond to
509 ecoregions with a large difference (> 0.33) between the model predictions and the data. **c,** Map of all
510 ecoregions with a large difference (> 0.33) between the fraction large pelagic fish in fisheries landings
511 and the model, following (4b). Grey ecoregions are excluded from the analysis due to limited data
512 availability. Fish illustrations by H. van Someren Gréve.

513

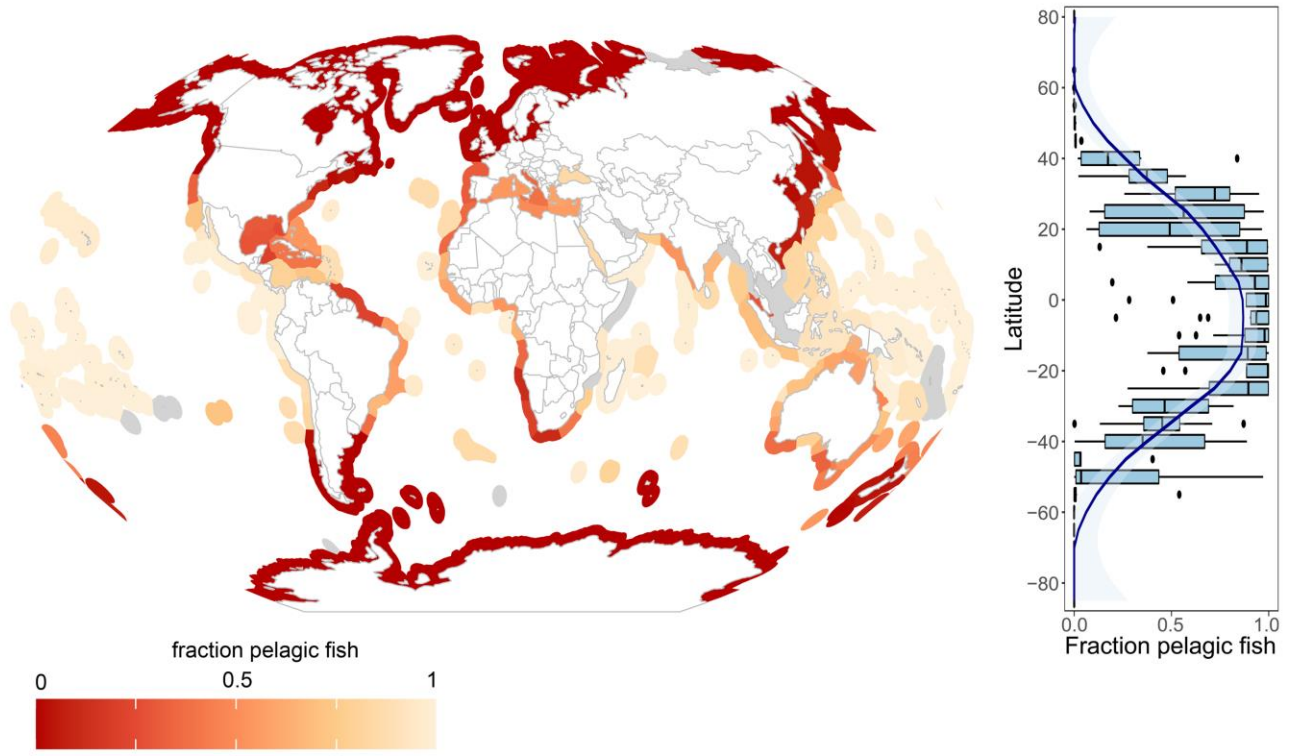
514 **Figure 1**



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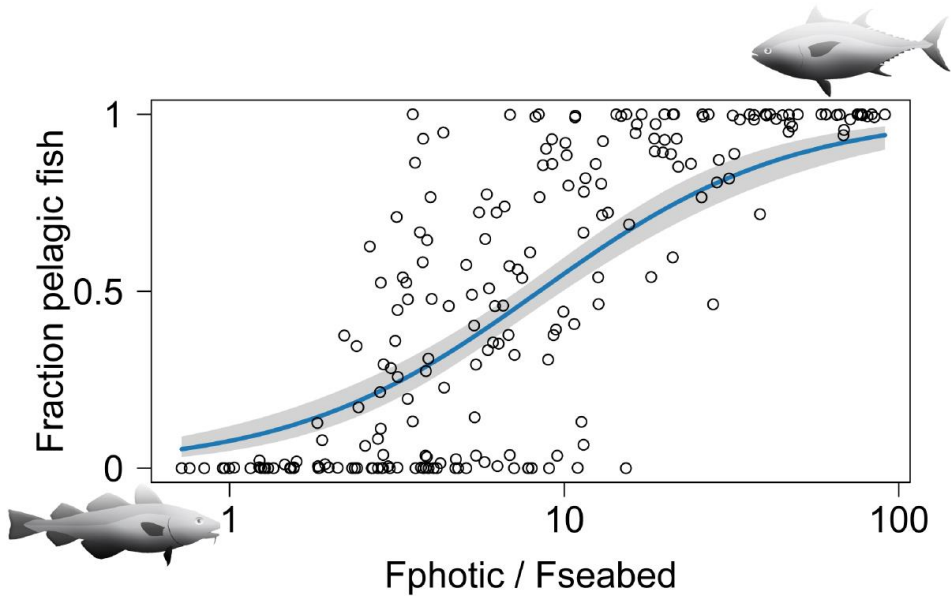
517 **Figure 2**



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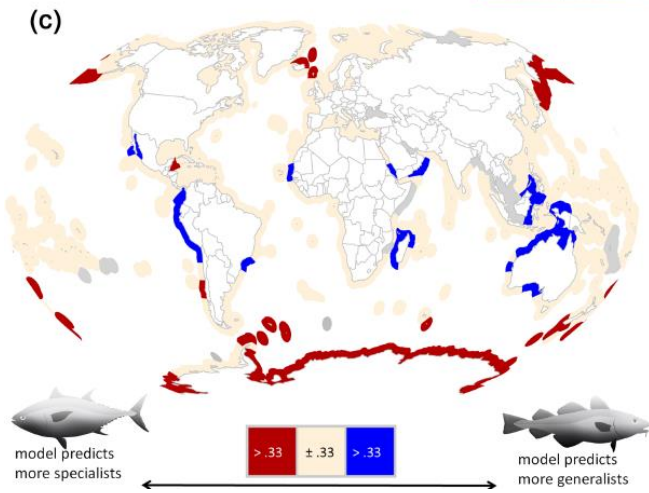
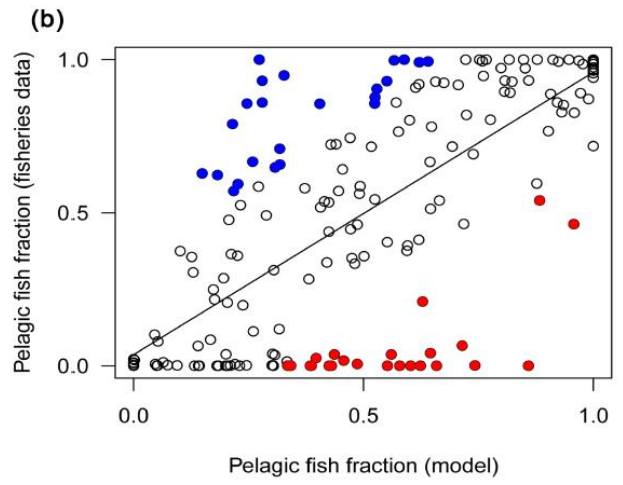
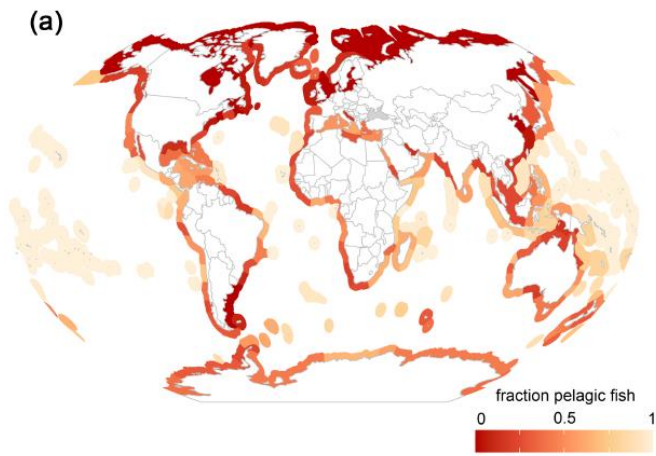
520 **Figure 3**



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523 **Figure 4**



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