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1 **Emergent global biogeography of marine fish food webs**

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10

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12

13 **Data availability statement:** Data and code for all analyses are available on github with DOI:

14 <https://zenodo.org/record/3923825>

15

16 **Biosketch:** Daniël van Denderen is a postdoctoral researcher at the Centre for Ocean Life in
17 Denmark. His research focuses on the importance of pelagic and benthic habitats for marine fish
18 communities, food webs and fisheries production. The authors are developing mechanistic trait-
19 based approaches to study fish life in the ocean.

20 **Emergent global biogeography of marine fish food webs**

21 **Running title:** Biogeography of fish food webs

22

23 **Abstract**

24 **Aim:** Understanding how fish food webs emerge from the planktonic energy flows that sustain
25 them is an important obstacle for predicting fisheries production under climate change and
26 quantifying the role of fish in carbon and nutrient cycling. A central complication is that energy
27 pathways from primary producers to fish vary across the global oceans.

28 **Location:** Global oceans

29 **Time period:** Predictions are representative of the early 1990s

30 **Major taxa studied:** Marine teleost fish

31 **Method:** We present a size- and trait-based fish community model that explicitly resolves the
32 dependence of fish on the varying pelagic and benthic energy pathways. We use the model to make
33 global predictions of fish food-web biogeography. We compare the predicted fish food webs with
34 regionally-calibrated models in three different ecosystem types.

35 **Results:** We demonstrate how variations in pelagic-benthic energy pathways and seafloor depth
36 drive the emergent biogeography of fish food webs from shelf systems to the open ocean, and
37 across the global ocean. Most shelf regions have high benthic production, which favors demersal
38 fish that feed on pelagic and benthic pathways. Continental slopes also show a coupling of benthic
39 and pelagic pathways, sustained through vertically migrating and interacting mesopelagic and
40 deep-sea demersal fish. Open ocean fish communities are primarily structured around the pelagic

41 pathway. From the emergent food-web structures, we estimate two fish ecosystem functions:
42 potential fisheries production and benthic-pelagic coupling by demersal fish.

43 **Main conclusion:** We mechanistically link variation in ocean productivity with the upper trophic
44 levels of marine ecosystems using a size- and trait-based fish community model. We show how
45 ocean productivity and seabed depth shape the dominant traits and energy flow in fish communities
46 across ocean biomes. The mechanistic basis of the model enables predictions of the upper trophic
47 levels of marine ecosystems under global change.

48

49 **Keywords:**

50 Benthic-pelagic coupling, Energy chains, Fish, Mesopelagic, Size-based models, Trait-based
51 ecology

52 **Introduction**

53 Fish are a globally important food source and are a key component of biodiversity and ecosystem
54 functions in marine systems worldwide (FAO, 2016; Villéger et al., 2017). With shifting climatic
55 conditions, there is a growing need to understand current links between ocean productivity and
56 fish food webs and predict future changes. These predictions are needed to address future changes
57 in fisheries production (Lotze et al., 2019; Stock et al., 2017) and the ecological role of fish in
58 marine systems, and to address how these changes impact nutrient cycling and carbon
59 sequestration (Wilson et al., 2009). Key to credible predictions is mechanistic models of the
60 relationship between fish food-web variations and the planktonic energy flows that sustain them.

61 The food-web structure of a fish community is traditionally described with species-based
62 approaches to quantify feeding interactions and energy flows (Plagányi, 2007). The ability of such
63 regional models to explore local food webs using sampled data has made them a valuable tool for
64 fisheries management. The models have been less useful to derive common structuring forces
65 across oceanic regions. For that reason, size- and trait-based models have been developed to
66 characterize the structure of fish communities (Andersen, 2019; Pope et al., 2006). These models
67 use body size to describe physiological processes and feeding interactions, have been used with a
68 pelagic as well as a benthic energy pathway (Blanchard et al., 2011) and have been implemented
69 across ecosystems in a global context (Jennings & Collingridge, 2015).

70 Despite body size being a key trait describing energy flow and the structure of marine ecosystems,
71 size-based models are a simplistic representation of the complex structure of observed food webs
72 (Link, 2002). Besides body size, there is a growing recognition of the importance of vertical
73 structure of zooplankton and fish communities, i.e., how biomass and feeding interactions are
74 distributed across the water column. The vertical structure is important for carbon fluxes (Bianchi,

75 Stock, et al., 2013; Steinberg & Landry, 2017), oxygen dynamics (Bianchi, Galbraith, et al., 2013)
76 and marine resources (Giraldo et al., 2017; Irigoien et al., 2014). The vertical structure is partly
77 driven by variation in diet, e.g. demersal fish are associated with bottom habitats, where they feed
78 on benthic invertebrates, whereas pelagic fish live in the water-column and have a planktivorous
79 diet. The vertical structure is further organized around the availability of light and oxygen, which
80 changes systematically with depth (Bianchi, Galbraith, et al., 2013; Klevjer et al., 2016). As a
81 result, there have been rapid developments in regional and global modelling systems to predict the
82 vertical structure of marine pelagic ecosystems (Anderson et al., 2018; Aumont et al., 2018;
83 Lehodey et al., 2010; Maury, 2010).

84 Here, we introduce a vertical trait axis into a size- and trait-based modelling framework previously
85 used to simulate pelagic and demersal fish (Petrik et al., 2019). This development allows us to
86 explore how the vertical structure of fish communities is determined by ocean productivity, size-
87 structured predation and seafloor depth. We implement the model for five fish guilds that differ in
88 their maximum body weight and vertical habitat strategy (Fig. 1). We assert that this functional
89 diversity ensures a generic representation of fish diversity to resolve global fisheries catches and
90 carbon export to depth. We build upon the guild classification of (Petrik et al., 2019) comprising
91 three guilds with fish species primarily important for global fisheries catches: 1) epipelagic fish,
92 such as sardines and anchovies commonly referred to as forage fish, with a small maximum weight
93 that feed in the upper water column on zooplankton, 2) large pelagic predators, such as billfish and
94 tunas, that feed on plankton in earlier life stages and prey upon fish later in life, and 3) large
95 demersal fish, such as cod, haddock and halibut, that feed as larvae in the water column and on
96 benthic invertebrates and pelagic fish later in life. Besides these three guilds, two other guilds are
97 common in open ocean environments and contribute to carbon export to depth: 4) most dominant

98 in the open ocean are mesopelagic fish, such as lanternfishes and bristlemouths (Irigoien et al.,
99 2014). These fish have a small maximum weight and are adapted to living in a twilight
100 environment. Mesopelagic fish are known for their diel vertical migration behavior, being at depth
101 during the day and at the surface during night. The migrations of the mesopelagic fish community
102 attract large pelagic predators to the twilight zone for feeding (Evans et al., 2008). Predation on
103 the mesopelagic fish community also occurs by demersal fish, e.g. slickheads and rattails, that feed
104 on the migrating mesopelagic community during day and migrate to deeper waters during night to
105 feed at the seafloor (Trueman et al., 2014). Research has shown that vertical migrations of
106 mesopelagic and demersal fish can make significant contributions to carbon export (Davison et al.,
107 2013; Trueman et al., 2014). Resolving the migrations therefore allows more accurate predictions
108 of fish carbon export in future work, see also (2018). Lastly, 5) the twilight zone is further occupied
109 by mid-water predators, e.g. sabertooths and barracudinas, which are a third predator group that
110 prey on the mesopelagic fish community (Drazen & Sutton, 2017; Hopkins et al., 1996).

111 It is our objective to describe large-scale variations in fish guilds and food-web structure. Our
112 objective does not require fine-scale resolution of precise migration depths of the different fish
113 guilds and zooplankton resources. The migrating behavior of resources and guilds are therefore
114 imposed (Fig. 2 and SI 1, Table S1.1). Our work thus assesses global patterns emerging from the
115 interaction of these observed behaviors across ocean biomes. The vertical behavior is combined
116 with the rule that big predators eat smaller prey and standard size-based food-web modelling
117 techniques to determine the emergent biogeography of marine fish food webs. The predictions are
118 based on zooplankton production and detrital export flux reaching the bottom derived from a high-
119 resolution Earth System Model (Stock et al., 2017), water column temperature and seafloor and
120 euphotic depth.

121 **Methods**

122 The fish food web is described by a stage-structured biomass model that follows the framework
123 developed by de Roos et al. (2008) and was used previously by Petrik et al. (2019) to estimate
124 global fish production of forage, large pelagic and demersal fish. The model incorporates food-
125 dependent somatic growth and reproduction following a standard bioenergetic budget for size- and
126 physiologically structured models (Andersen, Jacobsen, et al., 2015; de Roos et al., 2008) (SI 1,
127 Table S1.2). Parameterization is based on general fish physiology and mass-scaling principles
128 (Andersen, 2019) (SI 1, Table S1.3).

129 Below we describe 1) the model formulations of predator-prey interactions and 2) fish guild traits.
130 SI. 2 presents the remaining model formulations and model parameters of fish, zooplankton and
131 benthic resources. SI 2 further presents the environmental conditions used to model fish food webs.
132 SI 3 describes how we compared our modelling output with three regionally-calibrated Ecopath
133 with Ecosim (EwE) models that reflect different ecosystem types (Howell et al., 2009; Jarre-
134 Teichmann & Pauly, 1993; Mackinson & Daskalov, 2008), as downloaded from EcoBase (Coll  ter
135 et al., 2013).

136 Fish guilds and traits

137 The five fish guilds, epipelagic fish, large pelagic predator, mesopelagic fish, mid-water predator
138 and demersal fish are described by two traits, maximum (asymptotic) body weight and vertical
139 habitat strategy. Maximum weight is the most important trait in the structuring of fish communities
140 (Andersen & Beyer, 2006). The distinction between fish with small and large maximum weight
141 follows (Petrik et al., 2019). Two fish guilds, epipelagic fish and mesopelagic fish, have a weight
142 at maturity of 0.5 g and a maximum weight of 250 g. The other guilds mature at 250 g with a
143 maximum weight of 125 kg. The vertical habitat strategy of fish depends on seafloor depth and

144 varies between fish guilds. Epipelagic fish, large pelagics and demersal fish make up the fish
145 community in shelf regions, i.e. regions < 250 meters in depth. In slope (250-2000 meters) and
146 open ocean regions, all fish guilds may coexist. Some fish guilds and part of the zooplankton
147 community make diel vertical migrations. The vertical distribution of fish, zooplankton and
148 benthos in the water column is shown in Fig. 2 and explained in SI 2.

149 Emergent predator-prey interactions

150 Fish guilds in the fish community interact with each other and the resources through predator-prey
151 interactions that depend on size-based preference and vertical overlap (Fig. 1; SI 1, Table S1.2, eq.
152 1). Predators prefer smaller prey around a factor β smaller than themselves as described by a log-
153 normal size preference function (Ursin, 1973). To account for the size range of each stage we
154 integrate the size-preference function over the stage (eq. 2). The vertical distribution of each stage
155 and guild is modeled as a unimodal, or bimodal for vertically migrating groups, distribution
156 (Aumont et al., 2018; Maury, 2010), with the maximum concentration at depth(s) z_c (eq. 4). The
157 width of the distribution is assumed to be mass dependent (eq. 5), as larger individuals typically
158 have a wider home range (Jetz et al., 2004). This implies that smaller individuals have a vertical
159 distribution that largely mimics their prey, whereas larger individuals are more opportunistic. With
160 the chosen parameters, 90% of the distribution of a 0.001 g fish will be found in the top 40 m when
161 its maximum concentration is at the surface, while an 80 kg fish will roam across the top 170 m.
162 The vertical distribution is parameterized for day and night separately to incorporate diel vertical
163 migrations. The effective vertical overlap is calculated as the fraction of overlap of the predator
164 and prey vertical distribution curves (eq. 6), averaged over the day-night cycle, assuming 12 hours
165 of light/darkness (eq. 7). The final preference between individuals is the product of the size-based
166 preference and the vertical overlap (eq. 1).

167 **Results**

168 Emergent biogeography of fish food-web types

169 Food-web structure of the five fish guilds are predicted globally (Fig. 3). Maps of fish biomass for
170 each fish guild are shown in SI 1, Fig. S1.1. Continental shelf regions typically have a high detrital
171 flux reaching the seabed, supporting high benthic production. In these regions, demersal fish are
172 abundant as they can easily feed on both pelagic and benthic energy pathways (Fig. 3a and dark
173 orange in 3f). Demersal fish usually coexist with epipelagic fish and large pelagics. There are a
174 few shallow regions in the high arctic with low pelagic and benthic production where epipelagic
175 fish are the sole group present (not visible in Fig. 3f). Feeding on pelagic and benthic energy
176 pathways also occurs by demersal fish on continental slopes that still have a relatively high flux
177 of detritus reaching the seafloor (Fig. 3b, light orange in 3f). In these regions, adult demersal fish
178 make upward migrations during the day to feed on mesopelagic fish in the twilight zone, which
179 are further preyed upon by large pelagics. On both shelves and slopes, pelagic and benthic energy
180 pathways are therefore typically coupled through cross-habitat feeding (Fig. 3a-b).

181 In the deeper open ocean regions, pelagic and benthic energy pathways are decoupled. At high
182 zooplankton production, large pelagics coexist with epipelagic fish, mesopelagic fish and mid-
183 water predators (Fig. 3c, dark blue in 3f). Large parts of the open ocean are meso- and oligotrophic
184 areas with low nutrient mixing and consequently minimal new primary production and low
185 zooplankton production. The fish community in these areas is devoid of large predators and
186 gradually shifts from a community with epipelagic fish and mesopelagic fish (Fig. 3d, blue in 3f),
187 to mesopelagic fish only (Fig. 3e, light blue in 3f), to no fish in the least productive areas (Fig. 3,
188 white in 3f). The absence of fish in these limited areas indicates that fish present in nature in these
189 regions are either migratory or adapted to survive with low food in ways that are not accounted for

190 in our 5-guild model. Fish are also absent in large parts of the deep sea, indicating similar types of
191 adaptations to low food and/or pulsed food events.

192 Model comparison with regional models

193 We compared biomass and energy flow between our model predictions and three regionally-
194 calibrated models reflecting different ecosystem types. Despite the simplicity of our model, it well
195 captures the general features of the regional food webs (Fig. 4). As expected, shelf regions in both
196 models have higher benthic biomass and strong feeding fluxes towards demersal fish. Both models
197 also predict that the Peruvian shelf has a stronger pelagic pathway and higher biomass of pelagic
198 fish relative to the North Sea shelf. Finally, the slope region West of Scotland has a dominant mid-
199 water fish community in both models. A closer inspection shows that the regional model of the
200 North Sea predicts more benthic biomass and higher fluxes from benthos to fish as compared with
201 our prediction, whereas the biomass and fluxes in our model match well with the regional model
202 West of Peru. The regional model of the slope region predicts stronger feeding fluxes and no
203 epipelagic and/or large pelagic fish. Whether the absence of these fish guilds in this region is a
204 fisheries effect, the result of specific environmental conditions or a misclassification of fish species
205 into a specific guild as done in our study (see SI 3) is difficult to determine.

206 Fish ecosystem functions

207 Once the food-web structures are determined from the model, fish ecosystem functions can be
208 obtained. As examples, we show measures of potential fisheries production (Fig. 5a) and benthic-
209 pelagic coupling by demersal fish (Fig. 5b). Potential fisheries production is estimated as a fraction
210 of the energy flowing from juveniles to the fished adults. Classic surplus production fisheries
211 models show that the maximum sustainable yield to be taken from fisheries is about half of the
212 potential flux. For the small guilds, we first consider only a quarter of the total flux to leave

213 additional production as food for the larger fish guilds. The estimated fisheries production is 101
214 million tonnes per year, which compares well with the global fisheries output over the last decades
215 of 85 million tonnes per year (FAO, 2016). As expected, potential fisheries production per area is
216 highest in shelf seas and upwelling systems that have high new primary production (Fig. 5a). Shelf
217 and slope regions contribute 30% of the potential production. Mesopelagic fish have a potential
218 fisheries production of 30 million tonnes per year. The potential production can be increased by
219 taking a higher flux from the small guilds (i.e. half instead of a quarter), which will cause the
220 removal of large fish. This fishing patterns increases the potential global production to 168 million
221 tonnes per year. The prediction of increased catch when larger fish are removed matches other
222 studies showing theoretically (Andersen, Brander, et al., 2015) and empirically in the South-East
223 China Sea (Szuwalski et al., 2017) that a fishery narrowly targeting small fish can double the
224 fisheries production.

225 Benthic-pelagic coupling by demersal fish shows the relative flux of energy from pelagic and
226 benthic sources consumed by demersal fish (Fig. 5b). The pelagic flux is here defined as all energy
227 from pelagic zooplankton and the four pelagic fish guilds to demersal fish, whereas the benthic
228 flux represents demersal fish feeding on benthic invertebrates. In most shelf and slope regions, a
229 large fraction of energy consumed by all size-classes of demersal fish is of pelagic origin. For the
230 continental slope regions, this large fraction highlights that carbon is continuously transported to
231 the deeper waters through cross-habitat feeding. There is a small fraction of pelagic energy
232 consumed by demersal fish in decoupled open ocean systems, since the early life stages are pelagic
233 feeding.

234 Fish guild biomass as a function of seafloor depth and temperature

235 The changes in fish food-web structure in Fig. 3 from shelf to open ocean environments are driven
236 by changes in production of zooplankton, detrital flux and seafloor depth (Fig. 6). In regions with
237 a high pelagic production and a high detrital export flux out of the sunlit euphotic zone, demersals
238 are dominant in shallow shelf regions together with epipelagic fish (Fig. 6a-b). The demersals
239 decline in biomass with depth and this promotes large pelagics. At continental slopes, mesopelagic
240 fish become abundant and epipelagic fish decline. This shift happens due to the diel vertical
241 migrations of the zooplankton community that benefit mesopelagic fish (SI 1, Fig. S1.2).
242 Mesopelagic fish are preyed upon by large pelagics and adult deep-living demersal fish on slopes.
243 Deep-living demersals gradually decrease in biomass with depth and this decline promotes mid-
244 water predators (Fig. 6a-b). Around 2000 meters, demersals are unable to migrate the large
245 distance between the mid-water fish community and the bottom, resulting in a decoupling of the
246 energy pathways. Low pelagic production and low detrital export flux out of the euphotic zone,
247 i.e. oligotrophic regions, select for epipelagic and mesopelagic fish (Fig. 6c). The productivity and
248 abundance of these small fish is too low to support larger pelagic predators. Demersal fish do
249 survive in these conditions if there is sufficient benthic prey.

250 Temperature lowers the biomass of fish guilds in warmer waters due to increased maintenance
251 costs with temperature (SI 1, Fig. S1.3 - S1.6). The temperature dependencies in our model are
252 similar for all fish guilds and physiological rates and therefore have little influence on the relative
253 dominance of fish guilds. Yet, temperature does affect coexistence boundaries. With the
254 parameterization of Fig. 6, temperature excludes mid-water predators in temperate and tropical
255 regions (SI 1, Fig. S1.4 h, k, l). To promote these predators in the warmer waters, higher
256 zooplankton productivities are required (e.g. SI 1, Fig. S1.4 i).

257 **Discussion**

258 Fish food-web biogeography and the planktonic energy flows that sustain them

259 The transfer of energy from primary producers to the upper trophic levels varies across marine
260 regions throughout the ocean (Ryther, 1969). Broadly speaking, the transfer of energy varies cross-
261 regionally due to differences in 1) food chain lengths that connect phytoplankton to fish, and 2)
262 the strength of pelagic and benthic energy pathways (Friedland et al., 2012; Stock et al., 2017).
263 Such processes not only affect overall fish community biomass and potential fisheries catches, but
264 also the guild distribution of fish in a community (Cresson et al., 2020; Petrik et al., 2019; van
265 Denderen et al., 2018). Here we show that the distribution of biomass between fish guilds directly
266 depends on pelagic and benthic secondary production and is strongly mediated by seabed depth,
267 which (indirectly) controls the amount of detritus reaching the seabed, fish vertical behavior and
268 fish cross-habitat feeding. The importance of these individual processes for fish food-web structure
269 has been recognized for a long time. We show how these well-known bottom-up structuring forces
270 can be used to simulate fish guild biomass and feeding interactions across ocean biomes on a global
271 scale. Our study thereby mechanistically links variation in ocean productivity with the upper
272 trophic levels of marine ecosystems.

273 It is difficult to determine the extent to which the model reflects empirical patterns in nature. We
274 found a reasonable match between our modeled fish guild biomasses and feeding fluxes, and three
275 regionally-calibrated models that reflect different ecosystem types. Yet, estimates of fish biomass
276 are generally uncertain due to variation in gear catchability and acoustic backscatter. Moreover,
277 observed fish biomass is often changed due to historic fishing exploitation, making these
278 comparisons difficult. At global scales, one option is to compare modeled fisheries catches with
279 empirical catch reconstructions. This comparison has been done by Petrik et al. (2019), on which

280 our shelf model structure is based, and a reasonable agreement between modeled and empirical
281 catches was found for large pelagics and demersal fish across large marine ecosystems. Such a
282 comparison with empirical catch data is primarily useful for continental shelf and upwelling
283 regions where most of the fisheries production occurs. A more qualitative comparison of our
284 findings with empirical work in continental slope regions suggests that our model predicts larger
285 declines in demersal fish biomass with depth than is typically observed (Kallianiotis et al., 2000;
286 Mindel et al., 2016; Trueman et al., 2014). This may be due to migrations by demersal fish to
287 deeper waters, e.g. ontogenetic deepening, as well as an even larger capacity to exploit the
288 migrating mesopelagic resource. Nevertheless, eventually demersal fish biomass declines with
289 depth following the decline in the detrital flux that reaches the seafloor (Wei et al., 2011). For open
290 ocean pelagic systems, mesopelagic fish biomass has been found to strongly correlate with ocean
291 productivity (Irigoien et al., 2014) and such effects are also found in the model. One aspect that is
292 clearly misrepresented in the model is the simulated high abundance of large pelagics in productive
293 cold-water regions. Recent work suggests that large pelagic fish are outcompeted in these cold
294 waters by endotherms that can maintain a high body temperature and activity (Grady et al., 2019).

295 Fish and active carbon export

296 Active carbon transport by zooplankton and fish through diel vertical migrations is suggested to
297 contribute substantially to the total export of carbon (10-20% of the passive flux of carbon) to
298 deeper regions (Aumont et al., 2018; Bianchi, Stock, et al., 2013; Davison et al., 2013). These
299 predictions are focused on vertical migrations of the mesopelagic community that transport carbon
300 to depth by feeding at the surface at night and by respiring and excreting below the euphotic zone
301 during the day. Yet, the quantification of carbon flows to depth is not limited to the mesopelagic
302 community as vertically migrating mesopelagic fish are prey for deep-living demersal fish that

303 vertically migrate to deeper waters to feed at the seafloor (Trueman et al., 2014). Such vertical
304 migrations of prey and predator at continental slopes results in a demersal diet where a large
305 fraction of energy is from pelagic zooplankton and pelagic fish (Fig. 5b). Even though continental
306 slope regions are not that common on a global scale, these migrations ensure fast carbon transport
307 to depths up to about 2000 meters and highlight the need for further work on the quantification of
308 these fluxes.

309 The depth of vertically migrating species in open ocean systems was prescribed in our model using
310 the euphotic depth. For the sake of predicting fish food-web structures, depth of vertical migration
311 is of limited importance as the zooplankton and fish migrations are coupled to each other. Yet,
312 vertical migration depth is important to quantify active carbon fluxes. One way to improve the
313 model is to use a global empirical relationship between depth of vertical migration and oxygen,
314 temperature, surface chlorophyll and the mixed layer depth (Bianchi, Stock, et al., 2013).
315 Alternatively, the vertical migration strategies of prey and predators can potentially be obtained
316 through explicit applications of game theory (Pinti & Visser, 2018).

317 Fish trait-based ecology

318 We used a generic trait-based configuration to estimate the structural differences in energy flow
319 in fish communities across regions. The advantage of a trait-based approach is that it does not
320 require the quantification of feeding interactions from species-based parameterizations. It is
321 thereby also more robust in predicting the long-term effects of climate change as it implicitly
322 allows for invasions of new strategies and the extirpation of others (Kiørboe et al., 2018).

323 Our trait-based configuration diversified possible fish guilds, food-web structures and energy
324 flows compared to the more commonly used size-based models. Yet, some ecological processes

325 and behaviors had to be constrained in the model and can be further refined. Next to model
326 refinements related to the vertical migration behavior (as mentioned above), this is particularly the
327 case for the modelling of feeding strategies in shallow regions. In these regions, feeding strategies
328 were poorly resolved with the trait “vertical habitat strategy” as all fish had vertically overlapping
329 distributions. Even though fish in shallow regions make substantial use of both pelagic and benthic
330 pathways (Duffill Telsnig et al., 2019; Giraldo et al., 2017), preference for a pelagic or a benthic
331 diet seems to exist and was therefore imposed in the model. The fish feeding strategies did not
332 include obligate benthivorous fish as we expected that such a strategy is of limited importance for
333 total demersal guild biomass. One way to refine feeding strategies is by explicitly including a trait
334 axis that describes the ability of fish to feed on benthos relative to pelagic resources. A second
335 refinement is including light availability and adaptations to low or high light conditions explicitly
336 in the model to better incorporate pelagic feeding strategies in open ocean environments
337 (Langbehn & Varpe, 2017). Such an improvement may potentially shed further light on
338 bathypelagic fish that survive in low food environments in the open ocean, in regions where food
339 is now absent in the model. Yet, the inclusion of bathypelagic fish is unlikely to severely improve
340 predictions of active carbon export by fish or potential fisheries production as fish biomass will
341 always be low in these environments.

342 Conclusion

343 Our work demonstrates how inclusion of fish vertical habitat strategy in a well-established size-
344 and trait-based framework allows for global-scale prediction of fish community food-web
345 structure. Using the framework, we show how ocean productivity and seabed depth shape the
346 dominant traits and energy flows in fish communities. The modelling framework can be used to
347 1) predict dominance and potential fisheries production of different fish guilds, 2) assess the

348 indirect ecosystem effects of mesopelagic fisheries, which are a major potential resource for future
349 global fisheries, 3) quantify active export of carbon to depth through fish diel vertical migrations
350 and feeding interactions and 4) all of the above in the context of global change in primary
351 production and temperature. Our study thus highlights the trait-based approach to modelling fish
352 communities as a powerful tool to mechanistically predict links between ocean productivity and
353 fish production for fisheries, as well as quantify the ecological role of fish in marine systems.

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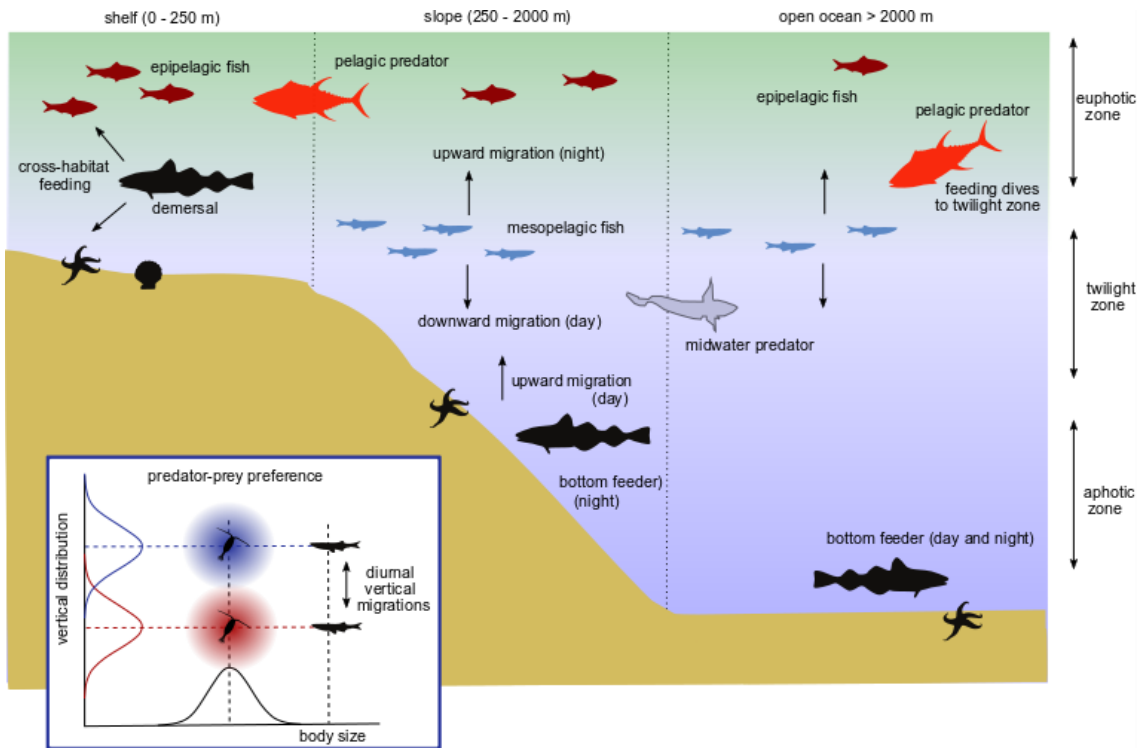
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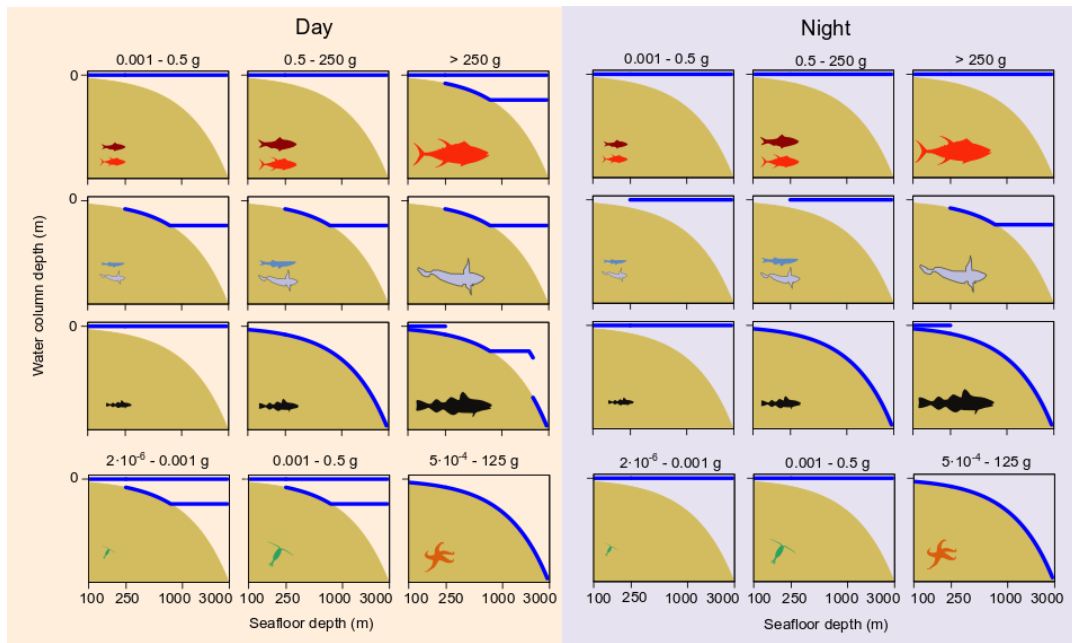
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514 **Figures**



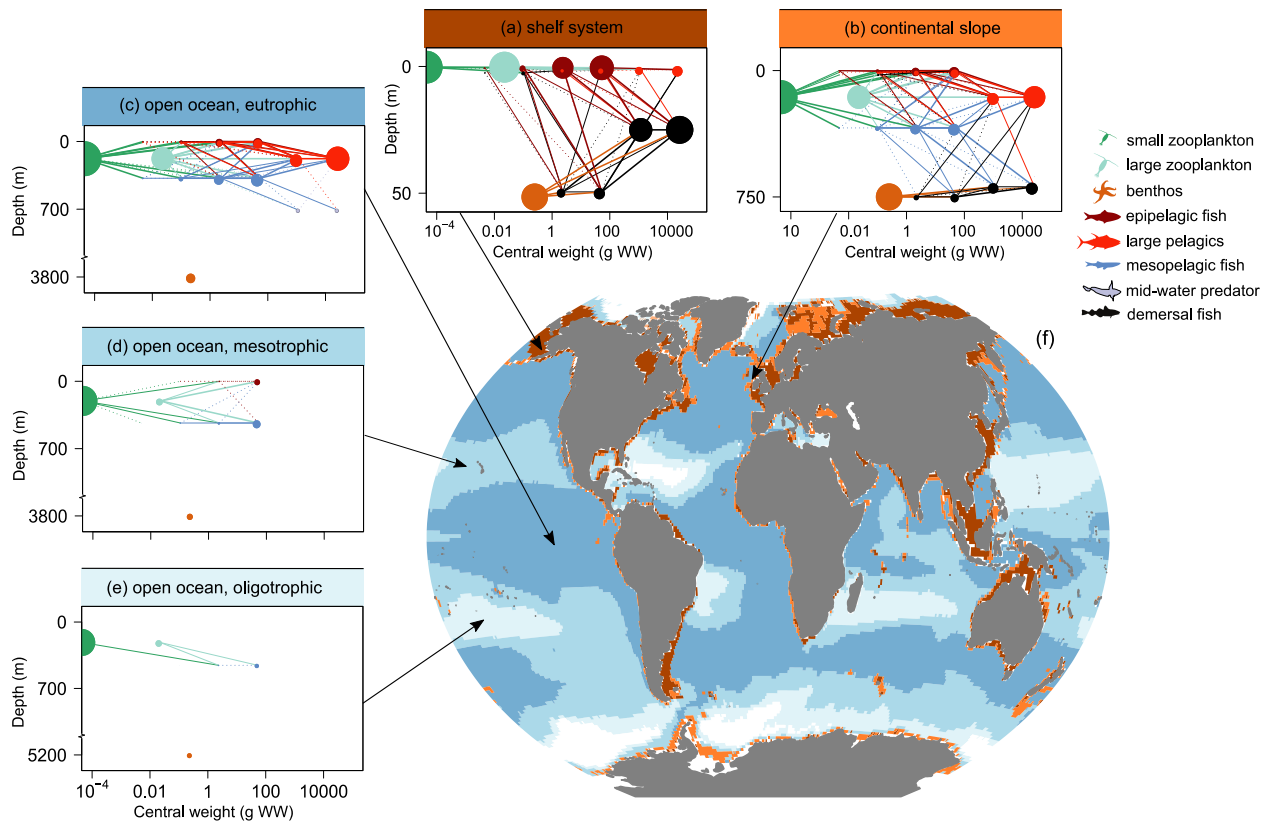
515

516 Figure 1. Illustration of fish guilds in the fish community deemed important for global fisheries
517 catches and active carbon export to depth. Fish interact with each other and the resources through
518 predator-prey interactions if they overlap in their spatial distribution in the water column and if
519 the prey is of preferred size (see inset).



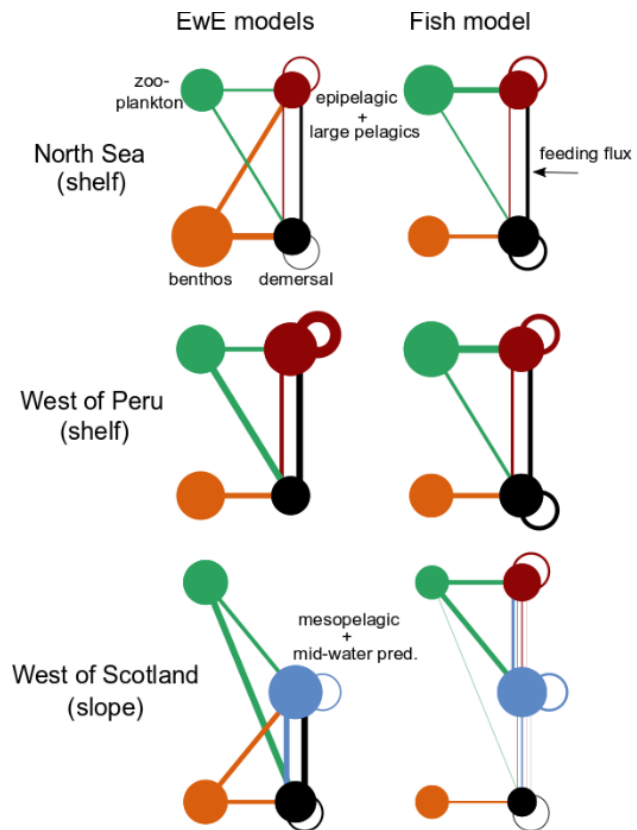
520

521 Fig 2. Vertical position (blue lines) of fish guild size-classes and resources from a seafloor depth
 522 of 100 to 3000 meters (upper edge of the sloping yellow shape in each panel). The vertical position
 523 shows the depth of maximum concentration z_c for day and night; when two positions are shown at
 524 the same seafloor depth it indicates a bimodal vertical distribution (SI 1, Table S1.1). The euphotic
 525 depth is at 150 m. Note that there are more fish size-classes than the groups presented here, but the
 526 classes align with the weight boundaries shown.



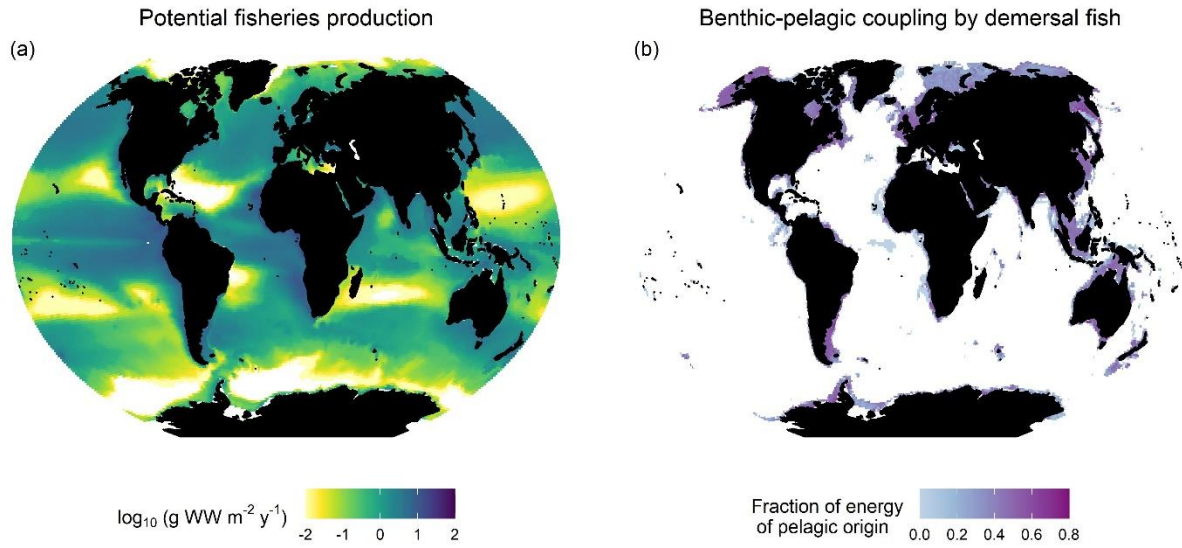
527

528 Figure 3. Emergent food-web types from shelf regions to open ocean environments due to seafloor
 529 depth, zooplankton production and detrital export. The food-web panels (a-e) show biomass
 530 (circles; surfaces are scaled with a \log_{10} transformation) and fluxes of biomass (lines) in a 1-degree
 531 grid cell. The vertical position of fish in the food-web panels is the average position of each size
 532 class. Dashed, solid thin and solid thick lines show weak (10^{-2} -0.1), intermediate (0.1-1) and strong
 533 (>1) feeding interactions in g wet weight $m^{-2} y^{-1}$. Interactions less than 10^{-2} g wet weight $m^{-2} y^{-1}$
 534 are not shown. The colors in the food-web panels correspond to the legend. The colors in the map
 535 (f) define regions with a similar food-web type, threshold values are presented in SI 1 Table S1.4.
 536 Food-web panels are not presented for the white areas where the resource production is too low to
 537 support fish biomass.



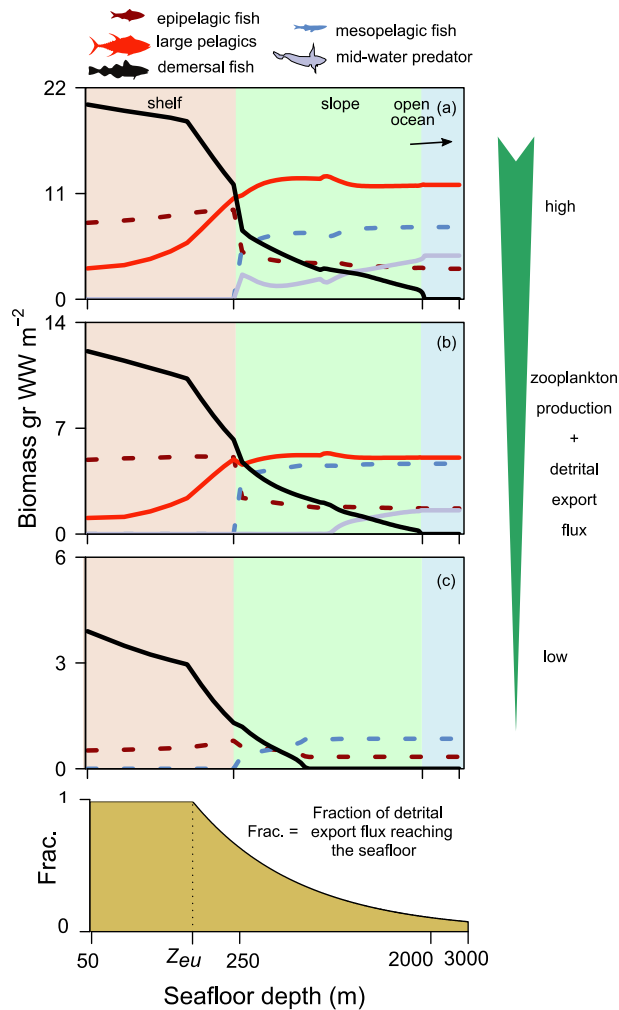
538

539 Figure 4. Comparison of biomass and energy flow between the trait-based fish model (right) and
 540 three regional-specific (Ecopath with Ecosim, EwE) food-web models (left). All panels show
 541 biomass (circles) and fluxes of biomass (lines), both scaled with a \log_{10} transformation. The
 542 internal loops present feeding fluxes within each grouping.



543

544 Figure 5. Map of two fish ecosystem functions: potential fisheries production (a) and benthic-
 545 pelagic coupling by demersal fish (b). Potential fisheries production is estimated as a fraction of
 546 energy flowing from juveniles to the fished adults. Benthic-pelagic coupling by demersal fish is
 547 estimated as the sum of all feeding fluxes from zooplankton/pelagic fish guilds to demersal fish in
 548 $\text{g wet weight m}^{-2} \text{y}^{-1}$ relative to the total flux. This prediction does not consider cannibalism by
 549 demersal fish and is only shown in areas where demersal biomass is $> 10^{-4} \text{ g wet weight m}^{-2}$.



550

551 Figure 6. Biomass of fish guilds as a function of seafloor depth for high (a), intermediate (b) and
 552 low (c) zooplankton production and detrital export flux out of the euphotic zone. Benthic
 553 maximum production depends on the detrital export flux and bottom depth, following eq. 21 in SI
 554 1, Table S1.2. The euphotic depth is at 150 m. Note the different scales on the y-axes. Resource
 555 values: maximum small and large zooplankton production is 100 (a), 50 (b) and 5 (c) g wet weight
 556 $\text{m}^{-2} \text{y}^{-1}$; detrital export flux is 380 (a), 250 (b) and 130 (c) $\text{g wet weight m}^{-2} \text{y}^{-1}$. There is no variation
 557 in temperature (see SI 1 Fig S1.4 for the effect of temperature).