Emergent global biogeography of marine fish food webs

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Biosketch: The authors are developing mechanistic trait-based approaches to study life in the ocean. These approaches are used for large-scale assessments of climate change, fisheries and marine ecosystem functions.

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

11

12   **Abstract**

13   **Aim:** Understanding how fish food webs emerge from planktonic and benthic production that

14   sustain them is an important challenge for predicting fisheries production under climate change

15   and quantifying the role of fish in carbon and nutrient cycling. We examine if a trait-based fish

16   community model using the fish traits of maximum body weight and vertical habitat strategy can

17   meet this challenge by globally representing fish food web diversity.

18   **Location:** Global oceans

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

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

21   **Method:** We present a size- and trait-based fish community model that explicitly resolves the

22   dependence of fish on pelagic and benthic energy pathways to globally predict fish food web

23   biogeography. The emergent food web structures are compared with regionally-calibrated

24   models in three different ecosystem types and used to estimate two fish ecosystem functions:

25   potential fisheries production and benthic-pelagic coupling.

26 **Results:** Variations in pelagic-benthic energy pathways and seafloor depth drive the emergent
27 biogeography of fish food webs from shelf systems to the open ocean, and across the global
28 ocean. Most shelf regions have high benthic production, which favors demersal fish that feed on
29 pelagic and benthic pathways. Continental slopes also show a coupling of benthic and pelagic
30 pathways, sustained through vertically migrating and interacting mesopelagic and deep-sea
31 demersal fish. Open ocean fish communities are primarily structured around the pelagic pathway.
32 Global model results compare favorably with data-driven regional food web models, suggesting
33 that maximum weight and vertical behavior can capture large-scale variations in food web
34 structure.

35 **Main conclusion:** Mechanistically linking ocean productivity with upper trophic levels using a
36 size- and trait-based fish community model results in spatial variations in food web structure.
37 Energy pathways vary with ocean productivity and seabed depth, thereby shaping the dominant
38 traits and fish communities across ocean biomes.

39

40 **Keywords:**
41 Benthic-pelagic coupling, Energy chains, Fish, Mesopelagic, Size-based models, Trait-based
42 ecology

43 **Introduction**

44 Fish are a globally important food source and are a key component of biodiversity and ecosystem
45 functions in marine systems worldwide (FAO, 2016; Villéger et al., 2017). With shifting climatic
46 conditions, there is a growing need to understand current links between ocean productivity and
47 fish food web variations in order to predict future changes. These predictions are needed to
48 assess future changes in fisheries production (Lotze et al., 2019; Stock et al., 2017), as well as to
49 address how the ecological role of fish in marine systems may change and impact nutrient
50 cycling and carbon sequestration (Saba et al., 2021; Wilson et al., 2009).

51 Recent advances in size-based ecology have resulted in models that are well-suited to estimate
52 energy transfer from plankton to the upper trophic levels, i.e. piscivorous fish, of marine pelagic
53 food webs. The size-based models derive fish communities as a size distribution and represent
54 differences among species only by the trait maximum body weight (Andersen, Jacobsen, et al.,
55 2015; Pope et al., 2006). The models link all physiological processes and patterns of predation

56 and mortality, i.e. big fish eat small fish, to individual body weight, which is a simplification that
57 enables characterizing fish communities with few parameters. As a result, size-based models
58 have been used across marine regions to describe fish communities and implemented in a global
59 context, e.g. Jacobsen et al. (2017) and Jennings & Collingridge (2015).

60 Empirical work on body size and food web structure has suggested that predictions of feeding
61 interactions can be considerably improved when body size is not used in isolation but in
62 interaction with other traits (Eklöf et al., 2013). For fish communities, there is a growing
63 recognition of the importance of a vertical-trait axis to incorporate the vertical structure of a fish
64 community, i.e. how biomass and feeding interactions are distributed across the water column
65 (Giraldo et al., 2017; Pecuchet et al., 2020). This vertical structure of a fish community is partly
66 driven by variations in diet, e.g. some fish are associated with the bottom habitat, where they
67 feed on benthic invertebrates, whereas other fish have a more planktivorous diet and live in the
68 water-column. The vertical structure is also organized by the availability of light and oxygen
69 (Bianchi, Stock, et al., 2013). Millions of fish migrate to the deeper ocean during the day to
70 escape predatory fish in the well-lit surface waters thereby actively transporting carbon to depth
71 through respiration and other processes, such as excretion and death (Irigoien et al., 2014). The
72 vertical structure of a fish community hence influences the biogeochemical fluxes of oxygen and
73 carbon in the water column (Bianchi, Galbraith, et al., 2013; Saba et al., 2021). The vertical
74 structure may further drive fish food web variations associated with important ecosystem
75 functions such as benthic-pelagic coupling and potential fisheries production (Petrik et al., 2019;
76 van Denderen et al., 2018). Consequently, there have been rapid developments in regional and
77 global modelling systems to predict the vertical structure of marine fish communities (Anderson
78 et al., 2018; Aumont et al., 2018; Blanchard et al., 2012; Lehodey et al., 2010; Maury, 2010).
79 Yet, none of these studies has so far considered vertically distinct pelagic habitats together with
80 the important role of the benthic seabed ecosystem as food for fish.

81 To represent fish in the benthic habitat and vertically distinct pelagic habitats, we introduce a
82 vertical trait axis into a size- and trait-based modelling framework (FEISTY) previously used to
83 simulate (epi)pelagic and demersal fish (Petrik et al., 2019). We implement the model for five
84 fish guilds that differ in their maximum body weight and vertical habitat strategy (Fig. 1). We
85 assert that this functional diversity ensures a generic representation of fish diversity to resolve

86 global fisheries catches and active carbon export to depth. The aims of this paper are: 1) to
87 predict the emergent biogeography of fish food web types based on large-scale variations in the
88 biomass of individual fish guilds and their feeding interactions with shifting environmental
89 conditions; 2) to compare the predicted fish food webs with regionally-calibrated models in three
90 different ecosystem types; and 3) to estimate two ecosystem functions, potential fisheries
91 production and benthic-pelagic coupling by demersal fish, from the emerging fish community
92 food web structures.

93 **Methods**
94 Overview of model structure
95 The fish food web is described by a size-structured biomass model that follows the framework
96 developed by de Roos et al. (2008) and was used previously by Petrik et al. (2019) to estimate
97 global fish production of forage, large pelagic and demersal fish. The model incorporates food-
98 dependent somatic growth and reproduction following a standard bioenergetic budget for size-
99 and physiologically structured models (Andersen, Jacobsen, et al., 2015; de Roos et al., 2008) (SI
100 1, Table S1.1). Differences among fish guilds are represented by the traits maximum body
101 weight and vertical habitat strategy. The trait maximum body weight represents a trade-off
102 between reproductive output and adult maximum size (Andersen & Beyer, 2006). The trait
103 vertical habitat strategy describes the vertical distribution of the different fish guilds and
104 resources along the water column. Fish vertical distribution varies within a guild by size and
105 day/night through vertical migrations and is imposed following observations from the literature
106 (SI 2). Fish interact through predator-prey interactions that depend on habitat overlap in the
107 water column and the rule that big predators eat smaller prey (Barnes et al., 2010).

108 We use the model to predict fish guild biomass and food web structure on a 1° spatial grid across
109 the global ocean. These predictions are driven by estimates of zooplankton and the energy supply
110 to the benthos from a high-resolution (1/10° spatial grid) Carbon, Ocean Biogeochemistry and
111 Lower Trophics (COBALT) ecosystem model from a climatology of GFDL's Earth System
112 Model (ESM2.6) representative of the early 1990s (hereafter termed ESM2.6-COBALT) (Stock
113 et al., 2014, 2017), water column temperatures and seafloor and euphotic depth (see SI 3 for data
114 sources). We further examine the changes in fish guild biomass and food web structure as a

115   function of seafloor depth for different idealized resource productivity and water column
116   temperature scenarios (see SI 4 for data sources).

117   Fish guilds

118   We implement the model for five fish guilds (Fig. 1). We build upon the guild classification of
119   Petrik et al., (2019) comprising three guilds with fish primarily important for global fisheries
120   catches: 1) epipelagic fish, such as sardines and anchovies commonly referred to as forage fish,
121   with a small maximum weight that feed in the upper water column on zooplankton, 2) large
122   pelagic predators, such as billfish and tunas, that feed on plankton in earlier life stages and prey
123   upon fish later in life, and 3) large demersal fish, such as cod, haddock and halibut, that feed as
124   larvae in the water column and on benthic invertebrates and pelagic fish later in life. These three
125   guilds largely ignore the mid-water habitats in open ocean environments.

126   Two other guilds are common in open ocean mid-water habitats where they contribute to carbon
127   export to depth: 4) mesopelagic fish and 5) mid-water predators. Mesopelagic fish, such as
128   lanternfishes and bristlemouths, are most dominant in the open ocean (Irigoien et al., 2014).
129   These fish have a small maximum weight and are adapted to living in a twilight environment
130   (Fig. 1). Mesopelagic fish are known for their diel vertical migration behavior, being at depth
131   during the day and at the surface during night. The migrations of the mesopelagic fish
132   community attract large pelagic predators to the twilight zone for daytime feeding (Evans et al.,
133   2008). Predation on the mesopelagic fish community also occurs by demersal fish, e.g.
134   slickheads and rattails, that feed on the migrating mesopelagic community during day and
135   migrate to deeper waters during night to feed at the seafloor (Trueman et al., 2014). Lastly, the
136   mid-water predators occupying the twilight zone, e.g. sabertooths and barracudinas, are a third
137   predator group that preys on the mesopelagic fish community (Drazen & Sutton, 2017; Hopkins
138   et al., 1996).

139   We assume that epipelagic fish, large pelagics and demersal fish make up the fish community in
140   shelf regions, i.e. regions < 250 meters in depth. On continental slopes (250-2000 meters) and
141   open ocean regions, all fish guilds may coexist. The vertical distribution of the different fish
142   guilds is shown in Fig. 2 and further explained in SI 2.

143 We parameterize epipelagic/forage and mesopelagic fish with a maximum body weight of 250 g

144 (lower limit of weight at maturation is 0.5 g) and the three larger guilds with a maximum body

145 weight of 125 kg (lower limit of weight at maturation is 250 g). For computational efficiency, we

146 represent the size-distribution of epipelagic and mesopelagic fish in four size-classes and the

147 three larger guilds in six classes. The model outcome is largely insensitive to the exact number of

148 size-classes used (SI 5).

149 All fish parameters beside maximum body weight and vertical habitat strategy are similar across

150 guilds and based on general fish physiology and mass-scaling principles (SI 1, Table S1.2). The

151 physiological rates (clearance, metabolic and maximum consumption rates) scale with

152 temperature. This scaling corresponds to a Q_{10} of 1.88, where Q_{10} shows the rate of change of the

153 parameters as a result of an increase of 10°C. This value, which originates with phytoplankton

154 growth studies (Eppley, 1972) and is within the range of values reported for zooplankton growth

155 and ingestion (Hansen, 1997), was used to scale all biological processes in the underlying

156 plankton food web model (Stock et al., 2014) and is carried through to the fish model

157 configuration. Since ambient temperatures vary in the water column, an average temperature per

158 guild and size class is estimated by integrating water column temperatures over the vertical

159 distribution of each fish guild and size class. More details on the model's equations, assumptions

160 and parameters can be found in SI 2.

161 Zooplankton and benthic resources

162 We include two zooplankton resources and one benthic resource following Petrik et al. (2019).

163 The smaller zooplankton group represents small to medium-sized copepods in the size range

164 $2 \cdot 10^{-6} - 0.001$ g (0.2 – 2 mm) and the larger group represents large copepods and krill in the size

165 range 0.001 – 0.5 g (2 – 20 mm). In shelf regions, the zooplankton groups are assumed to be

166 distributed in the upper water column with a maximum concentration at the surface of the water

167 column, whereas part of the zooplankton in each size group is assumed to make diel vertical

168 migrations in slope and open oceans regions (see further SI 2). Benthos consist of one size group

169 that represents benthic fauna from small annelids of $5 \cdot 10^{-4}$ g to larger organisms of 125 g, such

170 as echinoderms and bivalves, and are concentrated at the seafloor.

171 All resource groups follow semi-chemostat dynamics, with a turnover rate and a maximum

172 biomass density (SI 1, table S1.1 and SI 2). The maximum resource production, described as the

173   product of these two terms, is scaled to the medium and large zooplankton productivities on a 1°

174   grid from ESM2.6-COBALT (Stock et al., 2014, 2017). Such a scaling of zooplankton

175   productivities is both done for the global predictions as well as the theoretical scenarios, as

176   explained in SI 3 and SI 4 respectively. Benthic maximum production is modeled in two

177   different ways. In the global predictions, benthic maximum production is estimated from

178   ESM2.6-COBALT output of the detritus flux reaching the seabed (SI 3). In the theoretical

179   scenarios, benthic maximum production depends on both the detrital export flux out of the

180   euphotic zone and seafloor depth. For the latter, benthic maximum production declines for

181   seafloor depths that are deeper than the euphotic depth with a power law function that represents

182   remineralization of detritus in the water column (Martin et al., 1987; Suess, 1980) (SI 1, table

183   S1.1).

184   The ESM2.6-COBALT outputs drive fish guild biomass and food web predictions. The ESM2.6-

185   COBALT model, which is described and evaluated in Stock et al. (2017), has an ocean resolution

186   of 1/10°. The output is averaged to a 1° grid for use in this application. The 1° patterns still

187   reflect the integrated effect of fine scale processes, which is especially important to represent

188   coastal areas. There are two main shortcomings with the ESM2.6-COBALT predictions that are

189   likely to influence our outcomes: 1) it underpredicts very high chlorophyll in near-shore regions,

190   and 2) it is limited in representing the complex dynamics in inland seas. Nevertheless, both

191   across ocean biomes as well as across globally-distributed large marine ecosystems, ESM2.6-

192   COBALT robustly captures the primary differences in chlorophyll, primary production, export

193   fluxes, and medium and large zooplankton biomass (Stock et al., 2017). We may therefore

194   expect that despite the potential for regional bias, ESM2.6-COBALT encapsulates the primary

195   contrasts in zooplankton and benthic productivity across the disparate ecosystem types

196   considered in our analysis.

197   Analysis

198   At each grid cell, we run the fish model for 300 years and take the average of the last 60 years

199   (by which time the model has converged to an equilibrium or stable attractor). Initial conditions

200   of fish biomass are 0.01 g wet weight m^{-2} for each size class and resource biomass is 10% of

201   maximum biomass density.

202   We classify the observed food webs into different types, based on the relative biomasses of the

203   five fish guilds, to map the emergent biogeography of the fish food webs (objective 1). We

204   afterwards compare guild biomasses and the fluxes between them from our modelling output

205   with three regionally-calibrated Ecopath with Ecosim (EwE) models, downloaded from EcoBase

206   (Colléter et al., 2013) (objective 2). We use EwE models for validation as they offer a data-

207   driven inversion for the food web characteristics (Christensen & Walters, 2004; Polovina, 1984)

208   to assess against feeding fluxes between fish guilds and biomass of fish guilds arising in our

209   model. The three EwE models reflect different ecosystem types, 1) the North Sea shelf with a

210   relatively strong benthic pathway (Mackinson & Daskalov, 2008), 2) the Peruvian shelf with a

211   relatively strong pelagic pathway (Jarre-Teichmann & Pauly, 1993) and 3) a continental slope

212   region off the coast of Scotland (Howell et al., 2009). This comparison requires the classification

213   of the EwE fish species into one of the five fish guilds used in our model (see SI 6).

214   Lastly, we estimate two ecosystem functions, potential fisheries production and benthic-pelagic

215   coupling by demersal fish (objective 3). Potential fisheries production is estimated as a fraction

216   of the energy flowing from juveniles to the fished adults. Classic surplus production fisheries

217   models show that the maximum sustainable yield to be taken from fisheries is about half of the

218   potential flux. We calculate this energy flux for epipelagic and mesopelagic guilds (maximum

219   size is 250 g) based on the energy flowing from size-class 2 to 3 and for the other guilds

220   (maximum size >250 g) based on the energy flowing from size-class 4 to 5. For the epipelagic

221   and mesopelagic guilds, we first consider only a quarter of the total flux from size-class 2 to 3 to

222   leave additional production as food for the larger fish guilds. Benthic-pelagic coupling by

223   demersal fish shows the relative flux of energy from pelagic and benthic sources consumed by

224   demersal fish. The pelagic flux is here defined as all energy from pelagic zooplankton and the

225   four pelagic fish guilds to demersal fish, whereas the benthic flux represents demersal fish

226   feeding on benthic invertebrates and excludes cannibalism by demersal fish.

227   To disentangle the many processes from the global model output that affect fish guild biomass

228   and food web structure, we end with a theoretical analysis of the model. In this analysis, we

229   show the changes in fish guild biomass as a function of seafloor depth for different resource

230   productivity scenarios and water column temperatures. Variations in these three axes allow us to

231 mimic the primary contrasts across the range of ecosystems in the full global model, elucidating

232 drivers of cross-ecosystem contrasts.

233 **Results**

234 Emergent biogeography of fish food web types

235 Food web structure, defined by the relative biomasses of the five fish guilds at each 1° grid cell

236 (SI 1, Fig. S1.1), are predicted globally (Fig. 3). Continental shelf regions typically have a high

237 detrital flux reaching the seabed, supporting high benthic production. In these regions, demersal

238 fish are abundant as they can easily feed on both pelagic and benthic energy pathways (Fig. 3a

239 and dark orange in 3f). Demersal fish usually coexist with epipelagic fish and large pelagics.

240 There are a few shallow regions in the high arctic with low pelagic and benthic production where

241 epipelagic fish are the sole group present (not visible in Fig. 3f). Feeding on pelagic and benthic

242 energy pathways also occurs by demersal fish on continental slopes that still have a relatively

243 high flux of detritus reaching the seafloor (Fig. 3b, light orange in 3f). In these regions, adult

244 demersal fish make upward migrations during the day to feed on mesopelagic fish in the twilight

245 zone, which are further preyed upon by large pelagics. On both shelves and slopes, pelagic and

246 benthic energy pathways are therefore typically coupled through cross-habitat feeding (Fig. 3a-

247 b).

248 In the deeper open ocean regions, pelagic and benthic energy pathways are decoupled. In regions

249 with high zooplankton production, large pelagics coexist with epipelagic fish, mesopelagic fish

250 and mid-water predators (Fig. 3c, dark blue in 3f). Large parts of the open ocean are meso- and

251 oligotrophic areas with low nutrient mixing and consequently minimal new primary production

252 and low zooplankton production. The fish community in these areas is devoid of large predators

253 and gradually shifts from a community with epipelagic fish and mesopelagic fish (Fig. 3d, blue

254 in 3f), to mesopelagic fish only (Fig. 3e, light blue in 3f), to no fish in the least productive areas

255 (Fig. 3, white in 3f). The absence of fish in these limited areas indicates that fish present in

256 nature in these regions are either migratory or adapted to survive with low food in ways that are

257 not accounted for in our 5-guild model. Demersal fish are also absent in large parts of the deep

258 sea, indicating similar types of adaptations to low food and/or pulsed food events.

259 Model comparison with regional models

260   Despite the simplicity of our model, the predicted biomasses and energy flows capture the

261   general features of the regional EwE food webs well (Fig. 4). As expected, shelf regions,

262   exemplified by the North Sea and Peruvian shelves, have higher benthic biomass and strong

263   feeding fluxes towards demersal fish in both models. Both models also predict that the Peruvian

264   shelf has a stronger pelagic pathway and higher biomass of pelagic fish relative to the North Sea

265   shelf. Finally, the slope region West of Scotland has a dominant mid-water fish community in

266   both models. A closer inspection shows that the regional model of the North Sea estimates more

267   benthic biomass and higher fluxes from benthos to fish as compared with our prediction, whereas

268   the regional model West of Peru estimates higher pelagic fish biomass and feeding flux within

269   the pelagic fish community. The regional EwE model of the West Scotland slope predicts

270   stronger feeding fluxes and no epipelagic and/or large pelagic fish. Whether the absence of these

271   fish guilds in this region is a fisheries/sampling effect, the result of specific environmental

272   conditions or a misclassification of fish species into a specific guild for comparison with our

273   study (see SI 6) is difficult to determine. Regardless, the discrepancies between our simulations

274   and the EwE solution within a given system are small relative to the consistency of the cross-

275   ecosystem contrasts of primary interest herein.

276   Fish ecosystem functions

277   Fish ecosystem functions can be obtained from the food web structures determined by the model.

278   As examples, we show measures of potential fisheries production (Fig. 5a) and benthic-pelagic

279   coupling by demersal fish (Fig. 5b). The estimated fisheries production is 101 million tonnes per

280   year. As expected, potential fisheries production per area is highest in shelf seas and upwelling

281   systems that have high secondary production (Fig. 5a). Shelf and slope regions with seafloor

282   depths less than 2000 m contribute 30% of the potential production. Mesopelagic fish have a

283   potential fisheries production of 30 million tonnes per year. The potential production can be

284   increased by taking a higher flux from the small guilds (e.g. half instead of a quarter), which in

285   nature will cause a reduction in the biomass and catch of large fish due to a decline in prey fish.

286   This fishing patterns increases the potential global production to 168 million tonnes per year.

287   Benthic-pelagic coupling by demersal fish shows the relative flux of energy from pelagic and

288   benthic sources consumed by demersal fish (Fig. 5b). In most shelf and slope regions, a large

289   fraction of energy consumed by all size-classes of demersal fish is of pelagic origin. For the

290   continental slope regions, this large fraction highlights that carbon is continuously transported to

291   the deeper waters through cross-habitat feeding. There is a small fraction of pelagic energy

292   consumed by demersal fish in decoupled open ocean systems, since the early life stages are

293   feeding on zooplankton in the surface waters.

294   Theoretical analysis of fish guild biomass as a function of seafloor depth

295   The changes in fish food web structure (Fig. 3) from shelf to open ocean environments are driven

296   by changes in production of zooplankton and benthos, detrital flux and seafloor depth (Fig. 6). In

297   regions with a high pelagic production and a high detrital export flux out of the sunlit euphotic

298   zone, demersals are dominant in shallow shelf regions together with epipelagic fish (Fig. 6a-b).

299   The demersals decline in biomass with depth and this promotes large pelagics. At continental

300   slopes, mesopelagic fish become abundant and epipelagic fish decline. This shift happens due to

301   the diel vertical migrations of the zooplankton community that benefit mesopelagic fish (SI 1,

302   Fig. S1.2). Mesopelagic fish are preyed upon by large pelagics and adult deep-living demersal

303   fish on slopes. Deep-living demersals gradually decrease in biomass with depth and this decline

304   promotes mid-water predators (Fig. 6a-b). Around 2000 meters, demersals are unable to migrate

305   the large distance between the mid-water fish community and the bottom, resulting in a

306   decoupling of the energy pathways. Low pelagic production and low detrital export flux out of

307   the euphotic zone, i.e. oligotrophic regions, select for epipelagic and mesopelagic fish (Fig. 6c).

308   The productivity and abundance of these small fish is too low to support larger pelagic predators.

309   Demersal fish do survive in these conditions if there is sufficient benthic prey.

310   Changes in fish guild biomass are also affected by water column temperatures that change fish

311   physiological rates. The temperature dependencies in our model are similar for all fish guilds and

312   physiological rates and therefore have little influence on the relative dominance of fish guilds (SI

313   1, Fig. S1.3 - S1.5). As a result, higher water column temperatures mainly decrease the biomass

314   of each fish guild, and hence total fish community biomass, due to increased maintenance costs

315   (SI 1, Fig. S1.3).

316   **Discussion**

317   We modified a generic size- and trait-based fish community model (FEISTY) to predict the

318   emergent biogeography of fish food web types based on large-scale variations in fish guild

319   biomass and vertical feeding interactions with shifting environmental conditions. The result was

320   several structurally different food web types that predictably vary with seafloor depth and ocean
321   productivity. Below we expand upon the results of each of our objectives. This is followed by a
322   discussion on model limitations and a conclusion.

323   Fish food web biogeography

324   The transfer of energy from primary producers to upper trophic levels varies across marine
325   regions throughout the ocean (Ryther, 1969). Broadly speaking, the transfer of energy varies
326   cross-regionally due to differences in 1) food chain lengths that connect phytoplankton to fish,
327   and 2) the strength of pelagic and benthic energy pathways (Friedland et al., 2012; Stock et al.,
328   2017). Such processes not only affect overall fish community biomass and potential fisheries
329   catches, but also the guild distribution of fish in a community (Cresson et al., 2020; Petrik et al.,
330   2019; van Denderen et al., 2018). Our results show that the distribution of biomass between fish
331   guilds directly depends on pelagic and benthic secondary production and is strongly mediated by
332   seabed depth, which (indirectly) controls the amount of detritus reaching the seabed, fish vertical
333   behavior and fish cross-habitat feeding. The importance of these individual processes for fish
334   food web structure has been recognized for a long time. We show how these well-known bottom-
335   up structuring forces can be used to simulate fish guild biomass and feeding interactions across
336   ocean biomes on a global scale. Our study thereby mechanistically links variation in ocean
337   productivity with the upper trophic levels of marine ecosystems.

338   We used a generic trait-based configuration to estimate the structural differences in energy flow
339   in fish communities across regions. The advantage of a trait-based approach is that it does not
340   require the quantification of feeding interactions from species-based parameterizations, thereby
341   allowing characterizing fish communities with few parameters. Another advantage of a trait-
342   based approach is that its basis in physiological and ecological principles may be more robust in
343   predicting the long-term effects of climate change on fish guild biomass and associated
344   ecosystem functions than empirical relationships, e.g. Cheung et al (2016). For example, the
345   modeled fish guilds automatically adjust feeding interactions and physiological rates to new
346   environmental conditions, essentially reflecting a state where community re-assembly and
347   temperature adaptations have progressed (Kiørboe et al., 2018). Nonetheless, our predicted food
348   webs represent highly simplified fish communities that do not represent the myriad of species

349 that exist in natural systems. They are therefore primarily useful for large-scale assessments of
350 climate change, guild-based fisheries and fish ecosystem functions.

351 Model validation

352 It is difficult to determine the extent to which the model reflects empirical patterns in nature.
353 Estimates of fish biomass are available from scientific surveys for different regions, with
354 uncertainty due to variation in gear catchability, acoustic backscatter methodology and historic
355 fishing exploitation, whereas estimates of feeding fluxes are more difficult to obtain. Our initial
356 efforts at model validation were therefore to compare against regional ecosystem models whose
357 food webs have been calibrated for particular regions using data-driven inversion techniques, i.e.
358 Ecopath balances (Christensen & Walters, 2004). We found a reasonable match between our
359 modeled fish guild biomasses and feeding fluxes, and three EwE models that reflect different
360 ecosystem types. Yet, note that any difference (or similarity) could be due to the different
361 modelling frameworks.

362 At global scales, an alternative option to validate the model predictions is to compare modeled
363 fisheries catches with empirical catch reconstructions. This comparison has been done by Petrik
364 et al. (2019), using a model formulation upon which our model structure is based. This study
365 found a reasonable agreement between modeled and empirical catches of large pelagics and
366 demersal fish across large marine ecosystems. Such a comparison with empirical catch data is
367 primarily useful for heavily-fished continental shelf and upwelling regions where most of the
368 fisheries production occurs and catch provides a more reliable estimate of the relative fish
369 productivity between regions.

370 Other comparisons of our findings to observations, statistical models, and mechanistic models
371 agree on the large-scale food web structures, yet reveal nuanced differences. A more qualitative
372 comparison with empirical work in continental slope regions suggests that our model predicts
373 larger declines in demersal fish biomass with depth than is typically observed (Kallianiotis et al.,
374 2000; Mindel et al., 2016; Trueman et al., 2014). This may be due to ontogenetic migrations by
375 adult demersal fish to deeper and more offshore waters (Macpherson & Duarte, 1991), as well as
376 a larger capacity to exploit the migrating mesopelagic resource than was modeled. Nevertheless,
377 demersal fish biomass eventually declines with depth following the decline in the detrital flux
378 that reaches the seafloor (Wei et al., 2011). For open ocean pelagic systems, mesopelagic fish

379 biomass has been found to strongly correlate with ocean productivity (Irigoien et al., 2014) and
380 such effects are also found in the model. One aspect that is clearly misrepresented in the model is
381 the simulated high abundance of large pelagics in cold-water regions, where they are able to exist
382 in our model due to a high zooplankton productivity. Pelagic predators are indeed present in
383 these waters, although not as (teleost) fish but as pelagic-feeding endotherms, e.g., penguins and
384 pinnipeds, that can maintain a high body temperature and activity and outcompete large pelagic
385 fish (Grady et al., 2019).

386

387 Fish ecosystem functions
388 We estimated a potential fisheries production of 101 million tonnes per year in the model,
389 ignoring fisheries production of invertebrates. This estimate compares well with the global
390 industrial fisheries output over the last decades of approximately 100 million tonnes per year (up
391 to 130 million tonnes per year when the non-industrial fisheries are included), of which 15 to
392 20% is invertebrate fisheries (Pauly & Zeller 2016; Watson & Tidd, 2018). From our estimated
393 total, mesopelagic fish have a potential fisheries production of 30 million tonnes per year.
394 Mesopelagic fish are currently largely unfished but are seen as a major potential new food
395 resource for future global food security and nutrition through the production of fish-meal (St.
396 John et al., 2016). We found that the global potential fisheries production can be increased to 168
397 million tonnes per year when taking a higher flux from the small fish guilds, which in nature will
398 cause a reduction in the biomass and catch of large fish due to a decline in prey fish. The
399 prediction of increased catch when larger fish are at reduced biomass levels matches other
400 studies showing theoretically (Andersen, Brander, et al., 2015) and empirically in the South-East
401 China Sea (Szuwalski et al., 2017) that a fishery narrowly targeting small fish at the expense of
402 large fish can double the fisheries production. Despite the high yield, this shift in fishing strategy
403 will have a high environmental impact on biodiversity and the size-structure of marine
404 communities (Andersen & Gislason, 2017).

405 We quantified the amount of benthic-pelagic coupling by demersal fish across habitats. We
406 found that a large fraction of the demersal fish diet is prey inhabiting the pelagic realm
407 (zooplankton and/or pelagic fish) in both shelf and slope regions. As previously suggested by
408 Trueman et al. (2014), benthic-pelagic coupling by demersal fish in slope regions is driven by
409 vertically-migrating deep-living demersal fish that feed on vertically-migrating mesopelagic fish

410   in the water column. Such vertical migrations of prey and predator at continental slopes cover a

411   small proportion of the global ocean but may ensure fast carbon transport to depths up to about

412   2000 m, highlighting the need for further work on the quantification of these fluxes.

413   A natural next step is to assess how the vertical feeding strategies and vertical migrations of the

414   different fish guilds affect active carbon export to depth. Active carbon transport by fish (and

415   zooplankton) through diel vertical migrations is suggested to contribute substantially to the total

416   export of carbon (10-20% of the passive flux of carbon) below the euphotic zone (Aumont et al.,

417   2018; Bianchi, Stock, et al., 2013; Davison et al., 2013; Saba et al., 2021). For this study

418   however, we did not quantify active carbon export by fish as an ecosystem function, because the

419   depth of vertically migrating species was prescribed in the model. For the sake of predicting fish

420   food web structures, the specific depth of vertical migration is of limited importance as the

421   zooplankton and fish migrations are coupled to each other. Yet, vertical migration depth is

422   important to quantify active carbon fluxes and sequestration. One way to improve the model is to

423   use a global empirical relationship between depth of vertical migration and oxygen, temperature,

424   surface chlorophyll and the mixed layer depth (Bianchi, Stock, et al., 2013). Alternatively, the

425   depth of vertical migration of prey and predators may be obtained through explicit applications

426   of game theory (Pinti & Visser, 2018).

427   Limitations

428   The trait-based configuration used in our study diversified possible fish guilds, food web

429   structures and energy flows compared to the more commonly used size-based models. Yet, some

430   ecological processes and behaviors still had to be constrained in the model and can be further

431   refined. The primary shortcomings were: 1) feeding strategies were poorly resolved in shallow

432   regions (< 100 meters) by the trait "vertical habitat strategy" as most fish had vertically

433   overlapping distributions. Even though fish in shallow regions make substantial use of both

434   pelagic and benthic pathways (Duffill Telsnig et al., 2019; Giraldo et al., 2017), preference for a

435   pelagic or a benthic diet is evidenced in gut analyses and was therefore imposed in the model; 2)

436   feeding strategies excluded obligate benthivorous fish as we expected that such a strategy is of

437   limited importance for total demersal guild biomass; and 3) light availability and adaptations to

438   low or high light conditions were not explicitly incorporated in the model, which limited a

439   mechanistic implementation of some pelagic feeding strategies in open ocean environments,

440   sensu Langbehn & Varpe (2017). Our study further disregarded other upper trophic level
441   predators, such as elasmobranchs, cephalopods and mammals. The inclusion of any of these
442   predators requires further research to clarify their physiology and identify key traits and trade-
443   offs that foster coexistence.

444   Conclusion
445   Our work demonstrates how inclusion of fish vertical habitat strategy in a well-established size-
446   and trait-based framework allows for global-scale predictions of the food web structure of fish
447   communities. Using the model (which we name for recognizability FEISTY-VerticalTrait), we
448   show how ocean productivity and seabed depth shape the dominant traits and energy flows in
449   fish communities. Future developments of the model will allow 1) predicting dominance and
450   potential fisheries production of different fish guilds, 2) assessing the indirect ecosystem effects
451   of mesopelagic fisheries, which are a major potential resource for future global fisheries, 3)
452   quantifying active export of carbon to depth through fish diel vertical migrations and feeding
453   interactions and 4) examining all of the above in the context of global change. Our study thus
454   highlights the trait-based approach to modelling fish communities as a powerful tool to
455   mechanistically predict links between ocean productivity and fish production for fisheries, as
456   well as to quantify the ecological role of fish in marine systems.

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655 **Figures captions**

656   Figure 1. Illustration of simplified fish guilds in the fish community deemed important for

657   global fisheries catches and active carbon export to depth. Fish interact with each other and the

658   resources through predator-prey interactions if they overlap in their spatial distribution in the

659   water column and if the prey is of preferred size (see inset).

660   Fig 2. Vertical position (blue lines) of fish guild size-classes and resources from a seafloor depth

661   of 100 to 3000 meters, described by the upper edge of the sloping yellow shape in each panel.

662   The vertical position shows the depth of maximum concentration z_c for day and night; two lines

663   indicate a bimodal vertical distribution (SI 1, Table S1.3). The euphotic depth is here set at 150

664   m. Note that there are more fish size-classes (SI 2) than the groups presented here, but the classes

665   align with the weight boundaries in each panel.

666   Figure 3. Emergent food web types from shelf regions to open ocean environments due to

667   seafloor depth, zooplankton production and detrital export reaching the seafloor. The food web

668   panels (a-e) show biomass in g wet weight per m^{-2} (circles; see reference biomass in lower right

669   corner) and fluxes of biomass in g wet weight m^{-2} y^{-1} (lines) in a 1° grid cell. Dashed, solid thin

670   and solid thick lines show weak (0.01-0.1), intermediate (0.1-1) and strong (>1) feeding

671   interactions. Interactions less than 0.01 g wet weight m^{-2} y^{-1} are not shown. The vertical position

672   of fish in the food web panels is the average position of each size class. The colors in the food

673   web panels correspond to the legend. The colors in the map (f) define regions with a similar food

674   web type, corresponding to the color in the panel title bars; threshold values are presented in SI 1

675   Table S1.4. Food web panels are not presented for the white regions where the resource

676   production is too low to support fish biomass.

677   Figure 4. Comparison of biomass and energy flow between the trait-based fish model (right) and

678   three regional-specific Ecopath with Ecosim (EwE) food web models (left). All panels show

679   biomass (circles, with values in g wet weight m^{-2}) and fluxes of biomass (lines, with values in g

680   wet weight m^{-2} y^{-1}). The circles and lines are both scaled with a log$_{10}$ transformation for

681   visualization. The internal loops present feeding fluxes within each grouping. No values are

682   included for lines with a flux < 0.5 g wet weight m^{-2} y^{-1}.

683   Figure 5. Map of two fish ecosystem functions: potential fisheries production (a) and benthic-

684   pelagic coupling by demersal fish (b). Potential fisheries production is estimated as a fraction of

685   energy flowing from juveniles to the fished adults. Benthic-pelagic coupling by demersal fish is

686   estimated as the sum of all feeding fluxes from pelagic prey to demersal fish relative to the total

687   flux. This prediction does not consider cannibalism by demersal fish and is only shown in areas

688   where demersal biomass is $> 10^{-4}$ g wet weight m^{-2}.

689   Figure 6. Biomass of fish guilds as a function of seafloor depth for high (a), intermediate (b) and

690   low (c) zooplankton production and detrital export flux out of the euphotic zone. Benthic

691   maximum production depends on the detrital export flux and bottom depth, following eq. S21 in

692   SI 1 Table S1.1. The euphotic depth is at 150 m. Note the different scales on the y-axes.

693   Resource values: maximum small and large zooplankton production is 100 (a), 50 (b) and 5 (c) g

694   wet weight m^{-2} y^{-1}; detrital export flux is 380 (a), 250 (b) and 130 (c) g wet weight m^{-2} y^{-1}. There

695   is no variation in temperature (see SI 1 Fig S1.3 for results for three different water column

696   temperatures).

697

698   **Supplementary material information**

699   Supplement 1: Supplementary tables and figures

700   Supplement 2: Fish community model formulation

701   Supplement 3: Input parameters for the global predictions on a 1° grid

702   Supplement 4: Resource productivity and water column temperature scenarios

703   Supplement 5. Discretization of fish size-classes

704   Supplement 6: Model comparison with Ecopath with Ecosim