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Depth gradient on the resource use of a fish community from a semi-enclosed sea

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Abstract :

Depth is one of the environmental variables influencing the structure of marine food webs by directly or indirectly influencing benthic-pelagic coupling and predator-prey relationships. In shallow waters, the high degree of connectivity between pelagic and benthic networks results in complex systems with multiple interactions. Digestive tract (DT) and stable isotope (SI) analyses were used to investigate depth-related changes in feeding patterns for 33 fish species (eastern English Channel [EEC]) collected between 5 m and 80 m depth. Fish species were first arranged into functional groups based upon trophic and habitat similarities. DTs were used to determine the general topology of the food web and SIs were used to estimate the contributions of different sources to fish diets. At the scale of the aggregated EEC food web, the main food sources for all groups were of benthic origin (> 50%). The aggregated food web was then used as a template to explore the influence of depth on resource use by predatory fish. Mixing models including depth as a continuous covariate successfully untangled and identified different feeding strategies among functional groups. In shallow waters, fish species benefited from both pelagic and benthic prey whereas, in deeper waters, they fed predominantly on either benthic or pelagic sources depending on their habitat preferences. Our results support the hypothesis of a stronger benthic-pelagic coupling in shallow waters, notably through fish diet, and highlight the importance of including environmental factors such as depth as proxies of habitat variation to fully understand resource use and food web structure in epicontinental seas.

37 **Introduction**

38 Scientists have long recognized the importance of food web structure and functioning
39 to understand and predict the response of marine ecosystems to environmental change
40 (Woodward et al. 2010). The biotic compartment of marine ecosystems and its trophodynamics
41 respond to variability in the abiotic environment from the individual to the community level
42 (Keyl and Wolff 2008). Consequently, studying how food webs vary along natural gradients
43 from local to regional scales has been recognized as one of the fruitful avenues for future
44 research (Ings et al. 2009). Such environmentally-induced variability can be particularly
45 significant in semi-enclosed shallow seas that present low inertia to global (e.g., climate

46 change) and/or local variations (e.g., river systems, fisheries) (Mackenzie et al. 2007, Martin et
47 al. 2010). As a result, numerous epi-continental seas (e.g., Baltic Sea, North Sea) are highly
48 dynamic and productive areas fueled by a large number of sources (e.g., freshwater inputs,
49 marine organic matter), characterized by a large number of species and biological interactions,
50 and where commercially important fish are caught every year.

51 Transfer of energy or matter between benthic and pelagic compartments can be
52 described as a two-way process accounting for the amount of pelagic material that reaches the
53 sea floor (pelagic-benthic coupling) but also for the amount of benthic organic matter that is
54 available and consumed by pelagic species (benthic-pelagic coupling; Gaudron et al. 2016).
55 Studies on pelagic-benthic coupling in polar and temperate regions have successfully identified
56 a close relationship between primary production in the water column and benthic biomass or
57 abundance (Grebmeier 1993, Cresson et al. 2014b). Similarly, deep (> 500 m) benthic trophic
58 webs are largely dependent upon sinking organic matter of pelagic origin (Iken et al. 2001,
59 Cresson et al. 2014a). However, few studies have documented and recognized the importance
60 of benthic production to the whole food web in semi-enclosed shallow marine ecosystems
61 where its contribution is expected to be high due to the proximity between pelagic and benthic
62 species and the virtual absence of physical barriers such as thermoclines. Among the factors
63 influencing benthic-pelagic coupling (e.g., vertical current, primary production, nyctemeral
64 migrations, community composition), depth is one of the main forcing variables (Woodland
65 and Secor 2013) that can be easily measured and is usually available for all studies. Depth is
66 directly or indirectly related to different physical (e.g., water mixing, sinking time of organic
67 matter) and biological processes (e.g., vertical migration of species) (Baustian et al. 2014) and
68 can be used as a proxy of habitat variation to explore benthic-pelagic coupling and its impact
69 on aquatic food webs' structure (Kopp et al. 2015).

70 Energetic links can be studied using fish as integrators of benthic-pelagic coupling (and
71 the other way round pelagic-benthic coupling) by exploring fish trophic interactions and their
72 variation with depth (Romero-Romero et al. 2016). At the community level, fish are
73 characterized by a remarkable diversity of feeding strategies, life-history traits and associated
74 morphologies that are expected to respond differently to environmental variability. Flatfishes
75 (e.g., European plaice), generally characterized as endobenthos-feeders, spend most of their
76 time on the bottom and, for the majority, do not feed by sight (Gibson et al. 2014). Due to the
77 characteristics of such sedentary species, such as swimming short distances and creating
78 moderate disturbances of the bottom to forage (Link et al. 2002), we expect their diet to
79 originate from benthos regardless of depth. Benthic round fish (e.g., Gadoids) share a relatively
80 similar diet with endobenthos-feeders (mainly benthic prey). However, differences in their
81 morphological traits and feeding modes (visual predation) should allow them to take greater
82 advantage of available pelagic prey (e.g., copepods) when moving from deep to shallow
83 feeding grounds (Jönsson et al. 2013). Small forage fish (e.g., sprat, herring) are generally
84 identified as omnivorous pelagic planktivores (Mollmann et al. 2004). Yet, studies show that
85 larger specimens of some species (e.g., herring) can also be nectobenthos-feeders preying on
86 small benthic crustaceans and polychaete worms (Casini et al. 2004). Although the main food
87 sources of this functional group are expected to be of pelagic origin, benthic-derived material
88 may also play a significant role in its diet in shallow environments. Finally, piscivorous round
89 fish (e.g., European seabass) form a broad group that can occupy different habitats (pelagic or
90 demersal) and are among the largest specimens within the fish community. Although they
91 preferentially feed on fish (Juanes et al. 2002) thus occupying higher trophic levels, most
92 piscivores are opportunistic and have flexible diets. Piscivorous round fish are thus likely to
93 consume the most abundant food source regardless of its origin (Post et al. 2000).

94 In this study, we used data from the eastern English Channel (EEC), a semi-enclosed
95 sea, as a case study to address the following objectives: 1) identify the main trophic
96 interactions and describe the resulting food web structure at the EEC-scale; 2) explore variation
97 in fish resource partitioning with depth; and 3) compare the general structure of trophic
98 interactions within the fish community at the EEC-scale with other shallow semi-enclosed
99 systems. Based on a previous study (Kopp et al. 2015) and common knowledge on species'
100 habitat use and feeding strategy, we hypothesize that benthic-pelagic and pelagic-benthic
101 coupling vary with depth as the latter influences fish diets: pelagic-feeding species benefit from
102 benthic subsidies in shallow waters and the contribution of pelagic sources to their diet
103 increases with increasing depth as the benthic-pelagic coupling weakens; similarly, benthic-
104 feeding species benefit from pelagic subsidies in shallow waters and the contribution of benthic
105 sources to their diets increases with increasing depth as pelagic-benthic coupling weakens.

106 Diet estimates originating from digestive tract (DT) analysis and stable isotope (SI)
107 analysis provide a snapshot of the current prey sources and integrated information about food
108 resource use over several weeks to months, respectively. DTs of the main fish species (in terms
109 of commercial interest and/or ecological dominance) of the EEC have been reported by
110 Cachera et al. (2017) who studied sources of fish trophic niche variation at the individual level.
111 Additionally, SIs from the different compartments of EEC food web, including the main fish
112 species, were reported by Kopp et al. (2015) who showed an inshore-offshore gradient in the
113 food web structure and concluded that this gradient was related to a weakening of benthic-
114 pelagic and pelagic-benthic couplings towards offshore waters. To further understand the
115 processes underlying this phenomenon, we combined data from DTs and SIs within a Bayesian
116 framework, including depth as an environmental variable (Francis et al. 2011, Semmens et al.
117 2015). Species of the EEC food web were grouped into functional groups and DTs were used

118 to define the general topology of the food web whereas SIs were used to calculate proportions
119 of the different prey in the diet of the various functional groups. Lastly, for fish functional
120 groups, variation of diet (based on DTs and SIs) along a depth gradient from 7 to 80m was
121 explored.

122 **Materials and Methods**

123 *Data*

124 DT and SI data for fish and the majority of the epifaunal invertebrates ($n = 799$
125 samples) were collected using a GOV bottom trawl from R. V. “Gwen Drez” during the
126 Channel Ground Fish Survey (October 2009) that covers the whole EEC annually according to
127 a spatially stratified sampling scheme (Le Roy 2009). Additional SI data for zooplankton ($n =$
128 16) and for benthic suspension feeders ($n = 34$) were respectively collected in January 2010
129 with a WP2 zooplankton net (International Bottom Trawl Survey; Vérin 2010) and in July
130 2010 using a French dredge (COMOR survey; Foucher and Quinquis 2010). Finally,
131 particulate organic matter was obtained from water samples collected with Niskin bottles
132 during the French sampling program SOMLIT (October 2009 to June 2010). More details
133 about sampling protocols can be found in Kopp et al. (2015), Cachera et al. (2017) and
134 supplementary tables S1 and S2.

135 DT data were obtained by identifying prey to the lowest possible taxon in 853 digestive
136 tracts extracted from 16 fish species chosen to represent the main trophic guilds of the EEC
137 fish community (*Chelidonichthys cuculus*, *Chelidonichthys lucerna*, *Clupea harengus*,
138 *Dicentrarchus labrax*, *Gadus morhua*, *Merlangius merlangus*, *Mullus surmuletus*, *Mustelus*
139 *asterias*, *Pleuronectes platessa*, *Raja clavata*, *Sardina pilchardus*, *Scomber scombrus*
140 *Scyliorhinus canicula*, *Solea solea*, *Sprattus sprattus*, *Trachurus trachurus*; for more details on
141 digestive tract analysis see Cachera et al. 2017).

142 Nitrogen and carbon SI ratios, denoted by $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, were measured
143 from particulate organic matter, to zooplankton, epifaunal invertebrates, and fish collected
144 from 7 to 80m depth in the EEC. A biplot of the SIs for each fish species arranged in functional
145 groups can be found in Supplementary Figure S1. Specific details on tissue samples analyzed
146 for SI ratios and their preparation can be found in Kopp et al (2015). Briefly, SI data were
147 normalized to account for lipid content based on C:N ratios (Post et al. 2007) and corrected for
148 spatial variation in the isotopic baseline based on SI values of the suspension-feeding bivalve,
149 *Aequipecten opercularis*, taken as the baseline. SI values of the isotopic baseline at sampling
150 sites were obtained by kriging interpolation of published data (Jennings and Warr 2003a, b;
151 Barnes et al. 2009). For both nitrogen and carbon, the isotopic value of each consumer sample
152 was then corrected by subtracting the kriged baseline value at the sampling location and adding
153 the mean kriged baseline value averaged across the entire area (for all sampling sites:
154 $\delta[\text{corrected}] = \delta[\text{consumer}] - \delta[\text{local baseline}] + \delta[\text{mean baseline}]$ with δ the nitrogen $\delta^{15}\text{N}$ or
155 carbon $\delta^{13}\text{C}$ SI ratio). Any further mentioning of SI data in this paper refers to baseline-
156 corrected SI values.

157 *Food web modeling*

158 The topological food web of the EEC was constructed by aggregating qualitatively the
159 54 species sampled for SI into functional groups based on their taxonomic classification (e.g.
160 fish, cephalopods, bivalves), feeding strategies (e.g., filter feeders, scavengers), trophic guild
161 (e.g., herbivores, piscivores), habitat use (e.g., pelagic, demersal) and morphology (only for
162 fish, i.e., flatfish, round fish) using DT data reported by Cachera et al. (2017) for the main fish
163 species and completed by published data (see Supplementary Table 1 and 2 for references).
164 Aggregation resulted in 15 functional groups from primary producers to piscivorous fish and
165 cephalopods (Table 1). The trophic level (TL) of each species was estimated based on its $\delta^{15}\text{N}$

166 using the scaled method proposed by Hussey et al. (2014) where the trophic enrichment factor
167 (TEF) of the consumer's $\delta^{15}\text{N}$ is dependent on the $\delta^{15}\text{N}$ value of its prey:

168

$$TL_{consumer} = \left(\frac{\log(\delta^{15}\text{N}_{lim} - \delta^{15}\text{N}_{base}) - \log(\delta^{15}\text{N}_{lim} - \delta^{15}\text{N}_{TP})}{k} \right) + TL_{base}$$

169 where $\delta^{15}\text{N}_{lim}$ is the saturating $\delta^{15}\text{N}$ limit as TL increases, $\delta^{15}\text{N}_{base}$ is the $\delta^{15}\text{N}$ value of the
170 isotopic baseline, $\delta^{15}\text{N}_{TP}$ is the consumer's $\delta^{15}\text{N}$ value at a given TL, and k is a rate constant
171 (Hussey et al. 2014). Values for the parameters $\delta^{15}\text{N}_{lim}$, $\delta^{15}\text{N}_{TP}$, and k were taken from Hussey
172 et al. (2014). The bivalve *A. opercularis* was used as isotopic baseline ($TL_{base} = 2$). Trophic
173 level for each functional group was then calculated as the mean value for all individuals within
174 the group (Table 1).

175 The topological description of the food web consisted of trophic links between
176 functional groups expressed as a binary matrix. A trophic link was established if at least one
177 species of the consumer group fed on one species within the source group according to DT
178 analysis. The relative contributions of each source to consumers' diets were then estimated
179 using the Bayesian isotope mixing model IsoWeb (Kadoya et al. 2012). Isotope mixing models
180 are based on the principle that a consumer's isotopic ratios result from the mixing of the
181 isotopic ratios of its food sources according to their relative contributions to its diet after
182 accounting for TEF (Post 2002). While simple analytical mixing models can only estimate
183 contributions of a few food sources to a single consumer's diet at a time, IsoWeb has the
184 advantage of estimating dietary contributions for all consumers in a food web based on SI data
185 and a topological description of the food web given *a priori*. The model also allows for TEF
186 variation across links assuming that TEFs follow a normal distribution with a mean of 0.8 for
187 carbon and 3.4 for nitrogen (Post 2002, Saigo et al. 2015, Fukumori et al. 2016). The standard

188 deviations of these normal distributions are assumed to follow a half-Cauchy distribution, for
189 both carbon and nitrogen (see details in Kadoya et al. 2012). Nitrogen TEF values estimated
190 from Hussey's equation (TL calculations) were close to those proposed in IsoWeb (mean value
191 of 3.1). Hussey's equation provides TEF estimates between prey and predator species pairs,
192 while IsoWeb estimates TEF between functional groups (several species) preventing a direct
193 comparison of the estimates obtained by the two methods. The posterior probability densities
194 of TEFs for carbon and nitrogen from this study are provided in the supplementary Figure 2S.
195 The IsoWeb model was run with the following parameters: 10^6 chain length, burn-ins 500.000,
196 and thin number 500 for three parallel MCMC chains. Convergence was assessed using the
197 Gelman-Rubin test (Gelman et al. 2014).

198 *Estimation of predatory fish diet as a function of depth*

199 The resulting EEC-scale food web (referred to as IsoWeb model hereafter) was then
200 used as a template to further explore the effect of depth on food resource use by fish functional
201 groups using the Bayesian isotope mixing model MixSIAR (Stock and Semmens 2013).
202 Compared to IsoWeb, MixSIAR can incorporate continuous covariates as predictors of
203 sources' relative contributions to consumers' diet and multiplicative error structures. In this
204 study, depth was introduced as a continuous covariate affecting sources' contributions to
205 functional groups' diets. Because the model fits a continuous covariate (here depth) as a linear
206 regressor on sources contributions in Isometric Log-Ratio (ILR) transform-space (see Francis
207 et al. 2011; Egozcue and Pawlowsky-Glahn 2003 for details), it can also extrapolate changes in
208 sources' contributions to diet beyond the limits of the observed distribution of the covariate. As
209 results are presented in the space of sources' relative contributions to consumers' after
210 reciprocal transformation from the ILR transform space, depth effect may look non-linear
211 whereas it is linear in the ILR transform space. MixSIAR models were first run for each

212 functional group keeping the same trophic links, estimated TEFs, and Bayesian model
213 parameters as the ones previously used by IsoWeb. For every MixSIAR dietary estimate, mean
214 contributions and standard deviations are reported.

215 The “Planktivorous fish” group was excluded from this analysis due to insufficient
216 sample size (40 individuals) to explore diet variation with depth as a continuous covariate.
217 Visual inspection of the final isotopic space (referred to as IsoSpace hereafter) and correlation
218 coefficients between prey sources allowed for the determination of when two sources were
219 indistinguishable. For instance, if two sources presented high overlap in their SI ratios, then,
220 likely solutions could involve one of the two sources but not both at the same time (Inger et al.
221 2010). Sources were aggregated *a priori* only if the absolute value of the coefficient of
222 correlation was higher than 0.5 and if the combined sources had some functional or ecological
223 significance (e.g., “Benthic decapods-omnivores” and “Benthic decapods-carnivores”
224 combined into “Benthic decapods”) following suggestions by Phillips et al. (2005). Whenever
225 sources were combined, the model was re-run under the same settings (i.e., same MCMC
226 parameters). Convergence was assessed using the default MixSIAR diagnostic Gelman-Rubin
227 and Geweke tests. For each fish functional group, the plot of the IsoSpace and the mean
228 contribution of sources to the diet as a function of depth are reported. The resulting posterior
229 distributions of sources’ contributions to fish functional groups’ diets at the EEC-scale (i.e.
230 without accounting for the influence of depth) and at the minimum and maximum depths are
231 also provided in Supplementary Figure S3 to allow assessing uncertainty in the effect of depth
232 on functional groups’ diets.

233 **Results**

234 *EEC-scale food web (IsoWeb model)*

235 The EEC encompassed 5 TLs that, apart from the primary producers, ranged from TL 2
236 for benthic-suspension feeders (mainly bivalves and gastropods) to almost 5 for cephalopods.
237 Fish TLs varied from 3.17 for planktivorous to 4.4 for demersal piscivorous fish (Table 1).
238 Benthic-suspension feeders were the main food source for endobenthos-feeding fish (30% of
239 the diet) while copepods represented the main food source (27%) for benthos-feeding fish
240 (Table 2). Almost equal contributions of all sources to the diet of piscivorous fish (both
241 demersal and pelagic) and cephalopods suggest generalist diets for the higher TL species. The
242 combined contribution of benthic sources accounted for 54% of the diet of planktivorous fish
243 while pelagic subsidies (copepods and macro-zooplankton) represented 46%. Likewise, benthic
244 and pelagic sources represented 51% and 49%, respectively, of the diet of piscivorous pelagic
245 fish (Table 2). In contrast, the diet of benthos-feeding, endobenthos-feeding and demersal
246 piscivorous fish was largely dominated by benthic subsidies (73%, 100% and 100%,
247 respectively; Table 2). Overall, the contribution of benthic subsidies (i.e., benthic OM,
248 suspension feeders, deposit feeders, benthic predators, and benthic decapods) dominated the
249 diet (51 to 100%) of all fish functional groups, even for those that are commonly reported as
250 pelagic (e.g., planktivorous fish) (Table 2).

251 *Fish diet variation with depth (MixSIAR models)*

252 Using the previous model (IsoWeb) as a template (i.e., same topology and TEF factors),
253 changes in diet with depth, described as a continuous variable, were explored for each fish
254 functional group. Benthos-feeding fish ($n = 237$ individuals) were highly variable in terms of
255 $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}$ range: -15.45‰ to -18.98‰) suggesting that different carbon sources
256 contributed to their diet. An initial MixSIAR model run with the 5 potential sources of this
257 functional group (Figure 1a) showed a large overlap between SI ratios of copepods and deposit

258 feeders as prey (correlation of -0.90). However, these prey groups were not pooled together to
259 keep pelagic and benthic sources separate. As a result, large standard deviations (hereafter
260 referred to as SD) were observed for estimated sources' contributions to diet due to the
261 difficulty of the model to fully distinguish between the two sources. Overall diet (i.e.,
262 integrated across all depths) indicated that individuals fed mainly on copepods ($36.2 \pm 22.7\%$
263 of their diet) and deposit feeders ($31.3 \pm 19.5\%$) followed by benthic decapods-omnivores prey
264 ($13.5 \pm 5.3\%$). Cephalopods and benthic-suspension feeders were minor dietary items
265 representing less than 10% of individuals' diet each ($8.5 \pm 4.6\%$ and $10.5 \pm 8.3\%$ respectively).
266 Including depth as a continuous covariate of sources' contributions showed that individuals fed
267 primarily on copepods at shallow depths ($< 40\text{m}$) and increased their consumption of deposit
268 feeders with increasing depth (Figure 1b). The contribution of other sources remained low
269 ($<15\%$) and showed little variation with depth. Posterior distributions of sources' contributions
270 (Figure S3, 1st row) show that, despite some uncertainty in sources' contributions at the global
271 scale, there is a clear discrimination between benthic and pelagic sources as depth increases.

272 A first model for endobenthos-feeding fish ($n = 149$ individuals) showed a large
273 overlap between SI values of benthic predators and deposit feeders as sources (correlation of -
274 0.78). They were combined into a common "benthic predators-worms" group leading to a 4-
275 source mixing model (Figure 1c). Overall, individuals fed mainly on benthic-suspension
276 feeders ($63.8 \pm 5.0\%$) and benthos-feeding fish ($23.8 \pm 6.4\%$). The combined source "benthic
277 predators-worms" and benthic decapods-omnivores appeared as minor dietary sources ($6.2 \pm$
278 6.5% and $6.2 \pm 5.4\%$, respectively). Including depth as a continuous covariate showed that
279 individuals fed mainly on benthic-suspension feeders from shallow waters (7 m) up to 60 m
280 depth. Their contribution decreased substantially in deeper waters (from $\sim 60\%$ at 40 m depth to

281 ~10% at 80 m depth). The contribution of benthos-feeding fish also decreased with increasing
282 depth, whereas the contribution of “benthic predators-worms”, that represented a minor source
283 in shallow waters, increased strongly with depth to become the main source in the deepest
284 waters (Figure 1d). Posterior distributions of sources’ contributions (Figure S3, 2nd row) show
285 the clear shift of main sources as depth increases.

286 Demersal piscivorous fish ($n = 133$ individuals) were also trophically linked to benthic
287 predators and deposit feeders. Again, the SI ratios of these two sources overlapped largely
288 (correlation of -0.88) and they were thus combined into a “benthic predators-worms” group.
289 Similarly, the SI values of benthic decapods-omnivores overlapped with those of benthic
290 decapods-predators and these groups were combined into a “benthic decapods” group
291 (correlation of -0.52). The same held for benthos-feeding fish and benthic decapods
292 (correlation of -0.91) but these sources were kept separate because of functional difference,
293 which resulted in large SD values for sources’ contributions to diet (Figure 2a). Overall,
294 individuals consumed mainly “benthic predators/worms” ($51.2 \pm 6.4\%$) followed by benthos-
295 feeding fish ($29.2 \pm 12.8\%$) and “benthic decapods” ($19.7 \pm 14.9\%$). Little variation of diet
296 with depth was observed (Figure 2b). “Benthic predators/worms” remained the main food
297 source regardless of the depth, although its contribution decreased slightly (from ~60% to
298 ~40%) with increasing depth, while benthic decapods contribution increased but always
299 remained the lowest one. Posterior distributions of sources’ contributions (Figure S3, 3rd row)
300 show that besides the relative stability of the main sources, uncertainty in their contributions
301 increases with depth.

302 Pelagic piscivorous fish ($n = 106$ individuals) was the group with the highest number of
303 trophic links (7 sources), which increased uncertainty in the mixing models. As for the

304 previous group, benthic decapods species were combined into a single source (correlation of -
305 0.55). Similarly, “planktivorous fish” and “macro-zooplankton” were combined into a
306 “planktivores” group (correlation of -0.55). As a result, 5 potential sources instead of 7 were
307 considered (Figure 2c). Individuals were highly dispersed in terms of $\delta^{15}\text{N}$ values ($\delta^{15}\text{N}$ range:
308 from 11.78‰ to 18.29‰) suggesting feeding at different TLs. A large overlap in SI values was
309 still present between “planktivores” and “benthic decapods” (correlation of -0.85). However,
310 these sources were kept separate to distinguish pelagic and benthic sources. Overall,
311 individuals consumed mainly copepods ($37.6 \pm 10.2\%$) followed by “planktivores” ($27.21 \pm$
312 24.1%) and “benthic decapods” ($26.5 \pm 16.6\%$). Benthic-suspension feeders and benthic
313 predators were minor sources representing less than 5% of the diet ($3.9 \pm 3.8\%$ and $4.9 \pm 6.1\%$
314 respectively). When depth was included as a continuous covariate, individuals appeared to feed
315 mainly on a mixture of copepods and “benthic decapods” in shallow waters (~7m depth), but
316 their contribution progressively decreased with depth while the contribution of “planktivores”
317 increased to dominate diet in the deepest waters (Figure 2d). Posterior distributions of sources’
318 contributions (Figure S3, 4th row) show that, despite some uncertainty in benthic decapods’
319 contribution at the global scale, there is a clear discrimination between the main food sources,
320 notably of benthic and pelagic origin, along the depth gradient.

321 **Discussion**

322 We present the major trophic pathways towards the main fish species of a semi-
323 enclosed sea and how they vary with depth. Species are not studied in isolation, but instead are
324 positioned within the food web and grouped into functional groups that take into account
325 several biological (taxonomy, feeding strategy, trophic guild, and morphology) and habitat
326 (pelagic, demersal) characteristics that are frequently used in trophic web studies and modeling

327 approaches. Our results indicate high mixing of pelagic and benthic trophic pathways towards
328 fish in general over a large area (35.000 m²), but also highlight species' ability to forage
329 preferentially on different prey when moving from shallow to deep waters. With increasing
330 depth, benthic-pelagic and pelagic-benthic couplings weaken gradually (and almost linearly)
331 and species' diet more closely reflects their pelagic or benthic affinity (Figure 3). Some fish
332 functional groups related to the bottom, namely endobenthos-feeding fish and demersal
333 piscivorous fish, rely exclusively on benthic sources indicating some dietary specialization. In
334 contrast, benthos-feeding fish and pelagic piscivorous fish integrate both pelagic and benthic
335 sources as part of their diet depending on depth, suggesting a more opportunistic feeding
336 strategy. More precisely, the benthos-feeding group relies partly on pelagic sources at shallow
337 depth whereas they favor benthic subsidies as depth increases. Inversely, pelagic piscivorous
338 fish feed on benthic sources in shallow waters and focus more and more on pelagic subsidies as
339 depth increases. This conclusion was reached thanks to an original approach combining two
340 Bayesian modeling approach: IsoWEB and MixSIAR.

341 *Modeling considerations*

342 The combined use of two different Bayesian mixing models (IsoWeb Kadoya et al.,
343 2012 & MixSIAR Semmens et al. 2015), using DT and SI data simultaneously resulted in
344 better estimates than when used independently and compensated for some of each other's'
345 drawbacks. One of the main advantages of IsoWeb is the use of non-isotopic data, generally
346 DT or stomach contents, to identify main predator-prey relationships that are used to define the
347 general topology of the trophic network. The weaknesses of IsoWeb are the lack of visual
348 outputs to verify that the consumer's SI values lie inside the mixing polygon defined by the
349 sources' positions in the IsoSpace (created by the outer most values of the prey following TEF

350 adjustments; Phillips et al. 2014) and the lack of a correlation value between prey's SI ratios to
351 determine if sources can be discriminated based on their SI signatures. In this regard, the
352 combined use of IsoWeb with MixSIAR offers several advantages. First, MixSIAR can be
353 built upon IsoWeb calculations (e.g., trophic links, TEF estimates) and provides a simple
354 visual display of the IsoSpace for each node, combining source and TEF uncertainties
355 (Semmens et al. 2015). Second, MixSIAR provides correlation values between sources that can
356 help in making the decision of aggregating prey groups when appropriate. Finally, MixSIAR
357 can include environmental (e.g., depth) or biological variables as covariates affecting sources'
358 contributions to a consumer's diet.

359 In some cases, natural variability in SI signatures and TEFs of the different sources
360 reduced the discriminative power of the mixing models and resulted in large standard
361 deviations of sources' contribution estimates (see the full posterior distributions of sources'
362 contributions to fish functional groups, Figure S3). Higher uncertainty was especially observed
363 when the mixing model was unable to distinguish between two sources based on their SI
364 values (e.g., copepods and benthic deposit feeders as sources for benthos-feeding fish
365 considered at the EEC-scale). However, for all groups, major and minor dietary sources and
366 dominance of benthic *vs.* pelagic sources could be identified at the EEC-scale. Interestingly,
367 variation in fish's SI ratios was partly explained by depth. This resulted in a clearer
368 discrimination between food sources and therefore more certain sources' contribution estimates
369 when depth was included as a covariate (Figure S3: middle and right panels versus left panels),
370 thus ultimately providing more relevant and ecologically significant information. Diet
371 estimates from IsoWeb were slightly different from those provided by MixSIAR, which can be
372 explained by two factors. First, IsoWeb allows variation in TEFs that results in larger SD
373 estimates. MixSIAR models were built upon IsoWeb outputs, therefore using the resulting

374 mean TEFs and SDs calculated for every prey-consumer pair (out of the 10^6 iterations). Values
375 of TEFs used in MixSIAR had therefore narrower variances resulting in narrower SDs in
376 MixSIAR dietary estimates when compared to IsoWeb. Second, prey sources were grouped in
377 MixSIAR models if they overlapped and their grouping had ecological significance (see
378 discussion below). Thus, the number of sources for each predator differed between IsoWeb and
379 MixSIAR models resulting in different dietary estimates.

380 *Benthic-pelagic and pelagic-benthic couplings in shallow semi-enclosed marine ecosystems*

381 Our results at the scale of the entire EEC (IsoWeb model) indicated equally important
382 dietary contributions of benthic and pelagic subsidies for two functional groups of pelagic fish,
383 namely planktivorous and pelagic piscivorous fish, whereas these groups are usually known to
384 feed primarily on zooplankton and small fishes (e.g., Olaso et al. 2005). In parallel, benthos-
385 feeding and endobenthos-feeding fish are known to feed on a variety of bottom animals, but
386 preferentially on crustaceans and polychaete worms, respectively, whereas demersal
387 piscivorous fish also forage on bottom-living fish. For these three functional groups, our results
388 are in agreement with previous studies (Cohen 1990) and confirm that most of their energy is
389 of benthic origin, representing ~73% of their diet (IsoWeb).

390 Planktivorous fish are important prey for a large number of predators, including larger
391 fish, cephalopods, marine mammals and man (Mackinson and Daskalov 2007). A contribution
392 of benthic sources to their diet suggests that they could be key components of the benthic-
393 pelagic coupling by transferring benthic-derived carbon and energy towards higher trophic
394 levels in shallow semi-enclosed seas, which could potentially differentiate the structure and
395 functioning of their food webs from that of deeper open oceanic ecosystems (Pikitch et al.
396 2014). In the same vein, piscivores are characterized by generalist diets due to their mobility.
397 This includes a wide variety of prey from invertebrates to fish, of both pelagic and benthic

398 origin, thereby contributing to benthic-pelagic coupling (Schindler et al. 1996). This is
399 exemplified by the large range of $\delta^{15}\text{N}$ values observed in piscivorous pelagic fish that
400 indicates high dietary plasticity and the consumption of prey from different TL.

401 Numerous studies in large temperate lakes, with similar characteristics as the EEC (e.g.,
402 similar depth range, temperature, presence of benthic and pelagic invertebrates and fish) have
403 found patterns comparable to those of this study. Vander Zanden and Vadeboncoeur (2002),
404 using SI and stomach content data on 16 freshwater fish species (from both littoral and pelagic
405 habitats) showed that benthic-derived energy pathways accounted for more than 50% of total
406 fish energy intake and that this pattern is a general feature common to the large lakes of North
407 America (e.g., Lakes Superior, Michigan and Ontario). Similarly, several studies have
408 emphasized the role of predation and nutrient transfer by mobile predators in benthic-pelagic
409 coupling by showing that benthic invertebrates were the major prey source for pelagic fishes
410 (Stewart and Binkowski 1986, Schindler et al. 1996, Schindler and Scheuerell 2002). Due to
411 the proximity between pelagic and benthic compartments, shallow semi-enclosed seas and
412 large deep lakes (>20.000 km², ~80-100m depth) share similar physical and biological
413 constraints affecting benthic-pelagic coupling. Moreover, it seems clear that in shallow non-
414 stratified waters, the basis of the benthic and pelagic food webs (i.e., primary producers and
415 primary consumers) are not independent and should be studied as inter-dependent and highly
416 connected units (Boero et al. 1996, Cresson et al. 2014b) to fully understand processes
417 affecting the structure and dynamics of aquatic trophic networks.

418 *Variation of benthic-pelagic and pelagic-benthic couplings along the depth gradient*

419 The use of depth as a continuous variable partly explained the variation in consumers'
420 isotopic ratios and helped untangling complex interactions in the EEC over a large spatial

421 scale. In shallow waters, pelagic and benthic sources are highly connected and benefit primary
422 and secondary consumers in the two compartments, which are thus difficult to discriminate. It
423 is worth noting that strong links between zooplankton and zoobenthos from both functional
424 (energy fluxes) and structural (life cycle) perspectives (Boero et al. 1996), particularly in
425 coastal marine areas, may indicate even higher proportions of benthic-derived energy for
426 benthos-feeding and pelagic piscivorous fish. For example, the proximity of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
427 values of planktivores and benthic decapods rendered their discrimination by the mixing
428 models challenging. This observation highlights the strong connection between compartments,
429 where primary and secondary consumers (i.e., herbivores and omnivores) can have access to
430 both pelagic- and benthic-derived matter. Our results support the hypothesis of a greater
431 consumption of benthic prey by pelagic predators and of pelagic prey by benthic predators in
432 shallow waters. Our results, transposing the initial observations by Kopp et al. (2015) in a
433 depth continuum, suggest stronger benthic-pelagic and pelagic-benthic couplings with
434 decreasing depth through plasticity in fish diet, in addition to already known physical processes
435 (e.g., vertically mixed waters) and ecological features (e.g., vertical migration of zooplankton
436 and epibenthic fauna). In semi-enclosed marine ecosystems, depth is correlated with other
437 environmental and oceanographic variables (e.g., distance to shore, distribution of water
438 masses, currents) making it a suitable variable to account for habitat variation and its potential
439 effect on species diet. The gradual, almost linear, change in the strength of benthic-pelagic and
440 pelagic-benthic couplings along the depth gradient (Figure 3) is probably related to the fact that
441 waters are well-mixed in such ecosystems and the resulting absence of physical barrier in the
442 water column. In open oceanic ecosystems, it is likely that the strength of these couplings shifts
443 more abruptly with depth in relation to physical barriers such as thermoclines or transitions
444 between euphotic, dysphotic and aphotic zones. It is also expected that in such ecosystems

445 other parameters than depth need to be considered to fully account for the spatial heterogeneity
446 of benthic-pelagic and pelagic-benthic couplings. For example, at a given depth, varying
447 distance to marginal ice zones in the Barents Sea has been proven to influence pelagic-benthic
448 coupling (Tamelander et al. 2006). Similarly, seasonal or inter-annual variations in surface
449 primary and secondary productions modulate the amplitude of primary carbon sources that
450 reaches the bottom and different oceanographic features (e.g., currents, eddies, water column
451 stratification) and ecological features (e.g., structure of the pelagic-food web) can be better
452 proxies than depth to account for variation in the pelagic-benthic coupling (Grebmeier and
453 Barry 1991). Finally, the role of species that perform wide diel vertical migrations (fish and
454 zooplankton) in the pelagic-benthic coupling has also been highlighted in the North Atlantic
455 and Mediterranean seas. Most of these species concentrate at the upper and mid continental
456 slope depths (300-500 m) making them accessible to both, benthic and benthic-pelagic feeders,
457 resulting in relatively strong coupling between benthic and pelagic production (Tecchio et al.
458 2013, Trueman et al. 2014).

459 *Other sources of dietary variation*

460 Apart from benthic-pelagic and pelagic-benthic couplings, a change in diet with depth
461 is expected due to the mosaic of habitats (i.e., spatial differences in prey abundance or
462 composition due to different sediment types or other abiotic conditions). Endobenthos-feeding
463 fish had no trophic link identified (from previous DT analysis; Cachera et al. 2017) with
464 pelagic prey. Their main prey were all benthic and, due to their sedentary behavior, little
465 variation in diet was expected. However, endobenthos-feeding fish diet varied largely with
466 depth. This pattern could be linked to variation in the abundance of their various benthic prey.
467 Endobenthos-feeding fish fed mainly on benthic-suspension feeders in shallow waters (e.g.,
468 65.5% of their diet at 25m) and switched to benthic-predators and worms in deeper waters

469 (e.g., 76% at 75m depth). Unfortunately, the benthic-suspension feeders group included
470 bivalves and gastropods that are present in both shallow and deep waters. Similarly, there is no
471 published evidence of a higher abundance of worms in deeper waters in the EEC that could
472 explain the increase of their contribution with increasing depth and no high resolution data on
473 the spatial distribution of polychaetes worms is available for the area. The absence of a known
474 spatial trend in the abundance of both prey sources prevents from being conclusive about the
475 relationship between endobenthos-feeding fish's diet change and prey spatial distribution.
476 However, similar diet variability was found in flatfishes from the Bering Sea. In this area,
477 bivalves dominated flatfishes' diet on the inner shelf (shore to 50m), while polychaetes were
478 the main prey on the middle shelf (~50 to 100m). In this case, diet changes were associated
479 with estimated trends in prey abundance (Yeung and Yang 2014). The authors however
480 emphasized the possible mismatch between diet composition and infauna abundance in regions
481 with high prey availability, where endobenthos-feeding fish preferentially feed on polychaetes
482 even when they are not the dominant prey.

483 Demersal piscivorous fish had direct trophic links with benthic sources only. Small
484 variations with depth were observed, the diet being composed of benthic predators and worms
485 (~40-50%) followed by bottom-living fish (i.e., Benthos-feeder fish, ~31%) and benthic
486 decapods (15-25%). Our results suggest a more generalist diet than the other functional groups
487 with little intra- and inter-specific variability as shown by the weak dispersion of the
488 consumer's SI ratios. Previous studies have however highlighted high spatial and temporal
489 variability in the diet of species from this group (e.g., Atlantic cod, Daan 1973) that includes a
490 wide variety of prey. This discrepancy might be explained by the fact that we used SI data that
491 integrate diet over longer periods of time than stomach contents. Spatio-temporal diet
492 variability in highly mobile generalist species such as demersal piscivorous fish may integrate

493 out in terms of SI signature and result in rather similar SI ratios that are unrelated to the
494 sampling depth. Similar patterns have been observed in shelf and lacustrine fish assemblages,
495 where higher TL species integrate coupling of pelagic and benthic pathways, resulting into
496 intermediate $\delta^{13}\text{C}$ values (Woodland and Secor 2013, Schindler and Scheurell 2002). Although
497 the endobenthos-feeding and demersal piscivorous fish had trophic links with benthic prey
498 only, it is worth noting that our approach accounts only for direct predator-prey interactions
499 and that pelagic organic matter might still fuel benthic fish through indirect trophic links (i.e.,
500 contribution of pelagic organic matter to the diet of primary consumers), that would then
501 benefit indirectly from pelagic-benthic coupling.

502 *Concluding remarks*

503 The aim of this study was to provide information on the fundamental structure of the trophic
504 network involving fish functional groups in a semi-enclosed sea and over a large spatial scale.
505 The use of Bayesian mixing models integrating both DT and SI data indicated high connection
506 between benthic and pelagic compartments. Including depth as an environmental covariate, the
507 results showed that strong benthic-pelagic and pelagic-benthic couplings in shallow waters
508 result in fish benefiting from both benthic- and pelagic-derived matter as part of their diet. As
509 waters become deeper, these couplings weaken and species consume prey (either benthic or
510 pelagic) progressively more according to their habitat preferences. Future studies in epi-
511 continental seas should include environmental variables such as depth as proxies of habitat
512 variation to untangle consumers' resource use and highlight potentially varying energy
513 pathways structuring food webs. Results from this study enhance our comprehension of trophic
514 interactions sustaining the fish community, which is essential for management and informed
515 decision-making.

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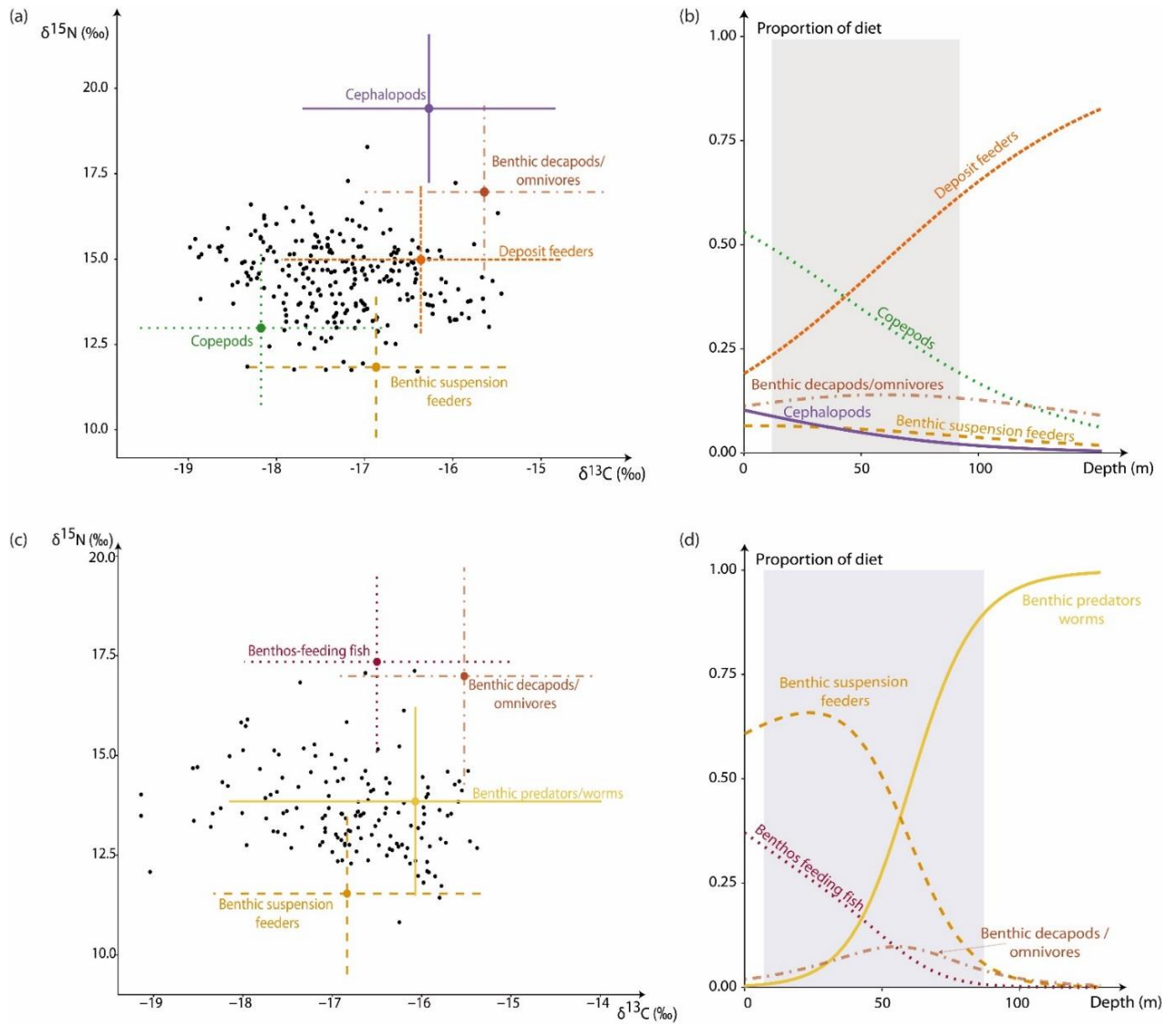
693 **Figure legends**

694 Figure 1: Diet composition of benthos-feeding (a, b) and endobenthos-feeding fish (c, d) as estimated
695 by the MixSIAR mixing model. Iso-Space (a, c) displaying consumer's individual SI values (individual
696 fish black dots) together with sources average SI values (e.g., "Copepods"; colored dots). The latter
697 have been adjusted by TEF means and are associated with error bars indicating ± 1 standard deviation
698 resulting from combined source and discrimination (TEF) uncertainty. Variation in diet as a function of
699 depth is illustrated in panels (b, d). Sampling depth range is illustrated by the grey box and spans from
700 7-12m to 80m. Extrapolations beyond this depth range were kept for illustration purposes. Figure 2
701 follows the same conventions as this figure.

702 Figure 2: Diet composition of demersal (a, b) and pelagic piscivorous fish (c, d) as estimated by the
703 MixSIAR mixing model. Iso-Space (a, c). Variation in diet as a function of depth (b, d).

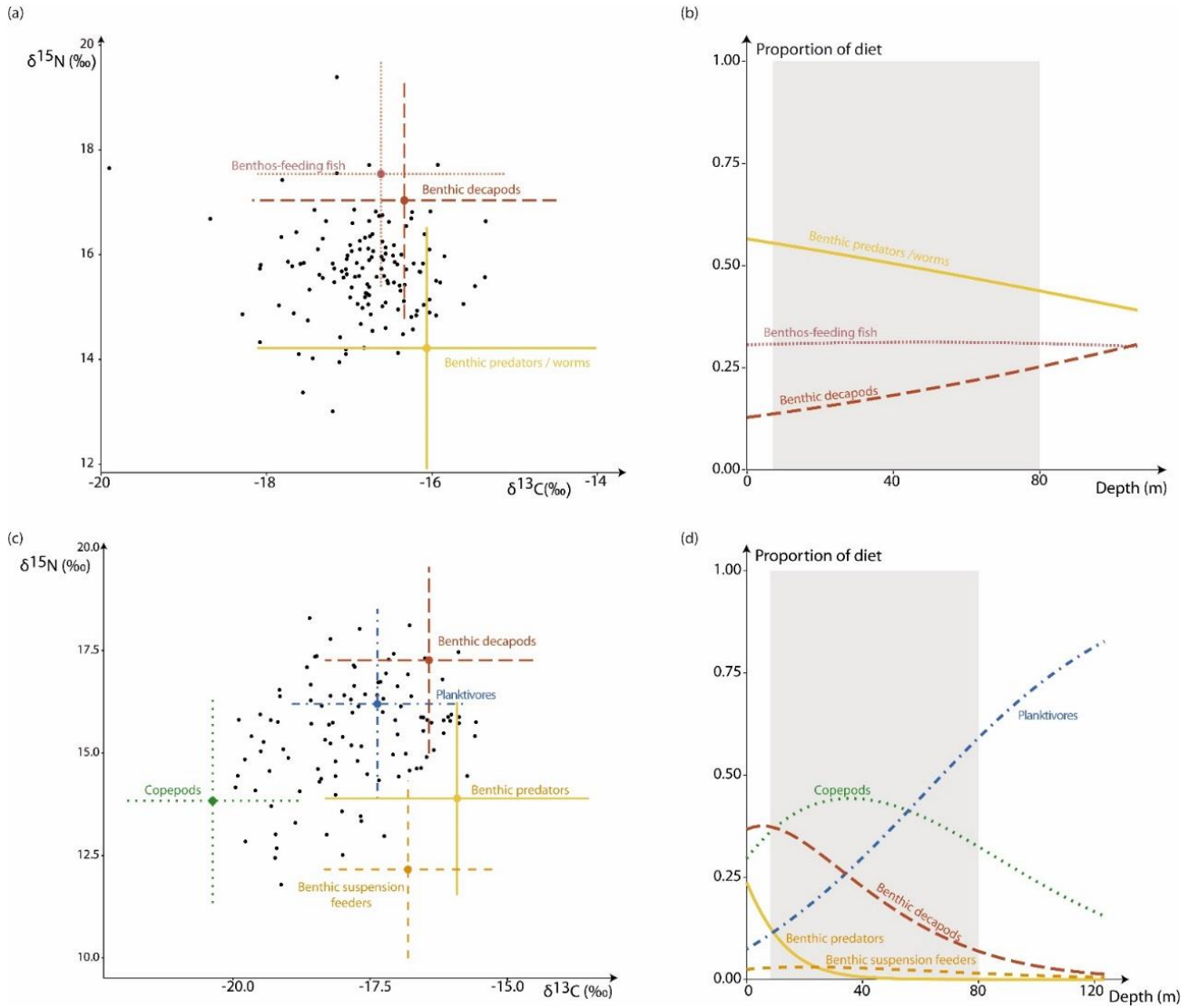
704 Figure 3: Variation of the proportional benthic contribution (all benthic sources summed) to the diet of
705 fish functional groups (proportional pelagic contribution is simply obtained as 1-benthic contribution).
706 Blue dashed line: pelagic piscivorous fish; orange dash-dot line: benthos-feeding fish; red continuous
707 line: demersal piscivorous and endobenthos-feeding fish

708 **Figure 1**



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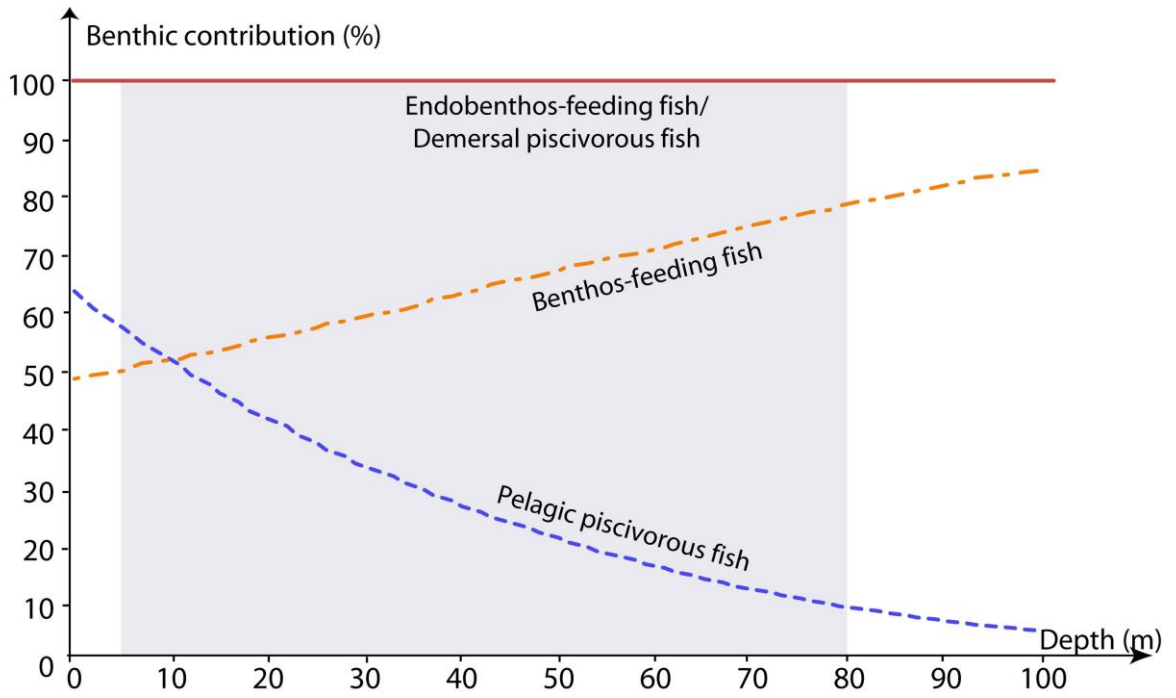
711 **Figure 2**



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714 **Figure 3**
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718 **Table 1: Functional groups of the Eastern English Channel food web. Species composition, reported diet and**
719 **mean trophic level (TL) based on SI are given for each functional group. Source data and references are**
720 **available in Supplementary Tables S1 and S2.**

Functional group	Composition	Reported diet	TL
1. Phytoplankton	POM	-	1
2. Benthic OM and detritus	BOM	-	1
3. Copepods	Copepods	Mostly herbivore, although some species are omnivorous/carnivorous or parasites	2.29 ± 0.32
4. Macro-zooplankton	Chaetognaths and fish larvae	Feed on copepods and other zooplankton	3.19 ± 0.03
5. Benthic-suspension feeders	Mainly bivalves and gastropods: <i>Aequipecten opercularis</i> , <i>Glycymeris glycymeris</i> , <i>Laevicardium crassum</i> , <i>Mimachlamys varia</i> , <i>Pecten maximus</i> , <i>Crepidula fornicata</i>	Suspension-feeder, deposit-feeder detrivore, planktivore, bacteria	2.01 ± 0.26
6. Deposit feeders	Mostly <i>Nereis</i> sp (this study) and <i>Aponuphis tubicola</i> , <i>Nephtys caeca</i> , <i>Dasybranchus gajolae</i> , <i>Glycera rouxii</i> (Le Loc'h, Hily, and Grall 2008).	Omnivores feeding on phytoplankton, zooplankton, crustaceans and other worms	2.72 ± 0.15
7. Benthic decapods/ omnivores	Shrimps <i>Palaemon serratus</i> , <i>Processa</i> sp. and Hermit crabs <i>Pagurus bernhardus</i>	Omnivores feeding on algae, crustaceans, gastropods and polychaetes	3.71 ± 0.79
8. Benthic decapods / predators/scavengers	Shrimp <i>Crangon crangon</i> and crabs <i>Liocarcinus holsatus</i> , <i>Maja brachydactyla</i> , <i>Necora puber</i>	Carnivores/scavengers feeding on echinoderms, crustaceans, marine worms, molluscs and dead fishes	3.56 ± 0.39
9. Benthic predators	Mainly echinoderms <i>Psammechinus miliaris</i> and the gastropod <i>Buccinum undatum</i>	Omnivores/scavengers feeding on marine worms, hydroids, small crustaceans, molluscs, diatoms, macroalgae and detritus	2.42 ± 0.37
10. Benthos-feeding fish	Rays <i>Raja clavata</i> , Gobiidae, Triglidae <i>Trigloporus lastoviza</i> , <i>Chelidonichthys lucerna</i> ,	Feed on all kinds of bottom animals, preferably crustaceans	3.83 ± 0.48

	small sharks <i>Scyliorhinus canicula</i> , <i>Scyliorhinus stellaris</i> , <i>Mustelus</i> sp., and small fish <i>Spondylisoma cantharus</i> , <i>Trisopterus luscus</i> , <i>Trisopterus minutus</i> , <i>Mullus surmuletus</i> , <i>Callionymus lyra</i> , <i>Eutrigla gurnardus</i>		
11. Endobenthos-feeding fish	Flat fishes <i>Buglossidium luteum</i> , <i>Limanda limanda</i> , <i>Microstomus kitt</i> , <i>Platichthys flesus</i> , <i>Pleuronectes platessa</i> , <i>Solea solea</i>	Feed on a wide range of small bottom-living organisms, mainly crustaceans (amphipods, shrimps), also polychaeta worms and bivalve mollusks	3.50 ± 0.44
12. Demersal piscivorous fish	<i>Dicentrarchus labrax</i> , <i>Gadus morhua</i> , <i>Hyperoplus lanceolatus</i> , <i>Merlangius merlangus</i> , <i>Scophthalmus rhombus</i> (flatfish feeding preferentially on fish)	Feeds on fishes and larger crustaceans	4.40 ± 0.49
13. Planktivorous fish	<i>Clupea harengus</i> , <i>Micromesistius poutassou</i> , <i>Sardina pilchardus</i> , <i>Sprattus sprattus</i>	Feeds on planktonic crustaceans	3.17 ± 0.55
14. Pelagic piscivorous fish	<i>Zeus faber</i> , <i>Scomber scombrus</i> , <i>Trachurus trachurus</i>	Feeds on zooplankton and small fish	4.32 ± 0.66
15. Cephalopods	<i>Alloteuthis subulata</i> , <i>Loligo vulgaris</i> , <i>Sepia officinalis</i>	Feed on a wide variety of animals, mainly bony fishes and crustaceans	4.75 ± 0.48

721 **Table 2: Diet matrix showing the contribution of each prey (columns) to the diet of consumers (rows) based on IsoWeb modeling (10⁶ iterations). Values**
722 **are expressed as mean proportions with standard deviations between square brackets. (*) POM. (**) Benthic organic matter. ΣB and ΣP correspond to the**
723 **sum of mean contributions of benthic (B) and pelagic (P) subsidies respectively.**

Consumer	Prey													ΣB	ΣP	Total
	POM	BOM	Copepods	Macro-zooplankton	Benthic suspension feeders	Deposit feeder	Benthic decapods omnivores	Benthic decapods /predators	Benthic predators	Benthos-feeding fish	Planktivorous fish	Pelagic piscivorous fish	Cephalopods			
Copepods	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Macro-zooplankton	0.37 [0.21]	-	0.63 [0.21]	-	-	-	-	-	-	-	-	-	-	-	1	1
Benthic-suspension feeders	0.35 [0.21]	0.65 [0.21]	-	-	-	-	-	-	-	-	-	-	-	0.65	0.35	1
Deposit feeder	0.37 [0.23]	0.63 [0.23]	-	-	-	-	-	-	-	-	-	-	-	0.63	0.37	1
Benthic decapods /omnivores	0.11 [0.09]	0.17 [0.14]	-	-	0.28 [0.21]	0.44 [0.20]	-	-	-	-	-	-	-	0.89	0.11	1
Benthic decapods /predators	-	0.18 [0.13]	-	-	0.23 [0.17]	0.23 [0.17]	0.17 [0.12]	-	0.19 [0.16]	-	-	-	-	1	-	1
Benthic predators	-	-	-	-	0.72 [0.24]	0.28 [0.24]	-	-	-	-	-	-	-	1	-	1
Benthos-feeding fish	-	-	0.27 [0.17]	-	0.24 [0.16]	0.21 [0.16]	0.15 [0.12]	-	-	-	-	-	0.13 [0.10]	0.73	0.27	1
Endobenthos-feeding fish	-	-	-	-	0.30 [0.18]	0.20 [0.16]	0.14 [0.12]	-	0.22 [0.17]	0.14 [0.11]	-	-	-	1	-	1
Demersal piscivorous fish	-	-	-	-	-	0.21 [0.16]	0.18 [0.14]	0.21 [0.15]	0.21 [0.15]	0.19 [0.15]	-	-	-	1	-	1

Planktivorous fish	-	-	0.30 [0.19]	0.16 [0.14]	0.32 [0.19]	-	0.10 [0.09]	0.12 [0.11]	-	-	-	-	-	0.54	0.46	1
Pelagic piscivorous fish	-	-	0.16 [0.12]	0.17 [0.13]	0.12 [0.10]	-	0.12 [0.10]	0.15 [0.12]	0.12 [0.10]	-	0.16 [0.12]	-	-	0.51	0.49	1
Cephalopods	-	-	-	-	-	-	0.19 [0.15]	0.21 [0.16]	-	0.19 [0.15]	0.23 [0.17]	0.18 [0.14]	-	0.82	0.18	1