
Reorganization of a marine trophic network along an inshore-offshore gradient due to stronger pelagic-benthic coupling in coastal areas

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Abstract :

Recent theoretical considerations have highlighted the importance of the pelagic-benthic coupling in marine food webs. In continental shelf seas, it was hypothesized that the trophic network structure may change along an inshore-offshore gradient due to weakening of the pelagic-benthic coupling from coastal to offshore areas. We tested this assumption empirically using the eastern English Channel (EEC) as a case study. We sampled organisms from particulate organic matter to predatory fishes and used baseline-corrected carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) to determine their trophic position. First, hierarchical clustering on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ coupled to bootstrapping and estimates of the relative contribution of pelagic and benthic carbon sources to consumers' diet showed that, at mesoscale, the EEC food web forms a continuum of four trophic levels with trophic groups spread across a pelagic and a benthic trophic pathway. Second, based on the same methods, a discrete approach examined changes in the local food web structure across three depth strata in order to investigate the inshore-offshore gradient. It showed stronger pelagic-benthic coupling in shallow coastal areas mostly due to a reorganization of the upper consumers relative to the two trophic pathways, benthic carbon sources being available to pelagic consumers and, reciprocally, pelagic sources becoming accessible to benthic species. Third a continuous approach examined changes in the mean and variance of upper consumers' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with depth. It detected a significant decrease in $\delta^{13}\text{C}$ variance and a significant increase in $\delta^{15}\text{N}$ variance as depth increases. A theoretical two-source mixing model showed that an inshore-offshore decrease in the pelagic-benthic coupling was a sufficient

condition to produce the $\delta^{13}\text{C}$ variance pattern, thus supporting the conclusions of the discrete approach. These results suggest that environmental gradients such as the inshore-offshore one should be accounted for to better understand marine food webs dynamics.

Highlights

► Marine food web is reorganized along a seaward gradient in the English Channel. ► Stronger coupling of the pelagic and benthic pathways from offshore to the coast. ► Shift of pelagic predators to the benthic pathway in shallow areas. ► Adaptive foraging of pelagic predators may explain food web reorganization.

Keywords : Food web, Spatial variation, Stable isotope, Megatidal shelf ecosystem

46 1. Introduction

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48 The structure of food webs has been the subject of increasing interest during the past
49 two decades. Research questions on food web structure lie in the field of ecological networks
50 that aims at understanding how community structure and trophic interactions affect ecosystem
51 functioning (Ings et al., 2009). Among the ecological functions studied are trophic resource
52 acquisition and biomass production, and their dependence on biodiversity and trophic
53 interactions in food webs (Duffy et al., 2007). Studies of the structure of food webs are thus
54 essential to predict the response of ecosystems to the effect of global change on biodiversity.
55 Nevertheless, studies of trophic network structure at large spatial and taxonomical scales in
56 marine ecosystems remain relatively scarce (e.g. Woodland and Secor, 2013).

57 Ings et al. (2009) considered the study of networks along environmental gradients as
58 well as from local to regional scales as “fruitful avenues”. However, there is a current lack of
59 knowledge on the way food web structure is affected by variation in environmental conditions
60 along gradients (but see Dézerald et al., 2013; Woodland and Secor, 2013). Most of the time,
61 when trophic network structure is studied at a sufficiently large geographical scale to address
62 this issue, only some compartments of the food web are considered in order to ensure a large
63 spatial coverage and a reliable sampling effort (e.g. pelagic fishes and zooplankton; Sholto-
64 Douglas et al., 1991 or top-predators and their prey; Revill et al., 2009). Then, the targeted
65 species or compartments are most often keystone species or strong interactors as their loss or
66 removal could cause dramatic changes in communities (e.g. Paine, 1969). However, it is
67 essential to consider most species of a community, as weak interactors, the removal or
68 addition of which is assumed to cause indiscernible changes, may have a preponderant role in
69 maintaining community stability (Berlow, 1999). Due to the multiplicity of ecological links
70 established by weak interactors in species-rich communities, the resulting complex network is

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71 able to buffer variations in keystone species (Brose et al., 2005) and to sustain community
72 stability under environmental variations such as stress and disturbance (Worm and Duffy,
73 2003). Another approach is to describe all the interactors of the food web but at a lower
74 spatial resolution. For instance, investigations have often focused on small dedicated areas
75 such as coastal nursery grounds (Rodríguez-Graña et al., 2008), marine protected areas
76 (Vizzini and Mazzola, 2009; Albouy et al., 2010) or emblematic zones such as reef areas
77 (Thomas and Cahoon, 1993; Jennings et al., 1997). However, such limited geographical scale
78 automatically prevents from addressing the question of the effect of environmental gradients.

79 Among others, a food web's structure is important as it determines its own dynamics,
80 be it in terms of energy or material fluxes (Dunne, 2006), but also its properties such as
81 resilience and stability. Notably, the relationship between diversity and stability depends
82 strongly on food web structure as for a given species richness food web stability is expected
83 to depend on connectance, i.e. the fraction of realized trophic links among all the possible
84 ones (Rooney and McCann, 2012). Therefore, knowledge of variations in food webs'
85 structure along environmental gradients is essential in understanding their dynamics and
86 evaluating their stability and resilience to natural and anthropogenic disturbances. Recent
87 theoretical considerations highlighted the importance of considering the coupling between
88 pelagic and benthic pathways in marine food webs to understand their structure (Woodland
89 and Secor, 2013), functioning (Blanchard et al., 2009) and resilience to perturbations
90 (Blanchard et al., 2011). Notably, pelagic food webs are supposed to be more strongly size-
91 structured, both in terms of trophic level (TL) and abundance, than benthic ones, because
92 large predators eat smaller prey in the former (Cohen et al., 1993), whereas predators share
93 unstructured and more diverse resources in the latter (Maxwell and Jennings, 2006). The
94 pelagic-benthic coupling is therefore specifically important in understanding the structure of
95 trophic networks in continental shelf seas where pelagic and benthic animals co-occur

1 96 spatially. Physical proximity between pelagic and benthic species and weaker physical
2 97 barriers such as thermoclines in shallow, mixed continental shelf waters may indeed allow a
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4 98 stronger benthic-pelagic coupling. Based on these theoretical premises, we hypothesized that
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7 99 in shelf seas (i) the coupling between pelagic and benthic pathways weakens from coastal to
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10 100 offshore areas, which results into changes in the trophic network structure along the inshore-
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12 101 offshore gradient; and (ii) these changes imply that the food web structure estimated from
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14 102 data varies according to the geographical scale considered, i.e. global versus local scale.

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17 103 We tested these hypotheses empirically in the eastern English Channel (EEC) - a
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19 104 shallow continental shelf sea taken as a case study. To this end, we sampled the largest
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21 105 possible range of organisms, from particulate organic matter to large predatory fishes, with a
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24 106 large spatial grid covering 35 000 km² (Fig. 1). We used carbon and nitrogen stable isotopes
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26 107 analyses to determine species' trophic position. Hierarchical clustering coupled to
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29 108 bootstrapping allowed us to identify trophic groups of species according to their isotopic
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31 109 ratios and thereby the trophic network structure at the scale of the whole sampling area
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34 110 (hereafter termed global scale). The strength of the benthic-pelagic coupling was assessed by
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36 111 estimating the relative contributions of pelagic and benthic sources of carbon to consumers'
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39 112 diet using a two-source mixing model. Then, we followed a discrete approach to test for an
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41 113 inshore-offshore gradient in the food web structure. Trophic groups and contributions of
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44 114 carbon sources were assessed using the same techniques but at the local scale, i.e. in three
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46 115 different depth strata distributed along the gradient. These are characterized by varying animal
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49 116 community composition and co-varying factors such as salinity, water temperature and soft
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51 117 bottom features (Martin et al., 2010). Finally, we developed a continuous approach in which
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53 118 we tested for an inshore-offshore gradient in the local food web structure through the
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56 119 influence of depth on the distribution (mean and variance) of nitrogen and carbon isotopic
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58 120 ratios of upper consumers (from secondary consumers upward, except for decapod
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121 crustaceans). The results of the continuous approach were completed and interpreted in terms
122 of the benthic-pelagic coupling by developing a theoretical two-source mixing model.

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124 **2. Materials and methods**

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126 *2.1. Study system and gradient approaches*

127 The eastern English Channel (EEC) is a shallow epi-continental sea located between
128 England and France, which presents an inshore-offshore gradient in habitats from the coast to
129 its central area (Vaz et al., 2007). After estimating the food web structure at the global scale,
130 two approaches were used to study variations of the local food web structure along the
131 inshore-offshore gradient, a discrete and a continuous one, both based on the use of depth as a
132 proxy of the gradient. Depth is indeed strongly correlated with the distance to the coast in the
133 EEC as well as with many environmental parameters (see below) and may be directly
134 involved in the benthic-pelagic coupling due to its obvious effect on the proximity between
135 the corresponding compartments.

136 - Discrete gradient approach

137 The EEC was sub-divided into three depth strata based on changes according to depth in the
138 taxonomic composition of the community of vertebrates (fishes) and invertebrates
139 (cephalopods and benthic epifauna) observed by trawling during the Channel Ground Fish
140 Survey (see sub-section „Sample collection“ below). More precisely, a Multivariate
141 Regression Tree (MRT) of the invertebrate and vertebrate species presence/absence data
142 matrix on depth was performed in order to identify depth thresholds at which the community
143 composition changed significantly. MRT is a constrained clustering method that identifies
144 clusters based on minimizing the within-group sums of squares but where partitioning occurs
145 at successive thresholds of a constraining or explanatory variable, here depth (Borcard et al.,

146 2011). Computation of sums of squares was based on Euclidian distance. A first split occurred
147 at 20m and a second one at 38m delineating three depth strata between 0 and 20m, 20 and
148 38m, and 38 and 79 m (Fig. 1). These were characterized by different taxonomic
149 compositions of the vertebrate and invertebrate community but also different physicochemical
150 features as these are known to co-vary with depth in the EEC. Salinity increases with depth as
151 the influence of continental freshwater fades away along the inshore-offshore gradient,
152 whereas average temperature along the water column decreases with increasing depth.
153 Sediment types also change from mud and fine sands in shallow waters through coarse sands
154 to gravels and pebbles in deeper areas as bed shear stress resulting from tidal currents
155 increases with depth (Martin et al., 2010).

156 - Continuous gradient approach

157 We complemented the discrete gradient approach by a continuous one, which consisted in
158 evaluating the influence of depth on the distribution (mean and variance) of nitrogen and
159 carbon isotopic ratios among all upper consumers (from secondary consumers upward, except
160 for decapod crustaceans which were under-represented in offshore areas) of the food web in
161 order to test for continuous changes in TL or trophic pathway along an inshore-offshore
162 gradient. This provides another way to look at potential reorganization of the local trophic
163 network structure in the EEC. This continuous approach based on observations was completed
164 by a theoretical approach (see below §2.7).

166 2.2. Sample collection

167 Particulate organic matter, zooplankton, epifaunal invertebrates and fishes were
168 sampled in the EEC for the purpose of the present study and represented a total of *ca.* 900
169 samples. Fishes and some epifaunal invertebrates were collected during the Channel Ground
170 Fish Survey (October 2009) using a GOV demersal trawl with a cod-end of 10 mm stretched

171 mesh, towed for 30 min at a speed of approximately 3.5 knots from R. V. “Gwen Drez” (Vaz
172 et al., 2007). Other samples of epifaunal invertebrates were gathered during the COMOR
173 survey (June 2010) using a French dredge towed for 5 to 6 minutes at a speed of
174 approximately 2.5 knots from R. V. “Thalia” (Delpech et al., 2007). As our samples were
175 collected by bottom trawling and dredging, small epifauna was underrepresented in the
176 samples and infauna was almost absent. Zooplankton was sampled during the International
177 Bottom Trawl Survey (February 2010) using a WP2 zooplankton net (Tranter and Smith,
178 1968) with a 200 μm mesh size fished from R.V. “Thalassa”. Diagonal tows were performed
179 at a speed of $0.75\text{m}\cdot\text{s}^{-1}$ from the surface to 3 m above the seabed. Finally, particulate organic
180 matter was obtained from water samples collected from R.V. “Sepia2” during the French
181 sampling programme SOMLIT (October to June) using a Niskin bottle and filtered until
182 clogged through precombusted Whatman GF/F filters ($0.5\ \mu\text{m}$) immediately after sampling.
183 All samples were kept frozen until processing in the laboratory.

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2.3. Stable isotope analysis (SIA)

186 Stable isotopes of carbon and nitrogen in tissues of organisms were used to examine
187 consumers’ trophic ecology. $\delta^{15}\text{N}$ values were used to define the trophic level of consumers
188 and $\delta^{13}\text{C}$ values were used to identify their position relative to the pelagic or the benthic
189 trophic pathways (De Niro and Epstein, 1978). Tissues were prepared for SIA as follows:
190 Whatman GF/F filters containing particulate organic matter (POM) were oven-dried and
191 subsequently exposed to HCl vapour for 4 hours in order to remove carbonates (Lorrain et al.,
192 2003). For zooplankton, after thawing samples in distilled water, copepods, fish larvae, and
193 chaetognaths were hand-picked from the detritus-rich samples and prepared whole. When
194 necessary, they were pooled by areas to ensure reliable C and N isotopic measurements. For
195 invertebrates, processing varied according to taxon. For annelids, analyses were done on the

196 remaining tissues once the digestive tracts and jaws were removed under a dissecting
 197 microscope. Muscle samples were taken from the abdomen of shrimps, the chelipeds of crabs
 198 and paguroids, the adductor muscle of bivalve molluscs, the foot of *Buccinum undatum* and
 199 *Crepidula fornicata*, and the mantle of cephalopods. Gonads were used for sea urchins. For
 200 fishes, a sample of white dorsal muscle was dissected (Pinnegar and Polunin, 1999). After
 201 dissection, tissue samples of all benthic taxa were washed with distilled water in order to
 202 prevent any contamination by sediment carbonates.

203 All samples were frozen at -80°C before freeze-drying. Each dried sample was then
 204 ground into a homogeneous powder using a mixer mill. Approximately 2 mg of powder was
 205 weighed into small tin cups, and determination of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and % content of C and N was
 206 carried out by Elemental Analysis Isotope Ratio Mass Spectrometry by Iso-analytical Ltd
 207 (Crewe, UK) using a Europa Scientific elemental analyser coupled to a Europa Continuous
 208 Flow Isotope Ratio Mass Spectrometer. In the present study, isotope ratios are reported in
 209 delta notation as per international standards: PeeDee belemnite carbonate for $\delta^{13}\text{C}$ and
 210 atmospheric nitrogen for $\delta^{15}\text{N}$. Data were corrected using working standards (bass muscle,
 211 bovine liver, nicotinamide; $\text{SD} < 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) that were previously
 212 calibrated against International Atomic Energy Agency (IAEA) standards. For all taxa, except
 213 mackerel (*Scomber scombrus*), the mean observed C:N ratio was lower than 3.5, the value
 214 above which lipid normalization is recommended (Post et al., 2007). Different techniques are
 215 available to account for the influence of lipid content on $\delta^{13}\text{C}$ ratios (Sweetings et al., 2006;
 216 Logan et al., 2008). Normalization of $\delta^{13}\text{C}$ ratios for mackerel was performed according to the
 217 following equation (Post et al., 2007):

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \text{ C:N} \quad (1)$$

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220 2.4. Trophic baseline and correction of isotopic values for spatial variation

221 The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of a species provide information about its trophic level and
222 pathway relative to a baseline. A suspension-feeding bivalve, queen scallop *Aequipecten*
223 *opercularis*, was chosen as the trophic baseline for this study (Jennings and Warr, 2003).
224 Using a primary consumer as a baseline has the advantage over primary producers such as
225 phytoplankton of buffering short term variations in isotopic values due to seasonality in
226 environmental factors or any other short-term source of temporal variability. One difficulty
227 though is that isotopic values of the trophic baseline, and thus of species at higher trophic
228 levels, may vary spatially due to environmental gradients. Specifically, along the inshore-
229 offshore gradient there is a diminishing influence of terrigenous influx of nutrients and
230 detritus that are characterized by $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios different from those of oceanic material.
231 It results that observed isotopic values of higher trophic level species (here consumers) must
232 be corrected for spatial variation in baseline values.

233 Unfortunately, the spatial coverage of our *A. opercularis* samples was insufficient (12
234 sampling sites; Fig. S1) to estimate properly spatial variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ baseline
235 values. To overcome this problem, we used published $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of *A. opercularis*
236 sampled with a better spatial coverage (23 sampling sites; Fig. S1) in summer 2001 (see
237 Jennings and Warr, 2003 and Barnes et al., 2009 for more details about the sampling protocol
238 and available isotopic). Published isotopic ratios at our disposal were averages of 3 to 6
239 individual values per sampling site (median = 5) except for one site with only 1 individual
240 value. We used these to predict $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ baseline values at all our sampling sites using a
241 geostatistical interpolation technique, namely kriging (Diggle and Ribeiro, 2007; see
242 Supplementary Material 1 for the detailed procedure). Despite our *A. opercularis* samples and
243 published data were collected in different years, the spatial structuring of isotopic values was
244 similar as predicted values at our sampling sites and observed baseline values from our
245 samples correlated significantly ($\delta^{15}\text{N}$: $r=0.58$, $n=19$, $t_{17} = 2.9452$, $p = 0.0090$; $\delta^{13}\text{C}$: $r = 0.74$,

246 n = 19, $t_{17} = 4.5073$, $p = 0.0003$; Fig. S1). For both nitrogen and carbon, the isotopic value of
 247 each consumer sample was then corrected by subtracting the predicted baseline value at the
 248 sampling location and by adding the mean predicted baseline value across all sampling sites.
 249 All isotopic ratios of consumers used in further analyses are corrected ones.

251 2.5. Trophic level and trophic sources

252 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ are enriched from a prey to its predator (trophic fractionation) by 2.5-
 253 4.5‰ (mean 3.4‰; Minagawa and Wada, 1984; Post, 2002) and 1-2‰ (mean 1.5‰; De Niro
 254 and Epstein, 1978; Wada et al., 1991), respectively. Therefore, we depicted the pelagic and
 255 the benthic trophic pathway according to the limits of the ranges of isotopic ratios expected
 256 for the trophic transfer of pelagic and benthic organic matter (Darnaude et al. 2004; Fig. 2).
 257 We used the maximum trophic increases of +4.5‰ in $\delta^{15}\text{N}$ and the minimum of +1‰ in $\delta^{13}\text{C}$
 258 to delimit the upper range of each trophic pathway, and the minimum of +2.5‰ in $\delta^{15}\text{N}$ and
 259 the maximum of +2‰ in $\delta^{13}\text{C}$ to delimit the lower range. The isotopic ratios of a pelagic
 260 primary consumer, namely copepods, and of a benthic primary consumer, namely *A.*
 261 *opercularis*, were used as starting point of the range for the pelagic and the benthic pathway,
 262 respectively.

263 As the $\delta^{15}\text{N}$ value provides indication of the trophic level of a consumer, the TL of
 264 each species was calculated following the equation from Post (2002):

$$265 \text{TL}_{\text{species}} = (\delta^{15}\text{N}_{\text{species}} - \delta^{15}\text{N}_{\text{base}}) / \Delta\text{N} + \text{TL}_{\text{base}} \quad (2)$$

266 where ΔN is the assumed average trophic fractionation corresponding to 1 TL for $\delta^{15}\text{N}$,
 267 estimated at 3.4‰ (Minagawa and Wada, 1984), $\delta^{15}\text{N}_{\text{species}}$ is the mean value of the focal
 268 species, $\delta^{15}\text{N}_{\text{base}}$ is the mean value of a species close to the base of the food web chosen as
 269 trophic baseline, here *A. opercularis*, and TL_{base} is its trophic level. As a primary consumer
 270 the trophic level of *A. opercularis* was set to $\text{TL}_{\text{base}} = 2$. The approximate standard errors (σ)

271 of species TLs were calculated based on the standard errors of $\delta^{15}\text{N}_{\text{species}}$, $\delta^{15}\text{N}_{\text{base}}$ and ΔN (see
 272 Supplementary Information 2 for details on the derivation)

$$273 \quad \sigma_{\text{TL}_{\text{species}}} = \left(\frac{1}{\Delta\text{N}^2} (\sigma_{\delta^{15}\text{N}_{\text{species}}}^2 + \sigma_{\delta^{15}\text{N}_{\text{base}}}^2) + \frac{(\delta^{15}\text{N}_{\text{species}} - \delta^{15}\text{N}_{\text{base}})^2}{\Delta\text{N}^4} \sigma_{\Delta\text{N}}^2 \right)^{1/2} \quad (3)$$

274 Equation (3) accounts for variability in observed $\delta^{15}\text{N}$ values ($\sigma_{\delta^{15}\text{N}_{\text{species}}}$ and $\sigma_{\delta^{15}\text{N}_{\text{base}}}$) but
 275 also for uncertainty in trophic fractionation value ($\sigma_{\Delta\text{N}}$). While $\sigma_{\delta^{15}\text{N}_{\text{species}}}$ and $\sigma_{\delta^{15}\text{N}_{\text{base}}}$
 276 were estimated from the data directly, $\sigma_{\Delta\text{N}}$ was estimated by assuming that the range of
 277 possible fractionation values for nitrogen 2.5-4.5‰ covers 99% of the distribution and that
 278 this distribution is Gaussian, which yields a standard deviation of $\sigma_{\Delta\text{N}} = 0.333\%$.

279 We calculated the contributions of pelagic and benthic sources of carbon to fish and
 280 cephalopod diet using a two-source mixing model with the $\delta^{13}\text{C}$ ratios of copepods and *A.*
 281 *opercularis* as the $\delta^{13}\text{C}$ ratios of the pelagic and the benthic carbon source, respectively. Since
 282 isotope mixing models can be highly sensitive to uncertainty surrounding the mean isotopic
 283 ratios of sources, we used a mixing model developed by Phillips and Gregg (2001), which
 284 incorporates the observed variation in source isotopic values to calculate the standard errors of
 285 contribution estimates. We calculated the proportion of benthic carbon (α) in fish diet using
 286 Phillips and Gregg's (2001) equation:

$$287 \quad \alpha = (\delta^{13}\text{C}_{\text{species}} - \delta^{13}\text{C}_{\text{P}}) / (\delta^{13}\text{C}_{\text{B}} - \delta^{13}\text{C}_{\text{P}}) \quad (4)$$

288 with $\delta^{13}\text{C}_{\text{species}}$, $\delta^{13}\text{C}_{\text{B}}$ and $\delta^{13}\text{C}_{\text{P}}$ the mean $\delta^{13}\text{C}$ values of consumer species, benthic and
 289 pelagic carbon sources respectively. The $\delta^{13}\text{C}$ value of the consumer ($\delta^{13}\text{C}_{\text{species}}$) was
 290 corrected for an average trophic fractionation of $\Delta\text{C} = 1.5\%$ per trophic level above the
 291 trophic level of the sources, i.e. 2:

$$292 \quad \delta^{13}\text{C}_{\text{species}} = \delta^{13}\text{C}'_{\text{species}} - \Delta\text{C}(\text{TL}_{\text{species}} - 2) \quad (5)$$

293 with $\delta^{13}\text{C}'_{\text{species}}$ the original value of the consumer and $\text{TL}_{\text{species}}$ its trophic level. The
 294 approximate standard error of α was computed according to Phillips and Gregg's (2001)
 295 equation modified to account for the correction for trophic fractionation (see Supplementary
 296 Information 2 for details on the derivation):

$$\sigma_{\alpha} = ((\sigma_{\delta^{13}\text{C}'_{\text{species}}}^2 + \Delta\text{C}^2 \sigma_{\text{TL}_{\text{species}}}^2 + (\text{TL}_{\text{species}} - 2)^2 \sigma_{\Delta\text{C}}^2 + \alpha^2 \sigma_{\delta^{13}\text{C}_\text{B}}^2 + (1 - \alpha)^2 \sigma_{\delta^{13}\text{C}_\text{P}}^2) / (\delta^{13}\text{C}_\text{B} - \delta^{13}\text{C}_\text{P})^2)^{1/2}. \quad (6)$$

298 As for $\sigma_{\text{TL}_{\text{species}}}$, this standard error accounts for variability in the data but also for uncertainty
 299 in fractionation value. Following the same reasoning as previously, if the range of possible
 300 fractionation values for carbon 1-2‰ covers 99% of the distribution and this distribution is
 301 Gaussian, the standard deviation is estimated as $\sigma_{\Delta\text{C}} = 0.167\%$.

2.6. Statistical analyses

304 Trophic groups of species at meso- and local scales (discrete gradient approach) were
 305 identified by hierarchical clustering analysis on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values using Ward's minimum
 306 variance method (Ward Jr, 1963). This method is based on the linear model criterion of least
 307 squares and its objective is to define groups that minimize the within-group sum of squares.
 308 Computation of within-group sums of squares is based on a Euclidean model. Given that
 309 sample size varied between taxa (from 3 to 63; Table 1), but that the intention was to account
 310 for within-sample variation in isotopic ratios, hierarchical clustering was performed on a
 311 bootstrapped matrix of distances between species that was computed as follows: since
 312 minimum sample size was 3, 3 individuals per species were sampled with replacement, the
 313 isotopic ratios of which were used as coordinates to compute a Euclidian distance matrix
 314 between species after standardizing coordinates to 0 mean and unit variance. This procedure
 315 was repeated 500 times, and the resulting distance matrices were averaged to obtain the

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316 bootstrapped distance matrix on which clustering was performed. The number of resampling
317 was sufficient to stabilize the values of the bootstrapped distance matrix. After clustering, the
318 optimal number of clusters was assessed by visual inspection of the resulting dendrogram and
319 confirmed using graphs of fusion level (Borcard et al., 2011).

320 The influence of depth (continuous gradient approach) on the mean and variance of
321 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios of upper consumers of the food web (continuous gradient approach) was
322 analysed using generalized least squares models that can account for heteroscedastic variance
323 of observations in linear regression models (Pinheiro and Bates, 2004). The following
324 procedure was used (Zuur et al., 2009): first, a classical linear model was fitted to $\delta^{15}\text{N}$ and
325 $\delta^{13}\text{C}$ values with depth as a continuous explanatory variable, and residuals were inspected for
326 normality and homoscedasticity. Residuals of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values exhibited clear
327 heteroscedasticity in relation with depth. As a second step, a generalized least squares model
328 was fitted with depth as a continuous explanatory variable of the mean and variance of $\delta^{15}\text{N}$
329 and $\delta^{13}\text{C}$ values. For variance, several sub-models were tested: a linear, an exponential, and a
330 power function of depth as well as a constant plus a power function of depth. The best
331 variance model was chosen on the basis of the Akaike Information Criterion (AIC), and the
332 significance of the effect of depth on variance was assessed by a likelihood ratio test between
333 the classical linear model and the generalized least squares model that is supposed to follow a
334 χ^2 distribution under the null hypothesis. The significance of the effect of depth on the mean
335 was assessed using an F test on the basis of the generalized least squares model. Primary
336 producers, primary consumers and decapod crustaceans were excluded from this approach
337 because the two first ones are known to present wider spread of isotopic ratios than high TL
338 organisms (i.e. Chauvelon et al., 2012), and because our sampling procedure would have
339 induced bias as these three compartments were under-represented in offshore areas (Table 1).

340 All analyses were performed in the statistical environment R (R Development Core Team,
341 2012). Multivariate regression trees were performed with package mvpart (Therneau et al.,
342 2013), geostatistical analyses were done with package GeoR (Ribeiro Jr and Diggle, 2001),
343 and generalized least squares models were fitted with package nlme (Pinheiro et al., 2013).
344 The data and R codes used in this study are available from the authors upon request.

2.7. Theoretical two-source mixing model

347 A theoretical two-source mixing model was developed to complement and interpret
348 the results of the continuous gradient approach on upper consumers. This model mimicked the
349 observed pattern in the contribution α of benthic carbon to upper consumers' diet according to
350 depth and predicted the resulting changes in the distribution (mean and variance) of upper
351 consumers' $\delta^{13}\text{C}$ ratios with depth.

352 Two groups of upper consumers composed of 376 individuals each were modeled (752
353 upper consumers were observed in our samples). They differed in terms of their affinity for
354 the pelagic and the benthic trophic pathway due to their position in the water column. This
355 difference in affinity translated into different contributions α of benthic carbon to consumers'
356 diet as observed in our data. α was therefore modeled as a truncated normal distribution
357 between 0 and 1 with mean 0.3 for consumers with a pelagic affinity (observed mean=0.32)
358 and 0.6 for those with a benthic affinity (observed mean=0.58). The weakening of the pelagic-
359 benthic coupling along the seaward gradient was modeled as a logistic decrease in the
360 variance of α from 0.06 to 0.02 with increasing depth, a pattern observed in our estimates of α
361 (observed variances of α centered around its mean according to species affinity being equal to
362 0.06, 0.03 and 0.02 for stratum 0-19m, 20-38m, and 38-78m, respectively). This agrees with
363 the line of reasoning according to which, in shallow waters, physical proximity facilitates
364 consumers' access to both pelagic and benthic carbon sources such that, because of

365 opportunistic behavior, the contribution of the two carbon sources to diet, and thus α , can vary
366 greatly whatever the consumers' affinity. In contrast, in deeper areas, consumers will access
367 to carbon sources according to their position in the water column and thus contributions α will
368 be more narrowly centered around consumers' affinity. The benthic and pelagic carbon
369 sources were modeled as having $\delta^{13}\text{C}$ ratios varying according to normal distributions with
370 means -17.4‰ and -21.1‰ and standard deviation 0.5‰ and 0.9‰ respectively, which
371 corresponded to our observations for *A. opercularis* and copepods respectively. At each depth,
372 each consumer C was then attributed a contribution α_C of benthic carbon to its diet randomly
373 drawn from the truncated normal distribution corresponding to its affinity. The consumer's
374 $\delta^{13}\text{C}$ value was then computed according to a two-source mixing model as
375 $\delta^{13}\text{C}_C = \alpha_C \delta^{13}\text{C}_B + (1 - \alpha_C) \delta^{13}\text{C}_P$, where the $\delta^{13}\text{C}$ values of the benthic and pelagic carbon
376 sources, $\delta^{13}\text{C}_B$ and $\delta^{13}\text{C}_P$ respectively, were randomly drawn from the corresponding
377 normal distributions. The changes with depth in the resulting mean and variance of
378 consumers' $\delta^{13}\text{C}$ values were then inspected and compared to observed data. Any agreement
379 between the observed and the predicted pattern in $\delta^{13}\text{C}$ values would suggest that variation in
380 the strength of the pelagic-benthic coupling was a sufficient condition to generate the pattern.

3. Results

3.1. Global-scale trophic network structure in the eastern English Channel

54 species, 3 pools of zooplankton and particulate organic matter (POM) were
analysed for stable isotopic ratios. $\delta^{15}\text{N}$ values ranged from 7.5‰ to 17.2‰ with POM
presenting the lowest $\delta^{15}\text{N}$ values, and a cephalopod, *Loligo vulgaris*, the largest ones (Table
1; Fig. 2). Organisms in the EEC formed a continuum of four trophic levels from POM
(TL=1.8) to fishes and cephalopods (max TL=4.6; Table 1). $\delta^{13}\text{C}$ values ranged from -21.5‰

390 to -15.5‰ with considerable overlap notably among fish species (Fig. 2; Table 1). $\delta^{13}\text{C}$
391 values varied greatly among primary consumers with deposit-suspension feeders exhibiting
392 larger values than zooplankton (Table 1). The difference between $\delta^{13}\text{C}$ values of pelagic (i.e.
393 copepods = $-21.1\text{‰} \pm 0.9$) and benthic primary consumers (i.e. *Aequipecten opercularis* =
394 $-17.4\text{‰} \pm 0.5$) provided evidence for two trophic pathways in the EEC: a pelagic pathway
395 rooted in POM on which zooplankton depends and a benthic pathway supplying benthic
396 suspension feeders.

397 Hierarchical clustering performed on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values illustrated that the trophic
398 network of the EEC at the global scale could be sub-divided into 6 trophic groups, from POM
399 to fishes and cephalopods (Fig. 2). Group 1 (mean $\delta^{15}\text{N} \pm \text{SD} = 7.55 \pm 2.35$; mean $\delta^{13}\text{C} \pm \text{SD}$
400 = -21.53 ± 1.32) corresponded to POM. Two groups of primary consumers could be
401 distinguished: a pelagic one, Group 2 ($\delta^{15}\text{N} = 9.96 \pm 1.48$; $\delta^{13}\text{C} = -20.77 \pm 1.14$), mainly
402 composed of copepods (detailed about the taxa included in this group and in the following can
403 be found in Fig. 2 and Table 1) and a benthic one, Group 3 ($\delta^{15}\text{N} = 8.81 \pm 0.88$; $\delta^{13}\text{C} = -17.75$
404 ± 0.75), composed of benthic suspension feeders.

405 $\delta^{15}\text{N}$ values allowed further discrimination of organisms with a TL around 3 and two
406 groups of secondary consumers could be distinguished: a pelagic one, Group 4, with low $\delta^{13}\text{C}$
407 values (-18.14 ± 1.34) and a benthic one, Group 5, exhibiting $\delta^{13}\text{C}$ values ($\delta^{13}\text{C} \pm \text{SD} =$
408 -16.46 ± 0.85) close to those of suspension feeders. Group 4 could be further sub-divided into
409 three sub-groups: i) sub-group 4.1 mainly composed of carnivorous zooplankton and a
410 zooplanktivorous fish ; ii) sub-group 4.2 formed by a mix of small zooplanktivorous pelagic
411 fishes, crabs and benthic fishes and iii) sub-group 4.3 characterized by pelagic fishes. The
412 group of benthic secondary consumers, Group 5, mostly gathered elasmobranchs, flatfishes,
413 and crustaceans.

414 Finally, a group of tertiary consumers, Group 6, with a TL around 4 was located at the
415 interface between the pelagic and the benthic pathway (mean $\delta^{13}\text{C} \pm \text{SD} = -17.08 \pm 0.85$). It
416 could be sub-divided into two sub-groups: sub-group 6.1 formed by a mix of benthic and
417 demersal fishes sub-group 6.2 mainly composed of large demersal fishes and cephalopods.

418 Dependency of the groups of upper consumers (4 to 6) on the pelagic and benthic
419 trophic pathway as determined from the limits of the ranges of isotopic ratios expected for the
420 trophic transfer of pelagic and benthic organic matter (dashed lines in Fig. 2) was confirmed
421 by the estimates of pelagic and benthic carbon contributions to upper consumers' diet by the
422 two-source mixing model: Group 4 belonged to the pelagic pathway with an average pelagic
423 contribution to consumers' diet of 0.69, whereas Group 5 depended on the benthic pathway
424 with an average benthic contribution of 0.76 and Group 6 depended on both pathways with an
425 average contribution of pelagic and benthic carbon of 0.59 and 0.41, respectively.

427 3.2. Local-scale trophic network structure in the eastern English Channel

428 3.2.1. Discrete gradient approach

429 The trophic structure of upper consumers was altered in the shallow depth stratum (0-
430 20m) compared to deeper strata (20-38m or 38-79m) and the global scale. Firstly, sub-group
431 4.2, mostly characterized by small planktivorous pelagic fishes, and group 5, comprising
432 flatfishes and elasmobranchs, merged into a new group (Fig. 3A and S2). This was mostly due
433 to species from sub-group 4.2, notably dragonet *Callionymus lyra*, pilchard *Sardinus*
434 *pilchardus* and herring *Clupea harengus*, that were enriched in ^{13}C compared to deeper strata
435 and the global scale. As a result, these species were positioned in the benthic pathway
436 together with flatfishes in shallow waters (Fig. 3A) whereas they preferentially preyed upon
437 pelagic sources of carbon in deeper areas (Fig.3B). Results of the two-source mixing model
438 confirmed this pattern. The benthic contribution to diet of *C. lyra*, *C. harengus* and *S.*

439 *pilchardus* decreased from 0.86, 0.75, and 0.75, respectively, in the 0-20m stratum to 0.35,
440 0.08, and 0.34, respectively, in the 20-38m stratum (Table 1 and Fig.4B). $\delta^{15}\text{N}$ values
441 confirmed that in the shallowest stratum pelagic species were able to feed on the benthic
442 pathway. The mean $\delta^{15}\text{N}$ ratio of *C. harengus* was indeed 1.5‰ lower in the 0-20m stratum
443 than in the 20-38m stratum (Fig.4A), probably because the base of the benthic pathway
444 (defined here by suspension-feeding bivalves; mean $\delta^{15}\text{N}$ of 8.7‰) had a lower $\delta^{15}\text{N}$ than the
445 base of the pelagic pathway (defined by copepods; mean $\delta^{15}\text{N}$ of 10.3‰).

446 Secondly, contrary to small pelagics such as *S. pilchardus* and *C. harengus*, pelagic
447 species from sub-group 4.3, such as mackerel *Scomber scombrus* or horse mackerel
448 *Trachurus trachurus*, confirmed their pelagic affinity by staying in the pelagic pathway even
449 in the shallow stratum (Fig. 3A and S2) where they either formed a distinct group (*S.*
450 *scombrus*) or clustered with large demersal fishes of sub-group 6.2 (*T. trachurus*). The
451 benthic contribution to their diet varied between 0.1 and 0.2 whatever the depth stratum
452 (Table 1 and Fig.4B).

453 Thirdly, it is interesting to note that the benthic contribution to the diet of most species
454 closely related to the bottom (flatfishes and rays in group 5 and Gobidae in sub-group 6.1)
455 increased with increasing depth (Table 1 and Fig.4B). This, together with the translation of
456 small pelagics towards the benthic pathway, confirmed that, in shallow waters, both pelagic
457 and benthic carbon sources are accessible to any species whatever its water column position
458 because of physical proximity. In contrast, in deeper areas, physical decoupling is such that
459 species access to carbon sources according to their water column position. For example, in the
460 0-20m stratum, plaice *Pleuronectes platessa* and dab *Limanda limanda* (group 5) lay at the
461 intersection between the pelagic and the benthic trophic pathway (see dotted lines in Fig. 3;
462 benthic contribution to diet of 0.57 and 0.60, respectively; Table 1 and Fig.4B), whereas in
463 the 20-38m stratum, they preferentially preyed upon benthic carbon sources (benthic

464 contribution of 0.77 and 0.81, respectively; Table 1 and Fig.4B). Another example is
 465 thornback ray *Raja clavata* (group 5), the benthic contribution to its diet increasing constantly
 466 with depth (0-20m: 0.62; 20-38m: 0.92; 38-79m: 0.99; Table1 and Fig.4B).

468 3.2.2 Continuous gradient approach

469 An inshore-offshore gradient in upper consumers' $\delta^{15}\text{N}$ values was evidenced by
 470 generalized least squares modelling. The mean of $\delta^{15}\text{N}$ values decreased significantly with
 471 increasing depth (slope = -0.0109 ; $F_{771}^1 = 7.33$, $p = 0.0069$) (Fig. 5A). In contrast, their
 472 variance increased significantly with depth according to an exponential function (
 473 variance = $1.106 \exp(0.0087 \text{ depth})$; $\chi_1^2 = 24.40$, $p < 0.0001$), so that the observed range of
 474 $\delta^{15}\text{N}$ values was larger offshore. An inshore-offshore seaward gradient was also found in
 475 upper consumers' $\delta^{13}\text{C}$ values. The mean decreased slightly, but non-significantly, as depth
 476 increased (slope = -0.0003 ; $F_{771}^1 = 0.01$, $p = 0.9114$). However, contrary to $\delta^{15}\text{N}$, the range of
 477 $\delta^{13}\text{C}$ values decreased offshore (Fig. 5B) as evidenced by a significant decrease in variance
 478 according to a power function of depth (variance = $3.0786 \text{ depth}^{-0.1286}$; $\chi_1^2 = 6.34$, $p =$
 479 0.0118).

480 Results of the theoretical two-source mixing model showed that the inshore-offshore
 481 gradient observed in upper consumers' $\delta^{13}\text{C}$ ratios could be linked to diminishing pelagic-
 482 benthic coupling as depth increases (Fig. 6). More precisely, the decrease in variance of the
 483 benthic contribution α to consumers' diet with increasing depth resulted in a unimodal
 484 distribution of α values with large variations in the consumer community at shallow depth that
 485 turned roughly bimodal with smaller variations as depth increased (Fig. 6A-C). Based on the
 486 distribution of the $\delta^{13}\text{C}$ values of benthic and pelagic carbon sources (Fig. 6D), resulting
 487 consumers' $\delta^{13}\text{C}$ values had a roughly constant mean (Fig. 6E) and a decreasing variance (Fig.

488 6F) with increasing depth. This theoretically-predicted gradient in upper consumers' $\delta^{13}\text{C}$
489 ratios corresponded qualitatively to the pattern observed in our data. This is consistent with
490 the hypothesis that the observed inshore-offshore gradient in upper-consumers' $\delta^{13}\text{C}$ values
491 detected by generalized least squares modelling is related to stronger pelagic-benthic coupling
492 in shallow coastal areas.

4. Discussion

495
496 Our results revealed that the food web of the EEC forms a continuum of four TLs with
497 trophic groups spread across two trophic pathways relying on pelagic and benthic carbon
498 sources, respectively. Besides this classical global-scale structure for a temperate coastal
499 ecosystem, we found an inshore-offshore gradient in the trophic network structure due to the
500 reorganization of the upper consumers relative to the two trophic pathways. More precisely,
501 the pelagic-benthic coupling was stronger in shallow waters where upper consumers, mostly
502 fishes, could access and use both pelagic and benthic carbon sources irrespective of their
503 water column position preference.

4.1. Global-scale trophic network structure in the eastern English Channel

506 The global-scale structure of the trophic network in the EEC was comparable with that
507 observed in other temperate coastal ecosystems although the taxonomic composition of
508 communities may differ. This suggests that some general principle may apply despite
509 potentially varying forcing factors. In the Bay of Biscay (west coast of France), three trophic
510 groups of primary and secondary consumers, similar to those in the EEC, have been identified
511 on the basis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios (Le Loc'h et al., 2008): zooplankton plus suprabenthos,
512 benthic suspension feeders, surface-deposit feeders, and a cluster of fishes, cnidarians and

513 polychaetes. Upper consumers were also organized in three to four trophic groups depending
514 on their TL and according to their feeding affinity, either pelagic, benthic or omnivores.
515 Similarly, on the continental shelf of south-eastern Australia, five groups of fishes were
516 identified, roughly comparable with those reported in this study (Davenport and Bax, 2002):
517 piscivorous predators, benthic-feeding sharks and rays, fishes preying on both benthic and
518 pelagic organisms, and two groups of pelagic feeders. This kind of structure was also
519 observed in the Middle Atlantic Bight on the eastern continental shelf of the United States
520 (Woodland and Secor, 2013). Upper consumers are thus organized in similar
521 functional/trophic groups in these ecosystems presenting significant pelagic-benthic coupling.

522 The existence of a pelagic and a benthic trophic pathway is a general feature in aquatic
523 ecosystems (Davenport and Bax, 2002; Le Loc'h et al., 2008; Syväranta et al., 2011).
524 Generally, the segregation between the pelagic and the benthic trophic pathway becomes
525 blurred when moving up the food web (higher consumers being at intermediate $\delta^{13}\text{C}$ values),
526 probably due to an increase in foraging area with consumers' size that results in more
527 connected food webs as the size, and thus the trophic level, of consumers increases. This
528 inherent structuring of aquatic ecosystems confers stability to their food webs (Rooney et al.,
529 2006). Also, the number of TLs identified at the global scale in the EEC (4) seems to be
530 common in marine food webs (e.g. Davenport and Bax, 2002; Le Loc'h et al., 2008;
531 Woodland and Secor, 2013). Even if some trophic networks may reach up to eight TLs, the
532 trophic scale of the EEC was indeed coherent with the average food chain length of roughly
533 four TLs found in marine food webs, be it in estuarine, coastal or pelagic systems (Vander
534 Zanden and Fetzer, 2007). It appears therefore, that the global-scale trophic network of the
535 EEC is mostly structured by trophic pathways and carbon sources, as highlighted by the large
536 range of $\delta^{13}\text{C}$ ratios, rather than by TLs. This pattern is expected in continental shelf seas
537 where predators share diverse food resources and where pelagic-benthic coupling is stronger

538 than in deeper oceanic ecosystems. In contrast, pelagic systems should be strongly structured
539 by TLs due to size-dependent predation. Although TLs were clearly distinct at the base of the
540 food web, they become more unclear higher in the food web (Fig. 2). Upper consumers' $\delta^{15}\text{N}$
541 ratios suggest that the fish assemblage crosses two TLs, meaning that some fishes are at least
542 partially piscivorous and could be defined as top-predators. The narrow ranges of $\delta^{15}\text{N}$ and
543 $\delta^{13}\text{C}$ values expressed by the five groups of secondary and tertiary consumers indicated that
544 many species share common trophic position and uptake carbon in relatively similar
545 proportions in the benthic and the pelagic trophic pathway. The positioning of organisms
546 along a continuum of trophic levels rather than in discrete ones may be considered as a sign of
547 prevalent omnivory (France et al., 1998), which is in line with the idea that species located
548 high in the food chain tend to become omnivorous, i.e., rely on resources exhibiting a large
549 range of trophic levels (Polis and Strong, 1996). The large size of top-predators promotes
550 their omnivory as they can prey on a larger range of prey sizes spread across the trophic
551 spectrum. This is consistent with the general finding of a slower increase of the predator-prey
552 mass ratio as predator size increases, which results in a slower rate of increase in trophic level
553 with body size and a lower efficiency of trophic transfer at higher trophic levels and larger
554 body sizes (Barnes et al. 2010).

556 *4.2. Reorganization of the trophic network structure along an inshore-offshore gradient*

557 While the mean of upper consumers' $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values remained approximately
558 constant with depth (non-significant change for $\delta^{13}\text{C}$ and significant change with a shallow
559 slope of -0.0109 for $\delta^{15}\text{N}$), we detected of an inshore-offshore gradient in their variance with
560 depth. The variance of upper consumers' $\delta^{15}\text{N}$ values increased significantly with increasing
561 depth, notably with rather low values of $\delta^{15}\text{N}$ (down to 10‰) for consumers located in deep
562 areas, whereas the variance of $\delta^{13}\text{C}$ ratios increased as depth decreased, with $\delta^{13}\text{C}$ values

563 down to -22‰ for some consumers in shallow areas, a carbon ratio that is usually observed
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2 564 for primary producers such as phytoplankton (France, 1995). The similarity with the pattern
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4 565 of $\delta^{13}\text{C}$ ratios with depth predicted by our theoretical two-source mixing model suggests that
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6
7 566 this feature was consistent with the hypothesis of a stronger pelagic-benthic coupling in
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10 567 shallow coastal areas that translates into wider variations of the contribution of pelagic and
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12 568 benthic sources of carbon to upper consumers' diet whatever their initial affinity and/or water
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14 569 column position.

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17 570 In parallel, the discrete approach showed a reorganization of the upper trophic levels
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19 571 of the food web in terms of the carbon sources utilized from coastal to offshore areas. This
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21
22 572 again can be interpreted as a stronger pelagic-benthic coupling in coastal areas, which resulted
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24 573 in a larger range of $\delta^{13}\text{C}$ values. More precisely, in coastal areas, benthic carbon sources were
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26 574 accessible to pelagic fishes such as *S. pilchardus* and *C. harengus* and, reciprocally, pelagic
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29 575 carbon sources were accessible to benthic species such as flatfishes and elasmobranchs.
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31 576 Basically, as depth decreased, diel vertical migrations of zooplankton (Hays et al., 2003) and
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33
34 577 epibenthic fauna (annelids, decapods and fishes; Vallet and Dauvin 2004; Woodland and
35
36 578 Seccor, 2013) in the water column as well as associated vertical migration of pelagic fishes
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38
39 579 following their prey (Casini et al., 2004) would facilitate the pelagic-benthic coupling. It is
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41 580 interesting to note that this effect of depth on the strength of the pelagic-benthic coupling has
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43
44 581 a parallel in some deep water systems off the continental slope (e.g. northeast Atlantic deep
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46 582 waters of the Rockall-Porcupine continental margin off northwest UK and Ireland). In these
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48
49 583 systems, the diel vertical migration of pelagic preys impinges on the benthic boundary layer
50
51 584 fauna of the slope during daytime. This allows demersal benthic-pelagic feeders to access
52
53 585 pelagic resources between 500 and 1000m but not deeper as diel vertical migration is limited
54
55
56 586 to the 0-1000m layer (Mauchline and Gordon, 1991; Trueman et al., 2014).

587 Taken together, these results suggest that marine shelf ecosystems such as the EEC
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2 588 can exhibit an inshore-offshore gradient in their trophic network structure underlain by a
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4 589 gradient in pelagic-benthic coupling strength. In coastal areas, the food web relied on a large
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6
7 590 basis in terms of carbon sources (large range of $\delta^{13}\text{C}$ values) and had a reduced number of
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10 591 TLs (small range of $\delta^{15}\text{N}$ values) probably due to the fact that predators shared diverse food
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12 592 resources irrespective of their body size or compartment of origin (pelagic or benthic). In
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14 593 contrast, in offshore areas, the trophic network depended mainly on pelagic sources of carbon
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16 594 (reduced range of $\delta^{13}\text{C}$ values) and was more strongly structured by TLs (large range of $\delta^{15}\text{N}$
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18
19 595 values), most likely because of a lower diversity of food resources being accessible. This may
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21
22 596 also be related to the fact that individuals feed on planktonic resources according to their body
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24 597 size (Blanchard et al. 2009; Woodland and Secor, 2013), since in pelagic size-structured
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26 598 systems smaller preys have a larger per unit biomass production rate (Heckmann et al., 2012).

29 599 Adaptive foraging could be hypothesized as the proximal process responsible for the
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31 600 reorganization of the food web along the inshore-offshore gradient. It is the ability of a
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33
34 601 species to adapt its foraging efforts to variability in its trophic environment, i.e., changes in
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36 602 prey abundance or prey specific composition. Notably, adaptive foraging is expected to favor
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39 603 the use of resources closer to the base of the food web (Heckmann et al., 2012), improve
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41 604 food-web stability (Uchida et al., 2007; Loeuille, 2010; Heckmann et al., 2012), and enhance
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43 605 food-web resilience and resistance against perturbations (Valdovinos et al., 2010), which
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46 606 could be an important feature in relatively perturbed coastal areas such as those in the EEC
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48
49 607 (Carpentier et al., 2009). Predator species that adapt their foraging behaviour are able to prey
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51 608 on lower trophic levels, and take advantage of trophic resources directly accessible and
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53 609 optimal without hunting high in the food chain. They focus on the most profitable prey and
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56 610 release unprofitable ones from predation (Heckmann et al., 2012). In coastal areas of the EEC,
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58 611 benthic food resources such as primary consumers are abundant and diversified (Foveau et al.,
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612 2013). The large range of their body sizes, their specific richness and their accessibility due to
1 shallowness may induce an adaptive change in the foraging behavior of some species that
2 613 shallowness may induce an adaptive change in the foraging behavior of some species that
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4 614 would target benthic preys in shallow coastal areas even if they have pelagic affinities.
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7 615 Contrarily, in deep offshore areas, only planktonic resources are available to pelagic upper
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10 616 consumers because of the distance to the seabed.

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12 617 The case of herring illustrates pretty well the changes observed in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios
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14 618 according to depth. In the intermediate depth stratum (20-38m), this species was located in the
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17 619 pelagic pathway ($\alpha=0.08$; Fig. 4) at a relatively high trophic level (TL=3.7; Fig. 3). In
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19 620 contrast, in the shallow depth stratum (0-20m), this species took advantage of both the pelagic
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21
22 621 and the benthic pathway ($\alpha=0.75$; Fig. 4), and occupied a lower trophic level (3.2; Fig. 3 and
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24 622 4). Even if herring does not express an ontogenetic diet shift and is identified as
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26 623 zooplanktivorous during its entire lifespan, it exhibits plasticity in feeding behaviour so that,
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29 624 according to prey availability, accessibility and profitability, it can exploit nekto-benthos and
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32 625 zoobenthos in addition to zooplankton (Casini et al., 2004). The low TL and strong
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34 626 contribution of benthic carbon to its diet are thus evidences that this species fed on benthic
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36 627 resources directly accessible in shallow coastal areas. The same type of pattern was observed
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39 628 by Jennings et al. (1997) in heterogeneous Mediterranean reefs environment where they found
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41 629 that a given fish species may present different trophic levels at different sites (deviations of
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43 630 $\sim 2\%$ in $\delta^{15}\text{N}$) and that the benthic pathway is an important carbon source even for fishes that
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45
46 631 are known to be pelagic feeders such as Atherinids. For fishes from the North Carolina
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49 632 continental shelf as well, Thomas and Cahoon (1993) found that isotopic ratios varied with
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51 633 location, fishes feeding on food items according to their availability in the environment rather
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53 634 than preying selectively. We hypothesize that many fish species that live in heterogeneous
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56 635 environments such as shelf seas are able to change their trophic position within food webs in
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58 636 response to local conditions, especially food resources availability. This ability of using
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637 alternative food resources from different trophic levels is defined by Darnell (1961) as one of
638 the main processes improving populations' stability in complex natural communities and
639 plasticity in feeding strategy would allow fishes to respond to local variations in food
640 availability.

641

642 *4.3. Strength and limitations of the study*

643 This study provides one of the largest, if not the largest, sampling plan of food web
644 structure in temperate coastal ecosystems where the implications of spatial scale and
645 variations along an environmental gradient are treated explicitly. A partly similar study by
646 Woodland and Secor (2013) extended over roughly 360 km² whereas the present study covers
647 nearly 35 000 km². At such scale, it is of course difficult to balance sampling effort across
648 space and species, especially when species diversity is high. Combined with the fact that most
649 of our samples were collected by bottom trawling, it resulted that small epibenthic fauna was
650 under-represented in and that infauna was almost absent from our sampling. However, given
651 that we sampled a high diversity of organisms in the EEC, from epibenthic macrofauna, to
652 phytoplankton and zooplankton, to large predatory fishes, we are quite confident that our
653 findings are representative of the trophic structuring of macro-organisms living on the seabed
654 and in the water column. Furthermore, the fine taxonomic resolution of our study, i.e. at the
655 species level in most cases, and the correction for spatial variation in stable isotopic ratios of
656 the trophic baseline, which is rare at such spatial scale (but see Jennings and Warr, 2003a,b or
657 Barnes et al., 2009), ensures unbiased estimates of TLs and contributions of carbon sources.
658 This may not be the case in food web studies with coarser taxonomic resolution (Hall and
659 Raffaelli, 1993) or neglecting spatial variation in baseline isotopic ratios.

660 Although our study provides a snapshot in time, isotopic imprint of muscle tissue is
661 representative of diet isotopic composition at a timescale of several months (Sweeting et al.,

662 2005; Barnes et al., 2009) and thus should provide a picture of the food web that holds at a
663 seasonal timescale at least. In this context, organisms' movements, notably in highly
664 migratory fishes, can be a source of potential error and we are aware that baseline corrections
665 for these species could be debatable. Fish movements can be of three kinds: movements
666 within the home range, migrations due to ontogenetic shifts, and spawning migrations
667 (Pittman and McAlpine, 2003). Regarding home range and foraging area, they usually scale
668 with body size in marine fishes but, although fishes are known as mobile species, they do not
669 exceed the order of 100 km² (e.g. for cod) and are linked to species' habitat (Pittman and Mac
670 Alpine, 2003). Given that, first, we considered a spatial scale that is roughly 350 times higher
671 than the home range of the biggest fishes sampled and, second, we focused on changes in
672 food web structure with depth, a very good proxy of habitat in continental shelf seas such as
673 the EEC (Vaz et al, 2007; Martin et al., 2010), we do not expect fish movement within their
674 home range (i.e. excluding migrations) to affect our results strongly. Regarding ontogenic
675 migration, given that our sampling scheme avoided nursery areas where are located juvenile
676 fish and targeted mostly adult fishes, our results on the inshore-offshore gradient in the
677 pelagic-benthic coupling should also not be influenced strongly by migrations related to the
678 processes of ontogenetic shifts. With respect to spawning migration, the reproductive season
679 of most fish species in the EEC spread from winter to summer (Carpentier et al., 2009) so that
680 spawning migrations should not affect deeply the composition of the fish assemblage as we
681 observed it in October.

682 Of course, even within a species' home range, individuals may feed at a given location
683 and be captured at another one. Likewise, the presence in our samples of non-resident
684 individuals originating from outside the EEC because of any type of migration cannot be
685 excluded. In both cases, the correction for spatial variation in baseline isotopic ratios may be
686 partly wrong. The maximum amplitude of variation in baseline ratios is roughly of 1.5‰ for

687 both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ be it within the eastern English Channel (home range; Fig. S1) or between
688 the EEC and the main areas of origin of potential migrating non-residents, namely the western
689 English Channel and the south North Sea (Jennings and Warr, 2003; Barnes et al. 2009). This
690 would generate a maximum bias of roughly ± 0.4 for TLs and ± 0.3 for the contribution of
691 benthic carbon to consumers' diet. As non-residents are most likely large predatory fish, this
692 may contribute to the blurring of the food web at high trophic levels. However, because bias
693 will be most often smaller than these maximum values and because it should be distributed
694 randomly across individuals, we believe that fish movement within their home range and fish
695 migration should not affect our qualitative results. Most importantly, the fact remains that
696 despite the potential noise generated by migrations and movements we found significant
697 variation in the structure of the EEC food web along the inshore-offshore gradient.

699 Conclusion

700 Spatial variability along environmental gradients has been rarely considered in studies that
701 have aimed at describing food web structure (but see Woodland and Secor, 2013). The
702 structure of the food web from the EEC, characterized by two main trophic pathways and four
703 trophic levels, seems relatively conventional for comparable marine ecosystems. The main
704 originality, which we believe could be generalized to most continental shelf seas, lies in the
705 particular depth structure of the EEC that confers specific properties to its food web, notably
706 an inshore-offshore gradient in its structure. More specifically our results highlighted that the
707 pelagic-benthic coupling is stronger in shallow coastal areas due to some upper consumers
708 that exhibit foraging plasticity and can extend their trophic niche to various sources of carbon
709 presumably according to the availability of prey. Given that the observed structure of food
710 webs can be highly variable depending on the resolution considered, our results suggest that

1 711 accounting for spatial variability (from local to regional scale as recommended by Ings et al.,
2 712 2009) is crucial to better understand trophic processes at play.

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4 713

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914 Figure and table captions

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2 915 Fig. 1 Map of the eastern English Channel (EEC) presenting the three depth strata (shades of
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5 916 grey) used for the discrete gradient approach and the geographical position of the sampling
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7 917 sites (filled circles).

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9 918 Fig. 2 Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for all the studied taxa. Circles (Part1) correspond to the
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12 919 results of hierarchical cluster analysis (Part2). (in color on the Web and in black-and-white in
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14 920 print)

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16 921 Fig. 3 Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for all the studied taxa in 1st depth stratum (A), 2nd depth
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19 922 stratum (B-), and 3rd depth stratum (C-). Circles correspond to the results of hierarchical
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21
22 923 cluster analysis (Appendix A). Correspondence for colors is the same as in Fig.2. (in color on
23
24 924 the Web and in black-and-white in print)

25
26 925 Fig. 4 Trophic level and contribution of benthic carbon to diet for secondary and tertiary
27
28
29 926 consumers in the 3 depth strata. A. Trophic level. B. Contribution of benthic carbon to diet.
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31 927 Dots are average values for 0-20m (black), 20-38m (gray) and 38-79m (white) stratum and
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33
34 928 surrounding black lines denote associated standard errors. Species were ordered according to
35
36 929 the contribution of benthic carbon to their diet in the 0-20m stratum.

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38
39 930 Fig. 5 Relationships between depth and isotopic ratios for secondary and tertiary consumers.
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41 931 A- $\delta^{15}\text{N}$ and B- $\delta^{13}\text{C}$. Quantile regressions (0.5: solid line; 0.05 and 0.95: dotted lines) are
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43
44 932 shown. The boxes represent the interquartile range, the line across is the median value, and
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46 933 the whiskers extend to the most extreme data points which are less than 1.5 times the length
47
48
49 934 of the interquartile range The white points show outliers.

50
51 935 Fig. 6 Theoretical inshore-offshore gradient in the $\delta^{13}\text{C}$ ratio of upper consumers resulting
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53 936 from diminishing coupling of the benthic and the pelagic pathway as depth increases. A, B
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55
56 937 and C: Distribution of the proportion of benthic source in consumers diet at increasing depth:
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58 938 10, 40 and 70 m. D. Distribution of the $\delta^{13}\text{C}$ ratio of the benthic and the pelagic source. E.

939 Resulting inshore-offshore gradient in the mean $\delta^{13}\text{C}$ ratio in consumers. F. Resulting inshore-
1
2 940 offshore gradient in the variance of the $\delta^{13}\text{C}$ ratio in consumers.
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4
5 941 Table 1 Names of all the studied species, zones of sampling, number of individuals (n), mean
6
7 942 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (\pm SD), estimated trophic level (TL, $\delta^{15}\text{N}_{\text{base}}=\textit{Aequipecten opercularis}$) and
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9 943 benthic contribution to fish diet (\pm SE). Species were considered in zones when $n>3$,
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11
12 944 otherwise, individuals were included in the community.
13

14 945 Supplementary material
15

16
17 946 Fig.S1. Maps of the isotopic ratios of the trophic baseline *A. opercularis* predicted by kriging
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19 947 from published data. A- $\delta^{15}\text{N}$ and B- $\delta^{13}\text{C}$. Plus signs correspond to sampling sites of this
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22 948 study whereas crosses correspond to sampling sites of the data published by Jennings and
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24 949 Warr (2003) and Barnes et al. (2009). Continuous lines are isolines of isotopic ratios.
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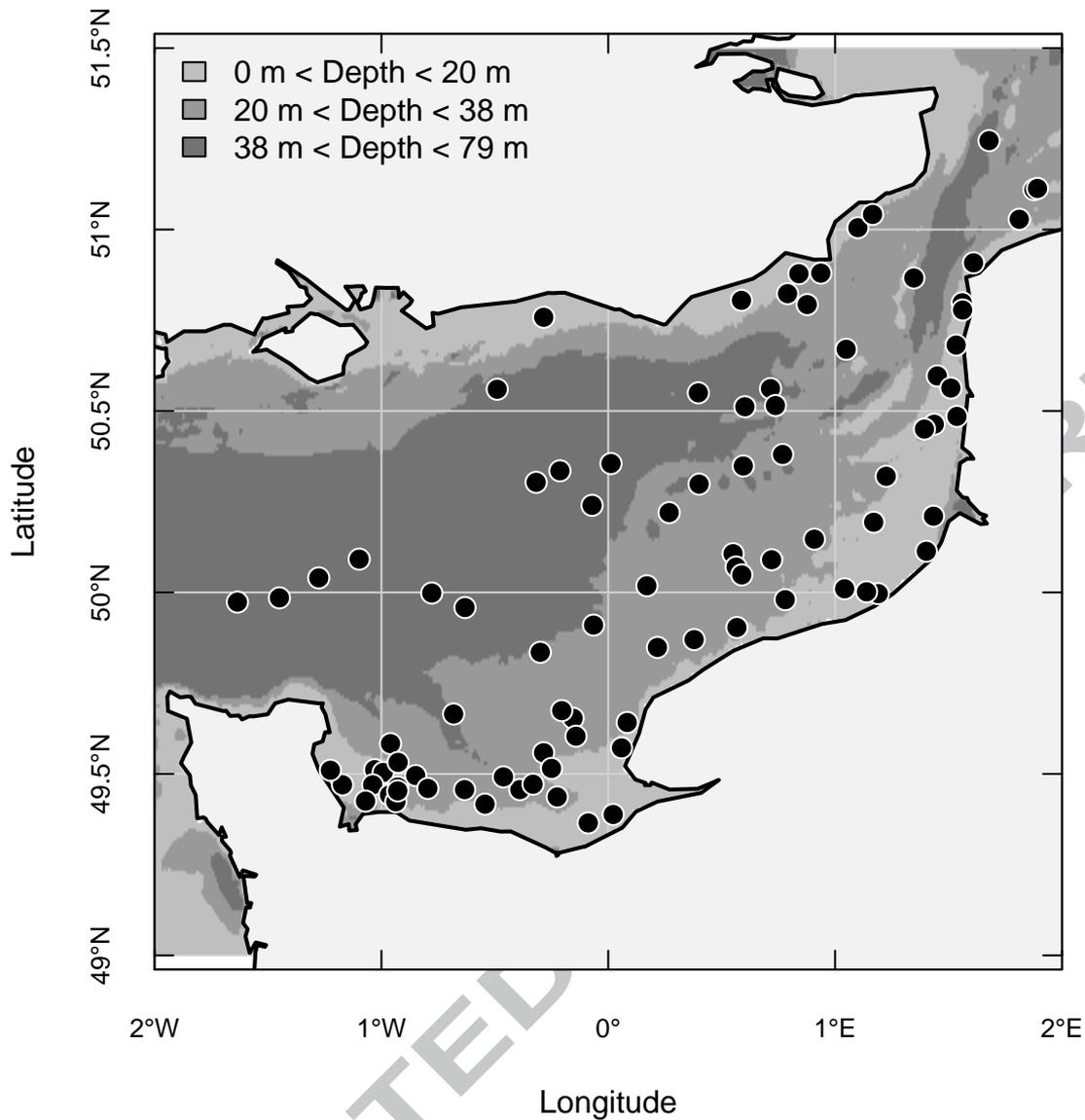
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27 950 Fig.S2. Hierarchical clustering for the three depth strata. A- 1st depth stratum, B- 2nd depth
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29 951 stratum, C- 3rd depth stratum.
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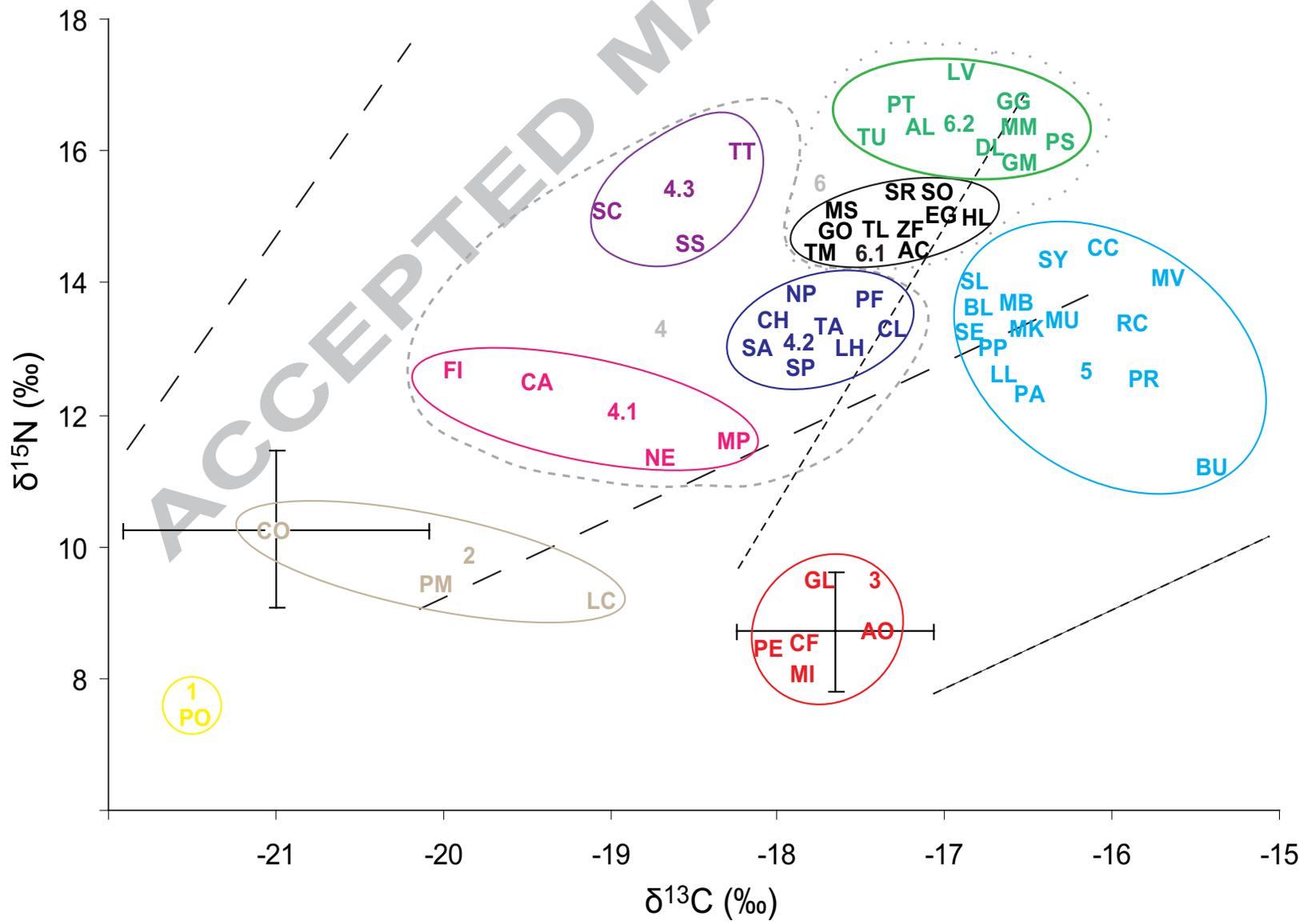
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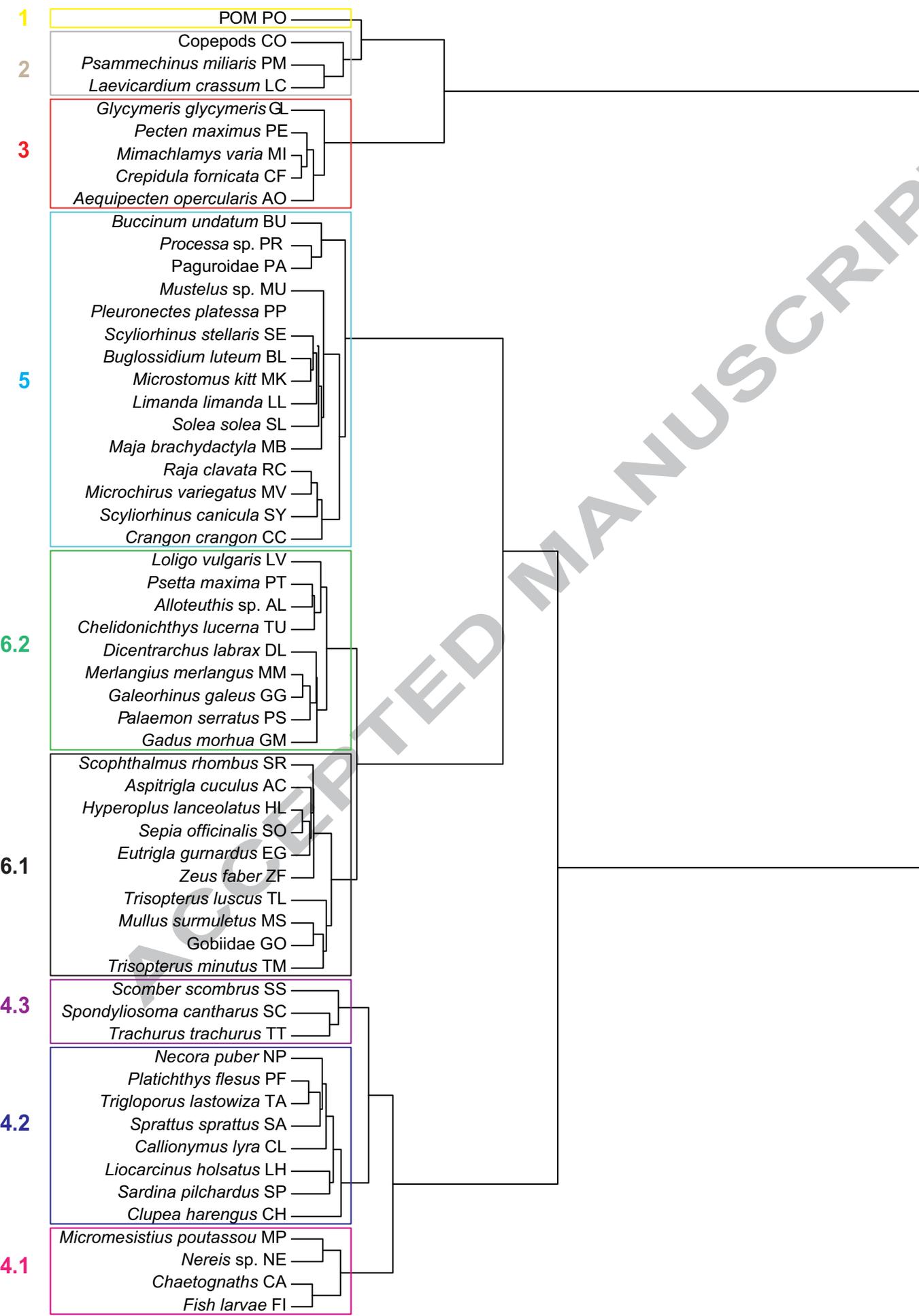
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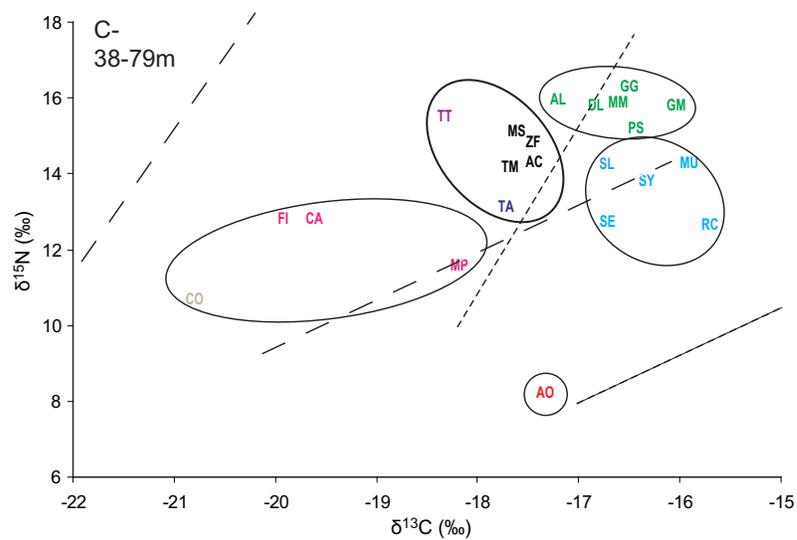
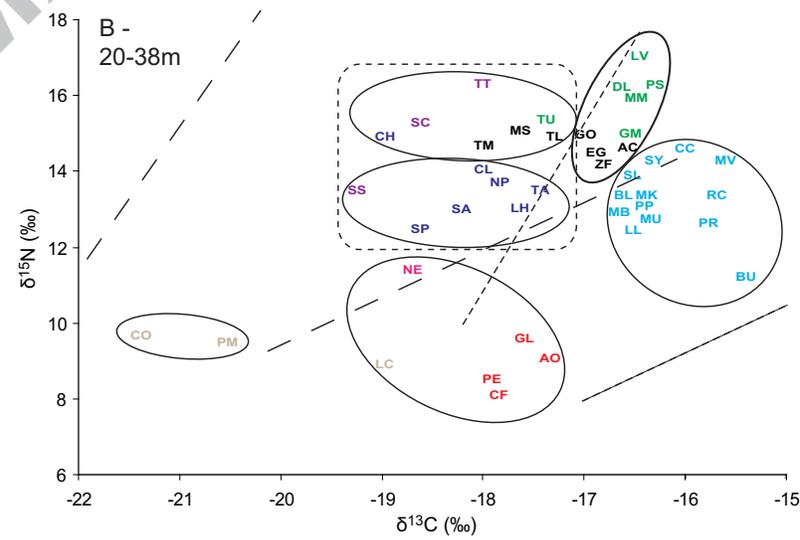
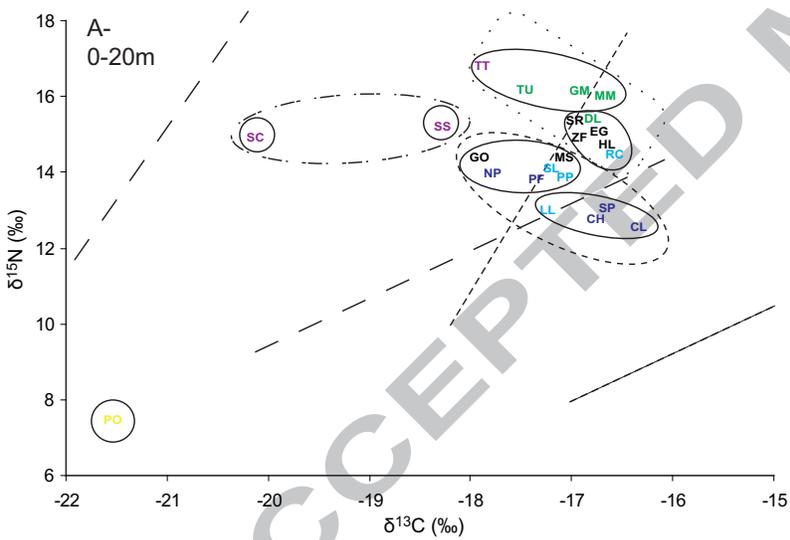
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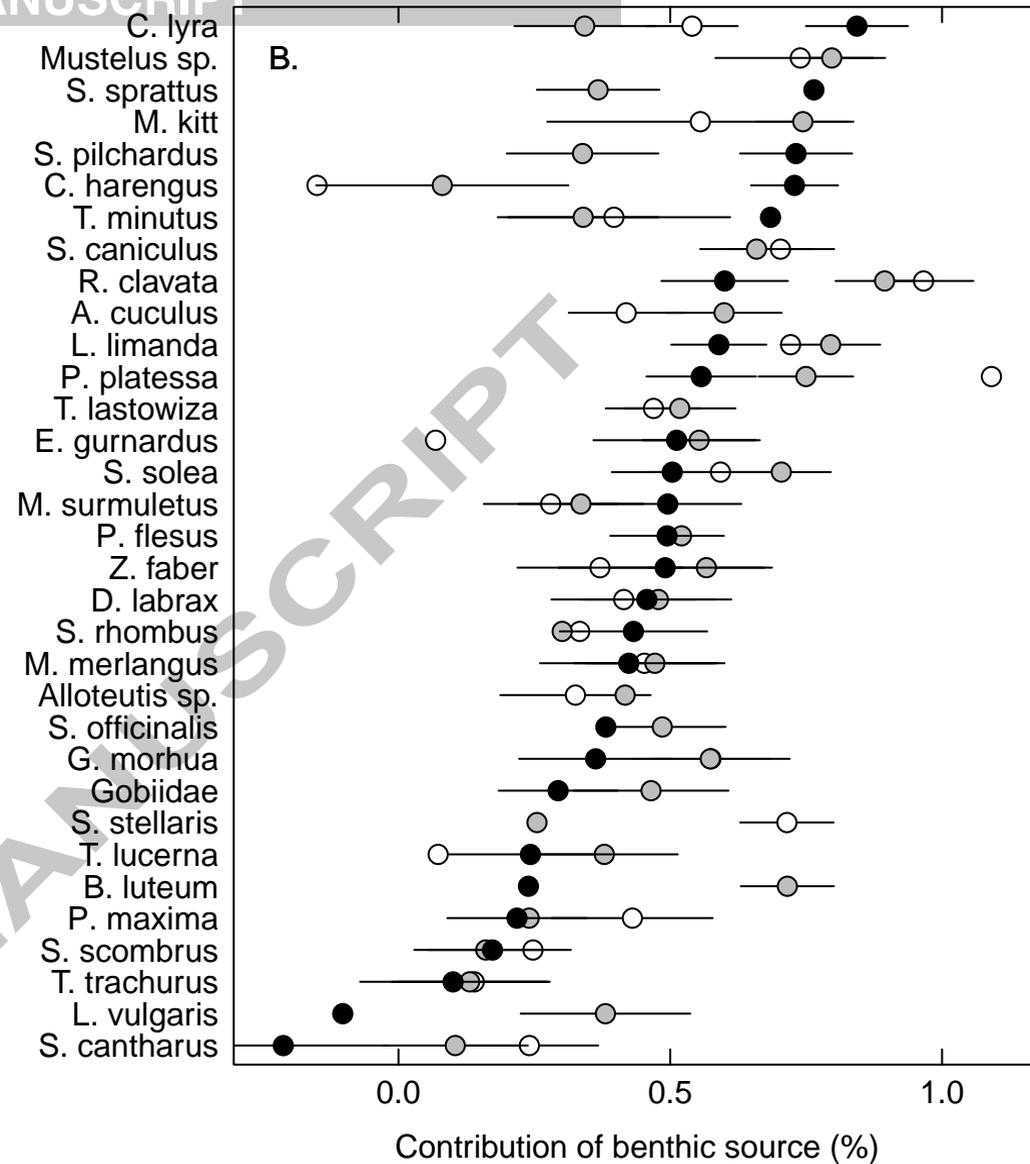
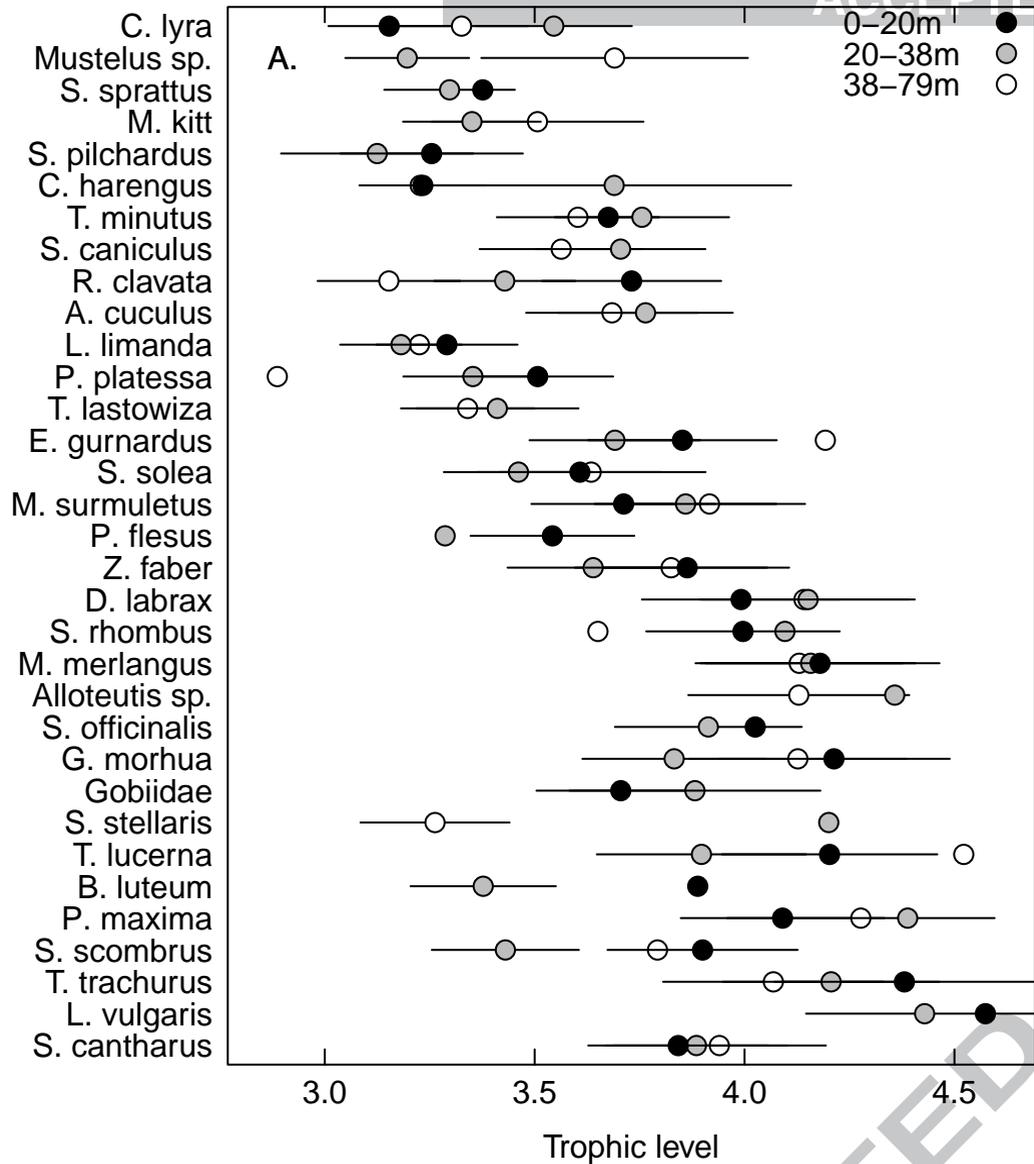


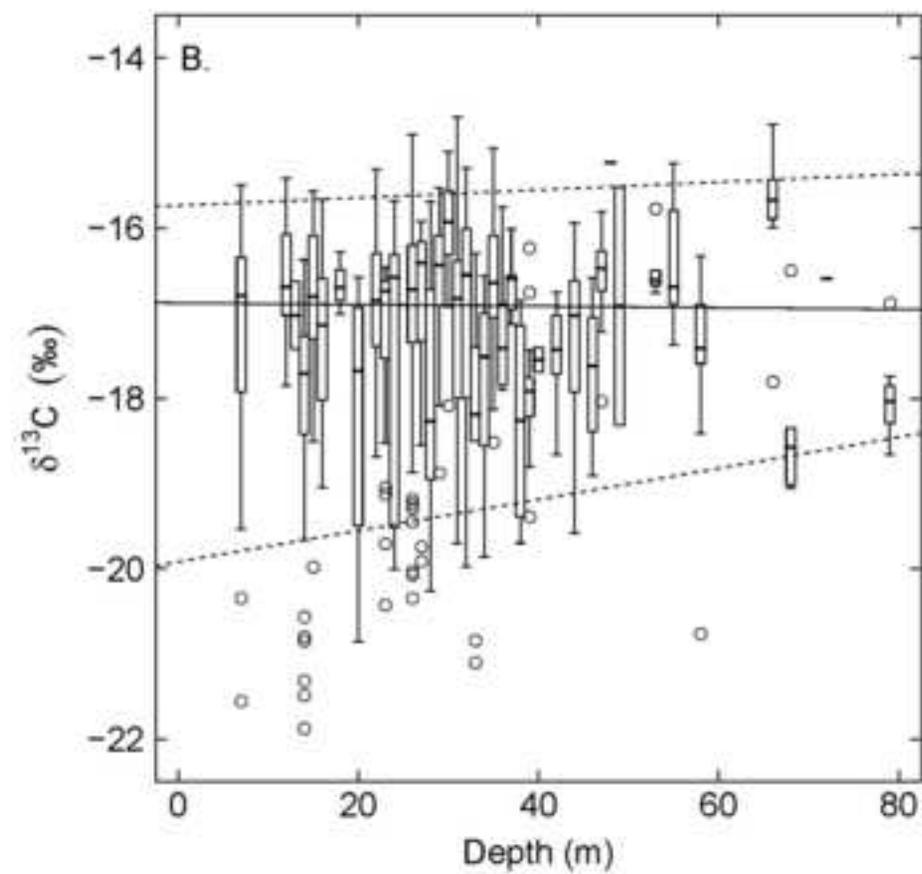
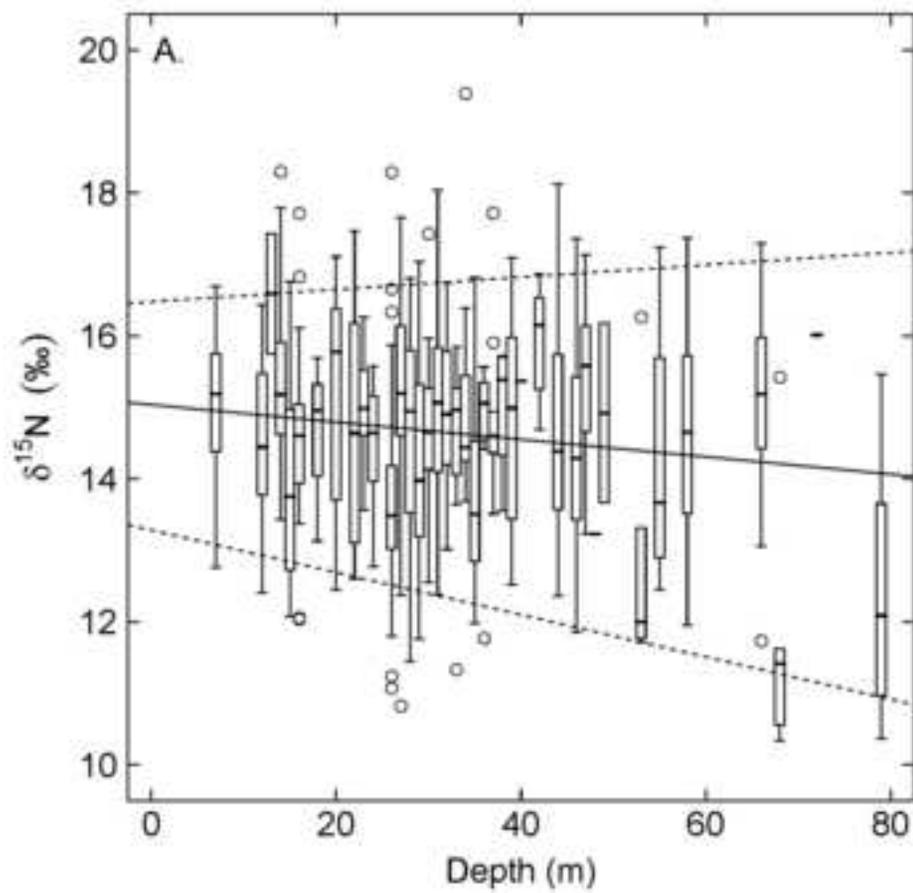


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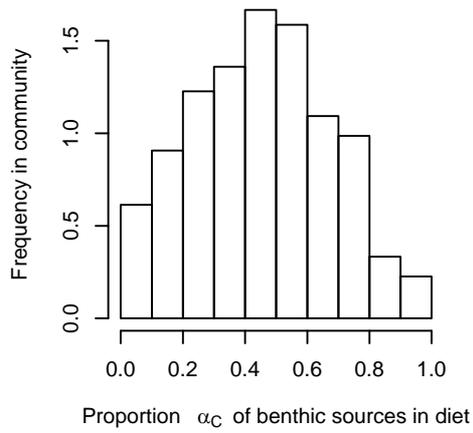




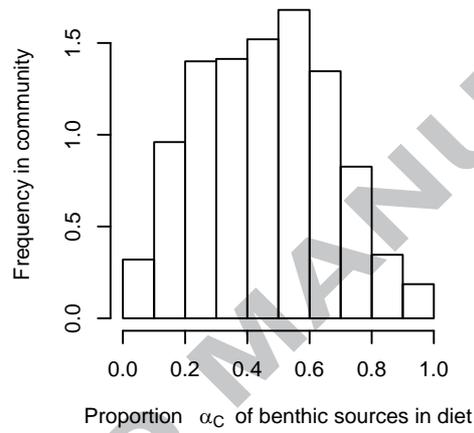




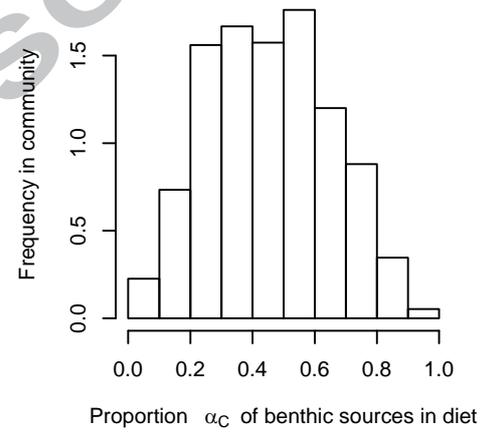
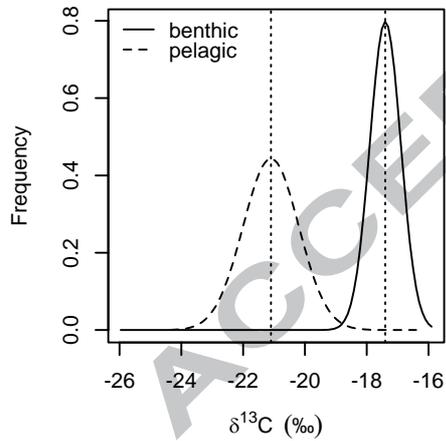
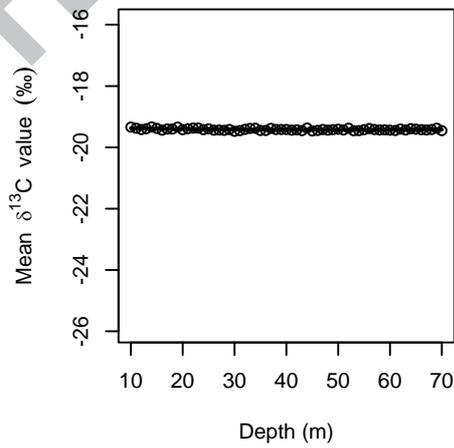
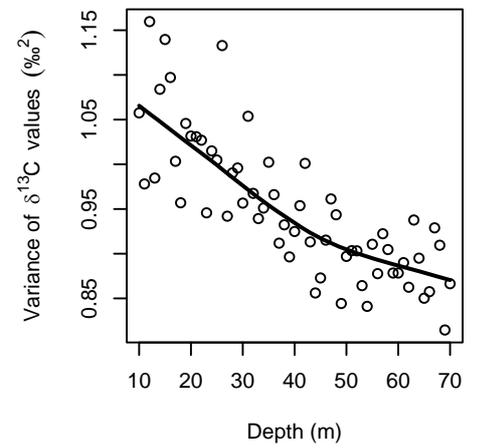
A. 10 m depth



B. 40 m depth



C. 70 m depth

D. Distribution of $\delta^{13}\text{C}$ values in sourcesE. Gradient of $\delta^{13}\text{C}$ in consumersF. Gradient of $\delta^{13}\text{C}$ in consumers

	Code	Zone	n	$\delta^{13}\text{C}$ (‰) \pm SD	$\delta^{15}\text{N}$ (‰) \pm SD	TL \pm SE	Benthic fraction \pm SE
Organic matter sources							
POM	PO	All depths	22	-21.53 \pm 1.32	7.55 \pm 2.35	1.76 \pm 0.16	0.16 \pm 0.10
		0-20m	22	-21.53 \pm 1.32	7.55 \pm 2.35	1.76 \pm 0.16	0.16 \pm 0.10
Zooplankton							
Chaetognaths	CA	All depths	3	-19.46 \pm 0.99	12.70 \pm 0.70	3.28 \pm 0.19	0.12 \pm 0.16
		38-79m	3	-19.46 \pm 0.99	12.70 \pm 0.70	3.28 \pm 0.19	0.12 \pm 0.16
Copepods	CO	All depths	11	-21.07 \pm 0.89	10.28 \pm 1.70	2.56 \pm 0.17	0.00 \pm 0.10
		20-38m	6	-21.43 \pm 0.77	9.68 \pm 1.51	2.28 \pm 0.19	0.01 \pm 0.11
		38-79m	5	-20.64 \pm 0.90	11.00 \pm 1.78	2.67 \pm 0.25	0.06 \pm 0.14
Fish larvae	FI	All depths	4	-20.03 \pm 0.42	12.89 \pm 0.09	3.33 \pm 0.16	-0.02 \pm 0.11
		38-79m	4	-20.03 \pm 0.42	12.89 \pm 0.09	3.33 \pm 0.16	-0.02 \pm 0.11
Crustaceans							
<i>Crangon crangon</i>	CC	All depths	12	-16.05 \pm 1.08	14.57 \pm 0.93	3.83 \pm 0.23	0.69 \pm 0.13
		20-38m	12	-16.05 \pm 1.08	14.57 \pm 0.93	3.83 \pm 0.23	0.69 \pm 0.13
<i>Liocarcinus holsatus</i>	LH	All depths	14	-17.56 \pm 1.46	13.10 \pm 0.99	3.40 \pm 0.18	0.50 \pm 0.12
		20-38m	12	-17.67 \pm 1.54	13.00 \pm 0.99	3.26 \pm 0.17	0.52 \pm 0.13
<i>Maja brachydactyla</i>	MB	All depths	8	-16.54 \pm 1.00	13.66 \pm 0.93	3.56 \pm 0.21	0.66 \pm 0.13
		20-38m	7	-16.58 \pm 1.07	13.43 \pm 0.70	3.38 \pm 0.18	0.72 \pm 0.12
<i>Necora puber</i>	NP	All depths	18	-17.84 \pm 1.19	13.95 \pm 0.69	3.64 \pm 0.20	0.35 \pm 0.12
		0-20m	8	-17.79 \pm 1.37	14.09 \pm 0.65	3.58 \pm 0.19	0.39 \pm 0.15
		20-38m	10	-17.87 \pm 1.11	13.84 \pm 0.74	3.50 \pm 0.19	0.39 \pm 0.12
<i>Palaemon serratus</i>	PS	All depths	7	-16.30 \pm 0.40	15.86 \pm 1.11	4.20 \pm 0.29	0.51 \pm 0.14
		20-38m	4	-16.17 \pm 0.47	16.15 \pm 0.73	4.18 \pm 0.27	0.54 \pm 0.14
		38-79m	3	-16.47 \pm 0.26	15.47 \pm 1.59	3.98 \pm 0.35	0.54 \pm 0.15
<i>Processa</i>	PR	All depths	6	-15.78 \pm 0.42	12.72 \pm 0.34	3.28 \pm 0.16	0.92 \pm 0.09
		20-38m	6	-15.78 \pm 0.42	12.72 \pm 0.34	3.28 \pm 0.16	0.92 \pm 0.09
<i>Paguroidea</i>	PA	All depths	3	-16.49 \pm 0.80	12.44 \pm 0.22	3.20 \pm 0.15	0.80 \pm 0.13
Echinoderms							
<i>Psammechinus miliaris</i>	PM	All depths	5	-20.09 \pm 1.45	9.30 \pm 0.43	2.28 \pm 0.08	0.31 \pm 0.15
		20-38m	5	-20.09 \pm 1.45	9.30 \pm 0.43	2.28 \pm 0.08	0.31 \pm 0.15
Polychaetes							
<i>Nereis</i> sp.	NE	All depths	4	-18.75 \pm 1.31	11.44 \pm 0.52	2.91 \pm 0.14	0.40 \pm 0.16
		20-38m	4	-18.75 \pm 1.31	11.44 \pm 0.52	2.91 \pm 0.14	0.40 \pm 0.16
Molluscs							
<i>Aequipecten opercularis</i>	AO	All depths	19	-17.36 \pm 0.32	8.36 \pm 0.76	2.00 \pm 0.07	1.00 \pm 0.03
		20-38m	6	-17.26 \pm 0.29	9.32 \pm 0.20	2.18 \pm 0.04	0.96 \pm 0.03
		38-79m	6	-17.47 \pm 0.31	8.12 \pm 0.30	1.82 \pm 0.05	1.03 \pm 0.04
<i>Alloteuthis</i> sp.	AL	All depths	8	-17.14 \pm 0.55	16.06 \pm 0.83	4.26 \pm 0.28	0.30 \pm 0.15
		38-79m	7	-17.24 \pm 0.52	15.96 \pm 0.85	4.13 \pm 0.26	0.33 \pm 0.14
<i>Buccinum undatum</i>	BU	All depths	6	-15.48 \pm 0.32	11.19 \pm 1.09	2.83 \pm 0.17	1.14 \pm 0.07
		20-38m	6	-15.48 \pm 0.32	11.19 \pm 1.09	2.83 \pm 0.17	1.14 \pm 0.07
<i>Crepidula fornicata</i>	CF	All depths	6	-18.04 \pm 0.31	7.92 \pm 0.67	1.87 \pm 0.10	0.89 \pm 0.05
		20-38m	6	-18.04 \pm 0.31	7.92 \pm 0.67	1.87 \pm 0.10	0.89 \pm 0.05
<i>Glycymeris glycymeris</i>	GL	All depths	8	-17.68 \pm 0.97	9.58 \pm 1.09	2.36 \pm 0.13	0.81 \pm 0.09
		20-38m	8	-17.68 \pm 0.97	9.58 \pm 1.09	2.36 \pm 0.13	0.81 \pm 0.09
<i>Laevicardium crassum</i>	LC	All depths	4	-19.03 \pm 0.96	9.26 \pm 1.15	2.27 \pm 0.18	0.55 \pm 0.12
		20-38m	4	-19.03 \pm 0.96	9.26 \pm 1.15	2.27 \pm 0.18	0.55 \pm 0.12
<i>Loligo vulgaris</i>	LV	All depths	7	-16.82 \pm 0.97	17.05 \pm 0.35	4.56 \pm 0.30	0.28 \pm 0.17
		20-38m	6	-16.54 \pm 0.68	16.98 \pm 0.33	4.43 \pm 0.28	0.38 \pm 0.16
<i>Mimachlamys varia</i>	MI	All depths	4	-17.89 \pm 0.51	8.41 \pm 0.32	2.01 \pm 0.07	0.88 \pm 0.06
<i>Pecten maximus</i>	PE	All depths	5	-18.18 \pm 0.62	8.27 \pm 0.35	1.97 \pm 0.07	0.83 \pm 0.07
		20-38m	5	-18.18 \pm 0.62	8.27 \pm 0.35	1.97 \pm 0.07	0.83 \pm 0.07
<i>Sepia officinalis</i>	SO	All depths	3	-16.93 \pm 0.21	15.35 \pm 0.25	4.06 \pm 0.24	0.42 \pm 0.13
Fishes							
<i>Aspitrigla cuculus</i>	AC	All depths	18	-17.01 \pm 0.53	14.58 \pm 0.55	3.83 \pm 0.22	0.47 \pm 0.11

		20-38m	9	-16.54 ± 0.21	14.72 ± 0.38	3.76 ± 0.21	0.60 ± 0.11
		38-79m	9	-17.48 ± 0.23	14.45 ± 0.67	3.68 ± 0.20	0.42 ± 0.11
<i>Buglossidium luteum</i>	BL	All depths	7	-16.79 ± 0.56	13.65 ± 0.81	3.56 ± 0.21	0.61 ± 0.11
		20-38m	6	-16.59 ± 0.18	13.40 ± 0.53	3.38 ± 0.17	0.72 ± 0.09
<i>Callionymus lyra</i>	CL	All depths	18	-17.31 ± 1.22	13.37 ± 0.78	3.47 ± 0.18	0.52 ± 0.11
		0-20m	7	-16.34 ± 0.75	12.64 ± 0.50	3.15 ± 0.14	0.84 ± 0.09
		20-38m	9	-18.04 ± 1.16	13.98 ± 0.48	3.55 ± 0.19	0.34 ± 0.13
<i>Chelidonichthys lucerna</i>	TU	All depths	11	-17.44 ± 0.60	15.74 ± 1.03	4.17 ± 0.27	0.27 ± 0.14
		0-20m	4	-17.51 ± 0.61	16.21 ± 0.26	4.20 ± 0.26	0.24 ± 0.15
		20-38m	6	-17.34 ± 0.67	15.17 ± 1.01	3.90 ± 0.25	0.38 ± 0.14
<i>Clupea harengus</i>	CH	All depths	10	-18.05 ± 1.72	13.53 ± 1.69	3.52 ± 0.24	0.35 ± 0.16
		0-20m	5	-16.74 ± 0.29	12.92 ± 0.37	3.23 ± 0.15	0.73 ± 0.08
		20-38m	4	-19.02 ± 1.48	14.47 ± 2.54	3.69 ± 0.42	0.08 ± 0.23
<i>Dicentrarchus labrax</i>	DL	All depths	52	-16.67 ± 0.83	15.84 ± 0.93	4.20 ± 0.26	0.43 ± 0.13
		0-20m	18	-16.85 ± 0.74	15.49 ± 0.77	3.99 ± 0.24	0.46 ± 0.13
		20-38m	27	-16.51 ± 0.95	16.04 ± 1.08	4.15 ± 0.25	0.48 ± 0.13
		38-79m	7	-16.81 ± 0.46	16.00 ± 0.34	4.14 ± 0.25	0.41 ± 0.13
<i>Eutrigla gurnardus</i>	EG	All depths	12	-16.96 ± 0.68	14.80 ± 0.67	3.89 ± 0.23	0.46 ± 0.12
		0-20m	4	-16.80 ± 0.95	15.02 ± 0.49	3.85 ± 0.22	0.51 ± 0.15
		20-38m	7	-16.86 ± 0.27	14.47 ± 0.48	3.69 ± 0.20	0.55 ± 0.10
<i>Gadus morhua</i>	GM	All depths	36	-16.55 ± 0.57	15.37 ± 1.06	4.06 ± 0.25	0.50 ± 0.13
		0-20m	7	-16.94 ± 0.43	16.25 ± 0.94	4.21 ± 0.28	0.36 ± 0.14
		20-38m	23	-16.55 ± 0.47	14.95 ± 0.96	3.83 ± 0.22	0.57 ± 0.11
		38-79m	6	-16.10 ± 0.77	15.95 ± 0.69	4.13 ± 0.26	0.57 ± 0.14
<i>Galeorhinus galeus</i>	GG	All depths	3	-16.62 ± 0.14	16.24 ± 0.21	4.32 ± 0.27	0.40 ± 0.14
		38-79m	3	-16.62 ± 0.14	16.24 ± 0.21	4.21 ± 0.26	0.43 ± 0.13
Gobiidae	GO	All depths	10	-17.71 ± 0.60	14.70 ± 0.69	3.86 ± 0.23	0.31 ± 0.12
		0-20m	7	-18.02 ± 0.30	14.52 ± 0.31	3.71 ± 0.20	0.29 ± 0.11
		20-38m	3	-16.98 ± 0.45	15.12 ± 1.22	3.88 ± 0.30	0.46 ± 0.14
<i>Hyperoplus lanceolatus</i>	HL	All depths	5	-16.72 ± 0.28	14.89 ± 0.57	3.92 ± 0.24	0.51 ± 0.12
		0-20m	5	-16.72 ± 0.28	14.89 ± 0.57	3.81 ± 0.22	0.54 ± 0.11
<i>Limanda limanda</i>	LL	All depths	18	-16.66 ± 0.90	12.81 ± 0.57	3.31 ± 0.16	0.72 ± 0.09
		0-20m	3	-17.29 ± 0.24	13.11 ± 0.43	3.29 ± 0.17	0.59 ± 0.09
		20-38m	14	-16.52 ± 0.97	12.74 ± 0.60	3.18 ± 0.14	0.79 ± 0.09
<i>Merlangius merlangus</i>	MM	All depths	48	-16.57 ± 0.44	16.05 ± 0.53	4.26 ± 0.26	0.43 ± 0.13
		0-20m	5	-16.71 ± 0.92	16.13 ± 1.03	4.18 ± 0.28	0.42 ± 0.16
		20-38m	34	-16.53 ± 0.38	16.06 ± 0.48	4.16 ± 0.25	0.47 ± 0.13
		38-79m	9	-16.66 ± 0.33	15.96 ± 0.37	4.13 ± 0.25	0.45 ± 0.13
<i>Microstomus kitt</i>	MK	All depths	15	-16.58 ± 0.66	13.38 ± 0.58	3.48 ± 0.18	0.68 ± 0.10
		20-38m	13	-16.50 ± 0.47	13.31 ± 0.53	3.35 ± 0.16	0.74 ± 0.09
<i>Micromesistius poutassou</i>	MP	All depths	12	-18.26 ± 0.68	11.64 ± 1.38	2.96 ± 0.17	0.49 ± 0.09
		38-79m	12	-18.26 ± 0.68	11.64 ± 1.38	2.96 ± 0.17	0.49 ± 0.09
<i>Microchirus variegatus</i>	MV	All depths	6	-15.65 ± 0.21	14.28 ± 0.20	3.74 ± 0.21	0.80 ± 0.10
		20-38m	6	-15.65 ± 0.21	14.28 ± 0.20	3.74 ± 0.21	0.80 ± 0.10
<i>Mullus surmuletus</i>	MS	All depths	72	-17.58 ± 0.69	15.04 ± 0.80	3.96 ± 0.23	0.30 ± 0.12
		0-20m	8	-17.09 ± 1.07	14.54 ± 0.91	3.71 ± 0.22	0.50 ± 0.14
		20-38m	46	-17.60 ± 0.61	15.04 ± 0.78	3.86 ± 0.22	0.34 ± 0.12
		38-79m	18	-17.77 ± 0.63	15.24 ± 0.75	3.92 ± 0.23	0.28 ± 0.12
<i>Mustelus sp.</i>	MU	All depths	14	-16.28 ± 0.70	13.51 ± 1.59	3.51 ± 0.22	0.74 ± 0.11
		20-38m	8	-16.49 ± 0.31	12.79 ± 0.49	3.20 ± 0.15	0.80 ± 0.08
		38-79m	6	-16.01 ± 1.00	14.47 ± 2.08	3.69 ± 0.32	0.74 ± 0.16
<i>Platichthys flesus</i>	PF	All depths	10	-17.38 ± 0.52	13.88 ± 0.78	3.62 ± 0.21	0.46 ± 0.11
		0-20m	9	-17.35 ± 0.54	13.97 ± 0.78	3.54 ± 0.20	0.49 ± 0.10
<i>Pleuronectes platessa</i>	PP	All depths	46	-16.61 ± 0.82	13.41 ± 1.02	3.49 ± 0.18	0.68 ± 0.09
		0-20m	11	-17.12 ± 0.64	13.85 ± 0.43	3.51 ± 0.18	0.56 ± 0.10

		20-38m	34	-16.47 ± 0.81	13.32 ± 1.09	3.35 ± 0.17	0.75 ± 0.09
<i>Psetta maxima</i>	PT	All depths	5	-17.18 ± 0.63	16.29 ± 0.62	4.33 ± 0.28	0.27 ± 0.16
<i>Raja clavata</i>	RC	All depths	32	-15.93 ± 0.73	13.66 ± 0.89	3.56 ± 0.19	0.80 ± 0.10
		0-20m	8	-16.58 ± 0.65	14.61 ± 0.69	3.73 ± 0.21	0.60 ± 0.12
		20-38m	18	-15.70 ± 0.65	13.58 ± 0.49	3.43 ± 0.17	0.89 ± 0.09
		38-79m	6	-15.78 ± 0.58	12.64 ± 0.84	3.15 ± 0.17	0.97 ± 0.09
<i>Sardina pilchardus</i>	SP	All depths	10	-17.89 ± 1.34	12.72 ± 1.34	3.28 ± 0.20	0.46 ± 0.13
		0-20m	4	-16.70 ± 0.44	12.99 ± 1.09	3.25 ± 0.22	0.73 ± 0.10
		20-38m	6	-18.69 ± 1.12	12.55 ± 1.57	3.12 ± 0.23	0.34 ± 0.14
<i>Scomber scombrus</i>	SS	All depths	48	-18.56 ± 1.63	14.57 ± 1.21	3.83 ± 0.22	0.13 ± 0.13
		0-20m	29	-18.28 ± 1.95	15.18 ± 1.00	3.90 ± 0.23	0.17 ± 0.14
		20-38m	18	-19.04 ± 0.82	13.58 ± 0.85	3.43 ± 0.18	0.16 ± 0.11
<i>Scophthalmus rhombus</i>	SR	All depths	10	-17.09 ± 0.81	15.43 ± 0.45	4.08 ± 0.25	0.37 ± 0.14
		0-20m	8	-16.95 ± 0.84	15.51 ± 0.24	4.00 ± 0.23	0.43 ± 0.14
<i>Scyliorhinus canicula</i>	SY	All depths	48	-16.36 ± 0.64	14.44 ± 0.87	3.79 ± 0.21	0.63 ± 0.11
		20-38m	40	-16.36 ± 0.68	14.52 ± 0.88	3.70 ± 0.20	0.66 ± 0.10
		38-79m	8	-16.37 ± 0.37	14.04 ± 0.71	3.56 ± 0.19	0.70 ± 0.10
<i>Scyliorhinus stellaris</i>	SE	All depths	10	-16.83 ± 0.39	13.33 ± 1.38	3.46 ± 0.22	0.63 ± 0.10
		38-79m	9	-16.76 ± 0.35	13.01 ± 0.99	3.26 ± 0.18	0.71 ± 0.09
<i>Solea solea</i>	SL	All depths	54	-16.75 ± 0.80	13.90 ± 1.00	3.63 ± 0.20	0.60 ± 0.10
		0-20m	16	-17.21 ± 0.96	14.19 ± 0.73	3.61 ± 0.19	0.50 ± 0.11
		20-38m	32	-16.51 ± 0.63	13.69 ± 0.96	3.46 ± 0.18	0.70 ± 0.09
		38-79m	6	-16.76 ± 0.73	14.28 ± 1.64	3.63 ± 0.27	0.59 ± 0.13
<i>Spondyliosoma cantharus</i>	SC	All depths	15	-19.02 ± 1.28	15.11 ± 0.24	3.98 ± 0.23	-0.02 ± 0.15
		0-20m	5	-20.12 ± 1.49	14.98 ± 0.16	3.84 ± 0.21	-0.21 ± 0.19
		20-38m	8	-18.61 ± 0.76	15.13 ± 0.18	3.89 ± 0.22	0.10 ± 0.13
<i>Sprattus sprattus</i>	SA	All depths	10	-18.10 ± 1.15	13.16 ± 0.32	3.41 ± 0.17	0.37 ± 0.12
		20-38m	9	-18.30 ± 1.03	13.13 ± 0.33	3.30 ± 0.16	0.37 ± 0.11
<i>Trachurus trachurus</i>	TT	All depths	57	-18.05 ± 1.04	16.16 ± 1.18	4.29 ± 0.27	0.09 ± 0.15
		0-20m	7	-17.89 ± 0.92	16.82 ± 1.31	4.38 ± 0.31	0.10 ± 0.17
		20-38m	33	-18.01 ± 1.20	16.22 ± 0.81	4.21 ± 0.26	0.13 ± 0.14
		38-79m	17	-18.18 ± 0.75	15.76 ± 1.58	4.07 ± 0.26	0.14 ± 0.14
<i>Trigloporus lastowiza</i>	TA	All depths	10	-17.67 ± 0.35	13.35 ± 0.40	3.47 ± 0.18	0.45 ± 0.10
		20-38m	3	-17.44 ± 0.35	13.52 ± 0.59	3.41 ± 0.19	0.52 ± 0.10
		38-79m	7	-17.77 ± 0.32	13.28 ± 0.32	3.34 ± 0.16	0.47 ± 0.09
<i>Trisopterus luscus</i>	TL	All depths	24	-17.34 ± 1.20	14.78 ± 0.86	3.89 ± 0.23	0.38 ± 0.13
		20-38m	24	-17.34 ± 1.20	14.78 ± 0.86	3.89 ± 0.23	0.38 ± 0.13
<i>Trisopterus minutus</i>	TM	All depths	15	-17.63 ± 1.29	14.57 ± 0.52	3.83 ± 0.22	0.34 ± 0.13
		20-38m	11	-17.73 ± 1.30	14.69 ± 0.55	3.76 ± 0.21	0.34 ± 0.14
		38-79m	3	-17.70 ± 1.49	14.17 ± 0.30	3.60 ± 0.19	0.40 ± 0.21
<i>Zeus faber</i>	ZF	All depths	13	-17.07 ± 0.79	14.67 ± 0.68	3.85 ± 0.22	0.45 ± 0.12
		0-20m	3	-16.88 ± 1.25	15.06 ± 0.66	3.86 ± 0.24	0.49 ± 0.20
		20-38m	6	-16.87 ± 0.40	14.30 ± 0.65	3.64 ± 0.20	0.57 ± 0.11
		38-79m	4	-17.49 ± 0.91	14.93 ± 0.60	3.82 ± 0.23	0.37 ± 0.15