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1 **Plasticity of trophic interactions in fish assemblages results in temporal stability of**
2 **benthic-pelagic couplings**

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20 **Highlights**

- 21 • Most fish species displayed trophic plasticity over time
- 22 • Trophic resources were used optimally through complementarity
- 23 • When considering biomass, dominant species were trophic generalists
- 24 • Couplings between benthic and pelagic habitats are a permanent feature of the EEC

25

26 **Abstract**

27 This study addresses the temporal variability of couplings between pelagic and benthic
28 habitats for fish assemblages at five periods in a shallow epicontinental sea, the Eastern
29 English Channel (EEC). Organic matter fluxes fueling fish assemblages and the relative
30 contribution of their different sources were assessed using stable isotope analysis and
31 associated isotopic functional metrics. Couplings between benthic and pelagic realms
32 appeared to be a permanent feature in the EEC, potentially favored by shallow depth and
33 driven by the combination of two trophic processes. First, trophic interactions exhibited
34 plasticity and revealed resource partitioning. Second, changes in the composition of fish
35 assemblages did not impact benthic-pelagic couplings, as most dominant species were
36 generalists during at least one time period, allowing complete use of available resources.
37 Examining both unweighted and biomass-weighted indices was complementary and permitted
38 a better understanding of trophic interactions and energy fluxes.

39

40 **Key-words:** Food webs, Stable isotopes, Biomass, Isotopic functional indices, Flux

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44 **1. Introduction**

45 Identifying and quantifying trophic interactions between organisms is crucial to
46 understand the structure and functioning of food webs (Ings et al., 2009; McCann, 2000).
47 Ecosystems with numerous trophic links are considered more stable and resilient to
48 perturbations (McCann, 2000; Rooney et al., 2006; Rooney and McCann, 2012) and trophic
49 interactions have been proposed as mediators between biodiversity and ecosystem functioning
50 (Hooper et al., 2005; Lynam et al., 2017; Rooney and McCann, 2012; Thompson et al., 2012).
51 Particularly, characterizing spatio-temporal variability of interactions in trophic networks is
52 considered a promising avenue for improving our understanding of the link between
53 biodiversity and ecosystem functioning (Ings et al., 2009; McMeans et al., 2015). However,
54 how this variability is impacted by environmental gradients and anthropogenic pressures has
55 been overlooked so far (Pellissier et al., 2018). Finally, the assessment of trophic interactions
56 and their spatio-temporal dynamics is also essential to sustainably manage marine ecosystems
57 (Seibold et al., 2018), notably for the implementation of the Ecosystem Approach to Fisheries
58 Management (Cresson et al., 2020; Garcia et al., 2003) or for aiming at good environmental
59 status such as recommended in the Marine Strategy Framework Directive in Europe.

60 Couplings between habitats, defined here as transfers of energy and organic matter
61 between them, have been widely studied both within and between aquatic and terrestrial
62 ecosystems (Darnaude et al., 2004). The existence, strength and variability of coupling fluxes
63 drive food web structure (Post et al., 2000), and functioning and resilience to perturbations
64 (Blanchard et al., 2011; Woodland and Secor, 2013). In particular, couplings can be mediated
65 by foraging when occurring across different habitats (Baustian et al., 2014; McMeans et al.,
66 2015; Quevedo et al., 2009). In marine ecosystems, a major coupling occurs between pelagic
67 and benthic realms, through a bidirectional process: on the one hand, sinking or vertically
68 migrating pelagic organic matter reaches the sea floor (pelagic-benthic coupling (Griffiths et

69 al., 2017)), while on the other hand, benthic organic matter can be feed upon by pelagic
70 species (benthic-pelagic coupling (Gaudron et al., 2016)). Most investigations have focused
71 on pelagic to benthic organic matter fluxes, as plankton sedimentation is considered to be the
72 main source of organic matter for most benthic ecosystems worldwide (Grebmeier and Barry,
73 1991; Polunin et al., 2001; Stasko et al., 2018; Tecchio et al., 2013). On the contrary, few
74 studies have investigated how benthic organic matter can be integrated in pelagic food webs.
75 Numerous chemical, biological and physical factors can affect couplings between benthic and
76 pelagic habitats (Baustian et al., 2014; Griffiths et al., 2017). These include primary
77 production intensity (Docmac et al., 2017; McMeans et al., 2015; Stasko et al., 2018; Udy et
78 al., 2019; Ying et al., 2020), filtering activity of suspension feeders (Cresson et al., 2016; Gili
79 and Coma, 1998), fish feeding activity (Snickars et al., 2015) or depth (Cresson et al., 2016;
80 Giraldo et al., 2017; Kopp et al., 2015). Despite the potential magnitude of spatial and/or
81 temporal variation of these factors, and of their effects on organic matter fluxes, most studies
82 performed one-off analyses of benthic-pelagic coupling, *i.e.* in one environment or at one
83 season (but see (Cresson et al., 2020; Hayden et al., 2019; McMeans et al., 2015; Silberberger
84 et al., 2018). In shallow waters, the physical proximity between pelagic and benthic habitats
85 and the absence of physical barriers, such as a thermocline, may allow for a strong coupling
86 between these habitats (Duffill Telsnig et al., 2018; Kopp et al., 2015; Woodland and Secor,
87 2013). Shallow marine ecosystems are thus good case studies to explore benthic-pelagic
88 coupling, its dynamics and its link with ecosystem functioning.

89 Multiple approaches are available for unraveling spatio-temporal variability in
90 benthic-pelagic coupling, particularly stable isotope analysis and functional diversity. On the
91 one hand, stable isotope analysis is an insightful tool in trophic ecology (Fry, 2006; Layman
92 et al., 2012), suited to quantify contributions of organic matter sources within an ecosystem
93 and to determine factors shaping communities. For instance, community-wide metrics based

94 on stable isotopes were developed by Layman et al. (2007) and by Jackson et al. (2011) and
95 have been widely used to study the isotopic structure of fish assemblages (*e.g.*, Abrantes et
96 al., 2014; Cresson et al., 2016; Hill et al., 2015; Jabot et al., 2017). On the other hand,
97 measuring functional diversity allows for a better understanding of ecosystem functioning and
98 trophic fluxes within biological communities (Cresson et al., 2019). According to Villéger et
99 al. (2008), the functional diversity of a community is the layout of its organisms and of their
100 relative importance (abundance or biomass) in a multi-dimensional functional space.
101 Functional diversity can be split into three components, functional richness (space occupied
102 by species in the functional space), functional divergence or dispersion (variance or degree of
103 clustering of species distribution in the occupied space) and functional evenness (regularity of
104 species distribution in the occupied space). Recently, functional diversity metrics have been
105 merged with stable isotope analysis, where isotopes are used as species traits (Cucherousset
106 and Villéger, 2015; Rigolet et al., 2015), to describe the isotopic diversity of a community.
107 One of the advantages of these new metrics is to deal with the heterogeneous distribution of
108 biomass among species of an assemblage. Accordingly, species with the highest biomass
109 should have the largest contribution to diversity metrics to reflect their expected highest
110 impact on ecosystem functioning (Rigolet et al., 2015). Accounting for species biomass
111 underlines the strength of trophic interactions, energy distributions and fluxes (Rigolet et al.,
112 2015) while ignoring species biomass assumes equitability between species (Cucherousset
113 and Villéger, 2015). Still, isotopic community metrics have drawbacks (Hoeinghaus and
114 Zeug, 2008) and do not necessarily grasp subtle details of food web structure when the
115 number of basal sources is high (Jabot et al., 2017). In particular, two key issues are the
116 failure to account for basal food sources (*i.e.*, the isotopic baseline) and the standardization of
117 isotopic values (Hoeinghaus and Zeug, 2008). One solution is to transform the isotopic niche
118 (in the δ -space, *i.e.*, $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ plot) into a trophic niche (expressed as dietary

119 proportions, i.e., in the p-space) through mixing models (Newsome et al., 2007), but using
120 few basal sources before calculating isotopic metrics to encompass changes both in isotopic
121 baselines and in diet proportions.

122 According to previous studies conducted in the Eastern English Channel (EEC), a shallow
123 epicontinental temperate sea, benthic-pelagic coupling intensity varies with depth and
124 predators' habitat preferences (Giraldo et al., 2017; Kopp et al., 2015). The present work aims
125 to build upon these initial results to study how benthic-pelagic coupling varies over time,
126 through the determination of the predominant organic matter sources (i.e. benthic vs pelagic)
127 fueling fish assemblages in the EEC and how these variations depend on (1) changes in the
128 trophic ecology of species over time and (2) changes in the species composition of the fish
129 assemblage. For this purpose, inferences from isotopic mixing models and functional indices
130 were used at five periods: autumn 2009, 2014, and 2015 and winter 2015 and 2016 to study
131 the topology of energy fluxes (Cucherousset and Villéger, 2015; Rigolet et al., 2015). We
132 used unweighted and biomass-weighted isotopic metrics as a complementary approach to
133 explore trophic interactions and energy fluxes (respectively) within the fish assemblage. We
134 hypothesize that variations in the three complementary facets (i.e. richness, dispersion, and
135 evenness) of trophic and functional diversity occur between periods for fish assemblages
136 because species respond differently to environmental conditions. We also hypothesize that
137 due to the strong benthic-pelagic coupling in this shallow ecosystem (Cresson et al., 2020;
138 Giraldo et al., 2017; Kopp et al., 2015), many species are generalists and can partition their
139 resources through complementarity. The inclusion of biomass will provide more information
140 about the trophic behavior of dominant fish species in the assemblage.

141

142

143 **2. Materials and methods**

144 **2.1 Study area and sampling**

145 Fish assemblages were sampled during five bottom trawl surveys conducted in the
146 EEC (49.3°N to 51.2°N, 2°W to 2°E, Fig. 1, Table 1). Additionally to providing information
147 on species composition and opportunities to collect fish individuals for further analysis, these
148 surveys also sample or observe most components of the ecosystem, from the abiotic
149 environment to top-predators (Travers-Trolet and Verin, 2014). The CGFS (Channel Ground
150 Fish Survey) occurred on board of R/V Gwen Drez in autumn 2009 (Le Roy, 2009) and on
151 board of the R/V Thalassa in autumn 2015 (Travers-Trolet, 2015). The CAMANOC
152 (“CAMpagne écosystémique en MANche OCCidentale”- Oct. 2014) and the IBTS surveys
153 (International Bottom Trawl Survey; Jan-Feb 2015 and 2016) were operated on board of the
154 R/V Thalassa (Travers-Trolet and Vérin, 2014; Vérin and Lazard, 2015; Vérin, 2016). A joint
155 dataset between the surveys was generated on the basis of common spatial boundaries, i.e.
156 filtering out data not located in the EEC to avoid any confusion between temporal and spatial
157 variability of the different surveys. The data used for autumn 2009 and winter 2015 were
158 reanalyzed from a previously published dataset (Cresson et al., 2020; Giraldo et al., 2017;
159 Kopp et al., 2015). The complete dataset was published at the following URL address:
160 <https://doi.org/10.17882/76378>.

161 Following the standard IBTS protocol (ICES, 2004), fish sampling was performed
162 using a Grande Ouverture Verticale (GOV) bottom trawl towed for 30 minutes during
163 daylight at a constant speed of 4 knots. The sampling scheme is spatially stratified by
164 subdividing the EEC into 1° longitude × 0.5° latitude rectangles. Immediately after trawling,
165 all fish were sorted, identified, weighed, and a subsample was measured for length. At each
166 station, when possible, a minimum of five individuals per species were collected in the modal
167 size-class and frozen onboard. The whole dataset comprises 35 fish species and 1419

168 individuals (Table S1). Sample size was then reduced to five individuals for each species by
169 random sampling, to limit the influence of some overrepresented species (see afterwards).
170 More than 35 species were encountered during the surveys but only these 35 were collected
171 for further trophic analysis. Therefore, we refer only to these 35 species hereafter when using
172 “fish assemblage”.

173 **Table 1**

174 Details of sampling. For each survey: number (n) and depth (mean \pm sd, min – max) of sampling stations used for laboratory analysis. Benthic
 175 and pelagic baselines correspond to isotopic values of benthic (*A. opercularis*) and pelagic (copepods) sources used in the mixing model for the
 176 five studied periods. Values for baselines were collected concomitantly with fish, with the exception of *A. opercularis* in autumn 2014 (S.
 177 Dubois, Ifremer/DYNECO, unpubl. data). Biomass representativeness corresponds to the sum of the biomass of the species sampled for stable
 178 isotopes analyses divided by the total biomass of the fish community.

Survey	Period	n station	Depth (m)		Benthic baseline (‰)		Pelagic baseline (‰)		Biomass representativeness (%)
			mean \pm sd	min - max	Carbon	Nitrogen	Carbon	Nitrogen	
CGFS 2009	Autumn 2009	48	37 \pm 13	20 - 79	-17.39 \pm 0.47	8.74 \pm 0.86	-21.07 \pm 0.89	10.28 \pm 1.70	98
CAMANOC	Autumn 2014	14	46 \pm 19	20 - 78	-17.58 \pm 0.24	6.93 \pm 0.30	-20.95 \pm 1.55	7.32 \pm 0.94	86
IBTS 2015	Winter 2015	12	43 \pm 7	30 - 54	-17.68 \pm 0.58	7.30 \pm 0.45	-19.77 \pm 0.46	6.42 \pm 0.89	95
CGFS 2015	Autumn 2015	15	28 \pm 9	23 - 53	-17.65 \pm 1.00	7.77 \pm 1.00	-20.73 \pm 0.83	7.77 \pm 1.00	92
IBTS 2016	Winter 2016	12	46 \pm 11	29 - 61	-17.58 \pm 0.69	7.81 \pm 0.68	-19.77 \pm 0.46	6.42 \pm 0.89	82

179 A suspension feeding bivalve (the queen scallop *Aequipecten opercularis*) and
180 zooplankton (copepods of the calanoid order) were collected to be used as proxies of benthic
181 and pelagic trophic baselines, respectively. *A. opercularis* feeds on a mix of phytoplankton
182 and associated bacterial and detrital material that supports benthic production (Barnes et al.
183 2009), and displays a $\delta^{13}\text{C}$ signature similar to deposit feeders and distinct from zooplankton
184 (Kürten et al., 2013). Following other papers on benthic-pelagic coupling (Cresson et al.,
185 2020; Hayden et al., 2019; Kopp et al., 2015), the use of zooplankton as proxy of pelagic
186 production pathway and bivalves as proxy of benthic production pathway is satisfactory.
187 Without any knowledge about fish diet, the use of these proxies will help determine the
188 relative importance of benthic or pelagic production in the food web to which the different
189 fish species belong (Kiljunen et al., 2020). Bivalves were sampled together with fish with the
190 GOV bottom trawl whereas zooplankton were collected with a WP2 net (200 μm mesh size)
191 and frozen for stable isotope analysis. As no copepods were collected in winter 2015, the
192 same isotopic values were used for the pelagic baseline in winter 2016 and 2015. Using
193 primary consumers rather than producers as trophic baselines is advocated (Jennings and van
194 der Molen, 2015; Jennings and Warr, 2003). Isotopic ratios of primary producers are highly
195 variable through time and thus should not be used as isotopic baseline for studies based on
196 muscle tissues, as muscles integrate isotopic signature of individuals' diet over several
197 months. In contrast, primary consumers' tissues integrate primary producers' isotopic
198 signatures on a time scale comparable to that of higher trophic level organisms' muscle,
199 providing a more relevant trophic baseline (Jennings and van der Molen, 2015). In the
200 laboratory, fish were thawed and measured (total length, to the nearest mm), then fish and
201 bivalves were dissected. One sample per individual of white dorsal muscle without skin (fish)
202 or adductor muscle (bivalves) (~ 2g wet mass) was dissected, stored frozen and then freeze-
203 dried for at least 24h. For zooplankton, several individuals were identified to the order or

204 genus level and sorted under a binocular microscope and pooled by sampling station in order
205 to have enough biological material for isotopic ratio analysis. All samples (fish muscle, *A.*
206 *opercularis* and copepods) were ground into a homogeneous powder (~ 1g dry mass) with a
207 mixer mill for stable isotope analysis.

208

209 ***2.2. Stable isotope analysis***

210 Stable isotopes are largely used as a tool to trace the trophic structure of marine food
211 webs, as they give an integrated view of trophic interactions and organic matter fluxes.
212 Nitrogen isotopic ratios ($\delta^{15}\text{N}$) are used to estimate the trophic level of consumers, because
213 consumers are enriched in ^{15}N relative to their prey (Peterson and Fry, 1987; Post, 2002). In
214 contrast, carbon isotopic ratios ($\delta^{13}\text{C}$) are used to identify the sources of organic matter
215 fueling trophic pathways since there are little changes of $\delta^{13}\text{C}$ values (commonly 1‰) at each
216 trophic level (DeNiro and Epstein, 1978). More specifically, it is an appropriate tracer of
217 couplings, since organic matter of different origin (*e.g.*, benthic or pelagic) exhibit markedly
218 different $\delta^{13}\text{C}$ values, and can be followed along food webs.

219 Isotopic ratios were measured with a Thermo Delta V isotope mass ratio spectrometer,
220 coupled with a Carlo Erba NC 2500 elemental analyzer. Ratios were expressed with the
221 classical δ notation,

$$222 \quad \delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 10^3, \quad (1)$$

223 where X is ^{13}C or ^{15}N respectively, and R the ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ respectively. Accuracy
224 of the analyses was checked with different standards for the five surveys, mink (autumn 2014,
225 2015, winter 2016), acetanilide (winter 2016) and sea bass muscle coupled with bovine liver
226 (autumn 2009). The analytical precision of measures was always ± 0.2 ‰ for both elements.

227 Since lipids tend to be depleted in ^{13}C compared to proteins, high lipid concentrations
 228 in tissues can bias $\delta^{13}\text{C}$ values (Logan et al., 2008). Using elemental carbon to nitrogen ratios
 229 (C:N) as a proxy of lipid content, the mathematical correction for lipids proposed by Post et
 230 al. (2007) was applied to all samples with C:N ratios higher than 3.5:

$$231 \quad \delta^{13}\text{C}_{\text{corrected}} = \delta^{13}\text{C}_{\text{uncorrected}} - 3.32 + 0.99 \times \text{C:N} \quad (2)$$

232

233 **2.3. Trophic level and benthic contribution calculations**

234 For each consumer, the relative trophic contribution of pelagic (copepods) and benthic
 235 organic matter (*A. opercularis*) was estimated with a mixing model taking into account the
 236 calculation of the benthic contribution and trophic level jointly. Combining the Post equation
 237 (Post, 2002) for the trophic level and a two-sources mixing model (Phillips and Gregg, 2003)
 238 by correcting for fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, the following system of equations was
 239 obtained:

$$240 \quad \begin{cases} TL_C = TL_{base} + (\delta^{15} N_C - (\alpha \delta^{15} N_B + (1 - \alpha) \delta^{15} N_P)) / \Delta^{15} N \\ \alpha = (\delta^{13} C_C - (TL_C - TL_{base}) \Delta^{13} C - \delta^{13} C_P) / (\delta^{13} C_B - \delta^{13} C_P) \end{cases} \quad (3)$$

241 where TL_C is the trophic level of the consumer C (fish), TL_{base} is the trophic level of the
 242 source ($TL_{base} = 2$ as the sources are primary consumers), α the fraction of the benthic source
 243 in fish diet, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ the nitrogen and carbon isotopic signature respectively, $\Delta^{15}\text{N}$ and
 244 $\Delta^{13}\text{C}$ the nitrogen (3.4‰) and carbon (1‰) trophic discrimination factor at each trophic level
 245 respectively, and C , B and P corresponds to the consumer, the benthic (*A. opercularis*) and
 246 pelagic (copepods) organisms respectively.

247 The following equation was obtained for α by solving the system of equations:

$$248 \quad \alpha = \frac{\Delta^{15} N (\delta^{13} C_P - \delta^{13} C_C) + \Delta^{13} C (\delta^{15} N_C - \delta^{15} N_P)}{\Delta^{15} N (\delta^{13} C_P - \delta^{13} C_B) + \Delta^{13} C (\delta^{15} N_B - \delta^{15} N_P)} \quad (4)$$

249 and TL_C was obtained replacing α with its value in (3).

250 For some individuals, values of benthic contributions lower than zero and higher than one
251 were obtained due to approximations regarding trophic discrimination factors. Trophic
252 discrimination factors values were set to 1‰ and 3.4‰ as suggested by Post (2002). but these
253 values can vary, according to several parameters, such as the species considered (Caut et al.,
254 2009). Furthermore, temporal differences between turnover rates of trophic baselines and fish
255 muscle or other sources of bias potentially unknown can affect values of benthic
256 contributions. Finally, contributions were scaled in order to obtain values strictly between 0
257 and 1.

$$258 \quad \%B = \frac{(\alpha - \min(\alpha))}{(\max(\alpha) - \min(\alpha))} \quad (5)$$

259 Hence, each individual position in the isotopic or δ -space, with coordinates $(\delta^{13}\text{C}, \delta^{15}\text{N})$, was
260 projected in the trophic or p-space, with coordinates $(\%B, TL_C)$, while accounting for benthic
261 and pelagic isotopic baselines.

262 ***2.4. Trophic interactions and energy fluxes***

263 Assessing fish assemblage functioning from stable isotope analysis classically does
264 not take into account the species unevenness observed in the field, as simultaneous sampling
265 of quantitative (biomass) and qualitative (stable isotopes) data requires a considerable amount
266 of work. However, trophic fluxes in marine ecosystems depend on species relative
267 dominance. Considering species biomass when analyzing stable isotopes might improve our
268 understanding of assemblage functioning particularly in regard to energy fluxes. Thus, for
269 each species, the benthic contribution $\%B$ in its diet was combined with its relative biomass
270 in the fish assemblage, as sampled by the trawl. Trophic structure was partly depicted by
271 isotopic functional indices (IFI), but also by violin plots representing the distribution of

272 consumer biomass across the fraction of contribution of benthic sources for the fish
273 assemblage. We propose to use both unweighted and biomass-weighted IFI and violin plots in
274 an attempt to consider trophic interactions and energy flux within the fish assemblage.

275 For each survey, species biomass density (B_i , expressed in $\text{kg}\cdot\text{m}^{-2}$) was calculated
276 according to the following formula:

$$277 \quad B_i = \frac{\sum_j B_{i,j} S_j}{\sum_{j'} S_{j'}} \quad (6)$$

278 with $B_{i,j}$ the average biomass density of species i across stations in stratum j , S_j the surface of
279 stratum j and $\sum_{j'} S_{j'}$ the sum of the stratum surfaces sampled during the survey. Relative
280 species biomass b_i among all fish species captured was then calculated as $b_i = B_i / \sum_{i'=1}^{S_T} B_{i'}$
281 where S_T is the total number of species captured during the survey. Relative species biomass
282 in the assemblage of 35 species used for isotopic analyses was calculated as $\beta_i =$
283 $B_i / \sum_{i'=1}^{S_S} B_{i'}$ with $S_S = 35$ the number of species used for isotopic analyses.

284 In order to account for the fluxes at the assemblage scale, the average benthic
285 contribution weighted by the relative biomasses of the species in the assemblage was
286 calculated as follows:

$$287 \quad \%B_w = \sum_{i=1}^{S_S} \beta_i \times \%B \quad (7)$$

288 Since the number of individuals sampled differed between species, a bootstrap
289 procedure was applied to avoid a possible bias in estimates of $\%B_w$ due to unequal
290 representation. Five individuals per species were sampled with replacement for all species
291 with $n > 5$. Resampling was based on a 100 000 iteration bootstrap procedure, to ensure that
292 the isotopic values for the pseudo individuals are representative of the isotopic variability of
293 the larger initial dataset. Scaled benthic contributions were then computed for each pseudo-

294 individual and their averages across pseudo-individuals are presented as results. After this
295 correction, all individuals had the same importance when biomass is not considered. To keep
296 inter-individual variability in violin plots, pseudo-individual benthic contribution was
297 considered rather than average contribution calculated for species, and one fifth of the
298 species' biomass was applied to each pseudo individual.

299 The Shannon-Weaver index (Shannon and Weaver, 1963) was used to measure the
300 diversity of the fish assemblage for each survey.

$$301 \quad H' = - \sum_{i=1}^{S_T} b_i \log_2(b_i), \quad (8)$$

302 where b_i is the relative biomass of the species i across the S_T species collected in the trawl. H'
303 is low when S_T is low and diversity is low (when one species dominate in the assemblage for
304 example). For a given S_T , the maximum diversity (*i.e.* all species are equally common), H_{max} ,
305 then equal $\log_2(S_T)$. The ratio between the measured diversity and the maximum theoretical
306 diversity for a given number of species is the Pielou Equitability Index (Pielou, 1976, J'),
307 which tends to zero when a species strongly dominates the assemblage or to one when species
308 are evenly distributed.

$$309 \quad J' = \frac{H'}{H_{max}} \quad (9)$$

310 ***2.5. Description of functional indices***

311 Each component of functional diversity (isotopic richness, isotopic dispersion and
312 isotopic evenness) was characterized using one index. These components must be quantified
313 independently to describe functional diversity (Mason et al., 2005; Villéger et al., 2008). As
314 trophic baselines might differ temporally, we followed Quevedo et al. (2009) or Kiljunen et
315 al. (2020) by calculating functional diversity indices in p-space, *i.e.* using (% B, TL_C), rather
316 than in δ -space (Cucherousset and Villéger, 2015). Average values of (% B, TL_C) per species,

317 i.e. across the five sampled individuals or pseudo-individuals depending on species, were
318 used for these calculations. Both an unweighted and biomass-weighted version of the
319 dispersion and evenness index were calculated for each of the five time-periods, whereas
320 richness can only be unweighted. by definition

321 2.5.1. *Isotopic Richness*

322 Isotopic Functional Richness (IFRic) is similar to the Total Area index developed by
323 Layman et al. (2007) and to the Functional Richness index (FRic) developed by Villéger et al.
324 (2008) but adapted for isotopic data. It represents the trophic diversity of the assemblage.
325 IFRic is the convex hull volume (or surface in a two dimensional space) surrounding species
326 in the trophic space, thus its value is not impacted by biomass consideration. For comparison
327 between time periods, IFRic was standardized by the IFRic value calculated when merging
328 the values of the five time periods (IFRic_{max} hereafter), so that its values were constrained
329 between zero and one (Rigolet et al., 2015). IFRic_{max} represents all values taken by
330 individuals whatever the time-period. By extension, we assume it corresponds to total
331 available trophic space for the assemblage. Then, IFRic represents the trophic resources used
332 at a given period, *i.e.* a subset of the total available trophic resources. When close to one,
333 available resources are efficiently used and/or resource availability is high. When close to
334 zero, resources potentially available to the assemblage are unused and/or resource availability
335 is unusually low.

336 2.5.2. *Isotopic dispersion*

337 Isotopic dispersion is an index of isotopic divergence, *i.e.* the variation in the position
338 or the dispersion of species in the isotopic space occupied. Isotopic Functional Dispersion
339 (IFDis) is based on FDis, developed by Laliberté and Legendre (2010). IFDis ranges from

340 zero, when all organisms have the same %B and trophic level, to one, when all organisms are
 341 far from the center of gravity.

$$342 \quad IFDis = \frac{\sum_{i=1}^{S_S} w_i \sqrt{\sum_k (x_{i,k} - c_k)^2}}{\max_{i'} (w_{i'} \sqrt{\sum_k (x_{i',k} - c_k)^2})} \quad (9)$$

343 where w_i is the relative weight of species i , with $\sum_{i=1}^{S_S} w_i = 1$ and x_{ik} is the coordinate of
 344 species i for trait k , here %B or TL_C . IFDis is thus the weighted mean distance to the weighted
 345 center of gravity $\mathbf{c} = (c_k)$ with

$$346 \quad c_k = \sum_{i=1}^{S_S} w_i x_{i,k}. \quad (10)$$

347 The unweighted version of this index, denoted IFDis hereafter, assumes an evenly
 348 distributed weight across species, i.e. $w_i = \frac{1}{S_S}$, whereas the biomass-weighted version,
 349 denoted IFDis_{biom} hereafter, takes species relative biomasses as weight, i.e. $w_i = \beta_i$. When
 350 IFDis_{biom} is close to zero, the assemblage is dominated by generalist species, whereas when it
 351 is close to one, it reveals trophic specialization.

352 2.5.3. Isotopic evenness

353 Isotopic Functional Evenness (IFEve), based on FEve, developed by Villéger et al.
 354 (2008) quantifies the uniformity in biomass distribution along the shortest tree that links all
 355 species in the trophic space (minimum spanning tree - MST).

$$356 \quad IFEve = \frac{\sum_{l=1}^{S_S-1} \min \left[\frac{\text{dist}_l(i,j)/(w_i+w_j)}{\sum_{l=1}^{S_S-1} \text{dist}_l(i,j)/(w_i+w_j)}, \frac{1}{S_S-1} \right] \frac{1}{S_S-1}}{1 - \frac{1}{S_S-1}} \quad (11)$$

357 where $\text{dist}_l(i,j)$ is the Euclidean distance between species i and j involved in branch l
 358 of the MST. As for IFDis, the unweighted version of this index, denoted IFEve hereafter,

359 considers evenly distributed weights w_i across species and the biomass-weighted version,
360 denoted $IFEve_{biom}$ hereafter, uses relative biomass as weight. An $IFEve_{biom}$ close to zero
361 reveals trophic redundancy and potential competition among species, whereas a value close to
362 one reveals optimal resource use through species complementarity.

363 All the indices used in this study and their significance were summarized in the Table
364 S2. All analyses and plots were produced using the R software and ggplot2 package (R Core
365 Team, 2019; Wickham, 2016); R scripts developed by Cucherousset and Villéger (2015) and
366 Mouillot et al. (2013) were used for computing isotopic functional indices (see supplementary
367 material in Cucherousset and Villéger (2015) and Mouillot et al. (2013)).

368

369 **3. Results**

370 ***3.1. Description of the fish assemblages of the different time periods***

371 The Shannon's index (H') results from a combination of two components, species
372 richness and the equitability of biomass between species. Among the five sampling periods,
373 the H' value in autumn 2009 was the highest ($H'= 2.64$), resulting from a high number of
374 harvested fish species and a moderate equitability ($J'= 0.44$, Table 2). The high biomass of *T.*
375 *trachurus* in autumn 2014 and 2015 (Relative biomass, $b_{T. trachurus} = 81$ and 70% respectively)
376 and the high biomass of *M. merlangus* in winter 2015 and 2016 ($b_{M. merlangus} = 69.5$ and 66%
377 respectively) led to a low diversity (H' between 1.39 and 1.78) and equitability (J' between
378 0.24 and 0.34). The lowest values of H_{max} were recorded in winter due to the lowest species
379 richness (S_T).

380

382 **Table 2**

383 Diversity and isotopic functional (unweighted and biomass-weighted) indices. For diversity
 384 indices, S_T corresponds to the species richness, H' to the Shannon-Weaver index, H_{max} to the
 385 theoretical maximum of diversity and J' to Pielou's equitability index (see Material and
 386 methods section for details). For functional indices, S_s corresponds to the number of species
 387 subsampled of species for stable isotope analysis, $IFRic$ to the isotopic richness, $IFEve$, to the
 388 isotopic evenness (unweighted, $IFEve$, and biomass-weighted, $IFEve_{biom}$, respectively), and
 389 $IFDis$ to the isotopic dispersion (unweighted, $IFDis$, and biomass-weighted, $IFDis_{biom}$,
 390 respectively).

Periods	Diversity indices				Isotopic functional indices					
	S_T	H'	H_{max}	J'	S_s	$IFRic$	$IFEve$	$IFEve_{biom}$	$IFDis$	$IFDis_{biom}$
Autumn 2009	62	2.64	5.95	0.44	28	0.34	0.71	0.41	0.38	0.27
Autumn 2014	67	1.45	6.07	0.24	11	0.21	0.79	0.57	0.58	0.23
Winter 2015	42	1.39	5.39	0.26	13	0.34	0.73	0.39	0.45	0.40
Autumn 2015	65	1.57	6.02	0.26	26	0.30	0.81	0.39	0.38	0.22
Winter 2016	39	1.78	5.29	0.34	25	0.37	0.73	0.30	0.38	0.24

391

392 The set of species used for isotopic analyses represented between 82% and 98% of the
 393 sampled biomass across all periods (Table 1). This subsample of species can thus be
 394 considered representative of the fish assemblage captured by the demersal trawl. The
 395 assemblage structure differed temporally because species with highest relative biomass b_i
 396 differed in time. In autumn 2009, the dominant fish species were *Scyliorhinus canicula*,
 397 *Trisopterus luscus* and *Mustelus asterias*, representing 18.5%, 13.5% and 12% of the relative
 398 biomass, respectively (Table 3). For the other periods, one species was largely dominant in
 399 the assemblage. In autumn 2014 and 2015, *T. trachurus* was clearly the most dominant
 400 species ($b_i = 81$ and 70%, respectively) while in winter 2015 and 2016, the dominant species
 401 was *Merlangius merlangus* ($b_i = 69.5$ and 66%, respectively).

402 **Table 3**

403 The three species with the highest relative biomasses in the ecosystem for each time period, their biomass density (kg.km^{-2}), benthic contribution
 404 ($\%B$) and associated trophic level (TL_C).

Periods	Dominant species in the ecosystem	Relative biomass (%)	Biomass ($\times 10^3 \text{ kg.km}^{-2}$)	Benthic contribution (mean \pm sd)	Trophic level (mean \pm sd)
Autumn 2009	<i>Scyliorhinus canicula</i>	18.5	0.63	0.56 ± 0.20	3.75 ± 0.58
	<i>Trisopterus luscus</i>	13.5	0.46	0.57 ± 0.27	3.71 ± 0.21
	<i>Mustelus asterias</i>	12	0.39	0.65 ± 0.09	3.29 ± 0.33
Autumn 2014	<i>Trachurus trachurus</i>	81	3.47	0.24 ± 0.11	3.56 ± 0.24
	<i>Merlangius merlangus</i>	6	0.24	0.56 ± 0.05	4.29 ± 0.10
	<i>Scyliorhinus canicula</i>	4	0.16	0.83 ± 0.08	3.41 ± 0.06
Winter 2015	<i>Merlangius merlangus</i>	69.5	4.05	0.56 ± 0.10	5.07 ± 0.13
	<i>Scyliorhinus canicula</i>	10	0.59	0.88 ± 0.08	4.02 ± 0.15
	<i>Limanda limanda</i>	9	0.53	0.78 ± 0.17	4.25 ± 0.16
Autumn 2015	<i>Trachurus trachurus</i>	70	8.75	0.14 ± 0.07	3.31 ± 0.19
	<i>Scomber scombrus</i>	9	1.18	0.07 ± 0.07	3.22 ± 0.35
	<i>Merlangius merlangus</i>	4	0.60	0.42 ± 0.07	4.40 ± 0.12
Winter 2016	<i>Merlangius merlangus</i>	66	6.03	0.51 ± 0.06	4.27 ± 0.13
	<i>Trachurus trachurus</i>	7	0.63	0.28 ± 0.18	4.73 ± 0.33
	<i>Mustelus asterias</i>	6	0.55	0.78 ± 0.07	3.60 ± 0.35

405 **3.2. Contributions of benthic and pelagic sources**

406 **3.2.1. Species scale**

407 Species with pelagic lifestyles had lower %B than benthic ones (Table 4). Both
408 *Scomber scombrus* and *T. trachurus* exhibited mean values lower than 30% regardless of the
409 studied period while mean %B values were always higher than 82% for benthic species (e.g.
410 *Raja clavata* (Fig. 2A)).

411 Among the species sampled at least twice, some of them (*Pleuronectes platessa*, *R.*
412 *clavata*, *M. asterias* or *Microstomus kitt*) always had a stronger benthic contribution (%B \geq
413 $55 \pm 5\%$), whereas others (*T. trachurus*, *Sprattus sprattus*, *Engraulis encrasicolus*, *C.*
414 *lucerna*) always had a stronger pelagic contribution (%B $\leq 45 \pm 5\%$ Fig. 2A). Despite some
415 variation and occasional high %B values, well-known pelagic species (e.g. *S. scombrus*, *C.*
416 *harengus*, *Spondylisoma cantharus* or *S. pilchardus*) generally exhibited low %B values.
417 However, many species displayed high trophic plasticity, i.e. shifted from a stronger benthic
418 to a stronger pelagic contribution depending on the period (Fig. 2A, Table S1). These species
419 were mainly benthic or demersal species (*Callionymus lyra*, *Chelidonichthys cuculus*,
420 *Dicentrarchus labrax*, *M. merlangus*, *Mullus surmuletus*, *Trisopterus* spp.)

421 The trophic level of most species sampled at least twice also varied among periods
422 (Fig. 2B). For most species sampled in autumn and winter (e.g. *C. lucerna*, *Gadus morhua*, *T.*
423 *trachurus*, *Trisopterus minutus*, *Eutrigla gurnardus*, *Limanda limanda*), their trophic level
424 was generally higher in winter than in autumn. Upper trophic level (>4) species (e.g. *D.*
425 *labrax*, *G. morhua*, *Zeus faber*, *M. merlangus*) generally displayed trophic plasticity (i.e.
426 differed in resource use over time) and generalism (i.e. predated on several trophic levels
427 and/or several food sources within a given period) and exhibited comparable contributions of
428 both benthic and pelagic sources.

429

Table 4

430

431

432

433

Results from the mixing model showing the mean contribution of the benthic organic matter source (*A. opercularis*; %*B*) to the community, whether weighing by species biomass or not. Values are reported as quantiles (25% - 50% and 75). The second and third column are expressed at specific scales and represented species with the lowest and highest benthic contribution. For these species, their mean and standard deviation (\pm sd) but also their minimum and maximum of benthic contribution are reported (See Table S1 for more details).

	Species with the min benthic contribution mean \pm sd. [min ; max]	Species with the max benthic contribution mean \pm sd. [min ; max]	Mean benthic contribution unweighted %<i>B</i> mean \pm sd. quantiles (25% - 50% - 75%)	Mean benthic contribution biomass-weighted %<i>B_w</i> mean \pm sd. quantiles (25% - 50% - 75%)
Autumn 2009	<i>S. scombrus</i> 0.18 \pm 0.10 [0.05 ; 0.32]	<i>R. clavata</i> 0.85 \pm 0.10 [0.71 ; 1.00]	0.46 \pm 0.20 (0.34 - 0.49 - 0.59)	0.50 \pm 0.20 (0.49 - 0.59 - 0.69)
Autumn 2014	<i>T. trachurus</i> 0.24 \pm 0.11 [0.14 ; 0.42]	<i>S. canicula</i> 0.83 \pm 0.07 [0.71 ; 0.93]	0.59 \pm 0.22 (0.48 - 0.62 - 0.73)	0.31 \pm 0.20 (0.22 - 0.25 - 0.42)
Winter 2015	<i>T. trachurus</i> 0.21 \pm 0.13 [0.00 ; 0.35]	<i>S. canicula</i> 0.88 \pm 0.08 [0.78 ; 0.98]	0.57 \pm 0.23 (0.38 - 0.59 - 0.72)	0.62 \pm 0.17 (0.57 - 0.62 - 0.75)
Autumn 2015	<i>S. scombrus</i> 0.07 \pm 0.07 [0.00 ; 0.19]	<i>S. stellaris</i> 0.82 \pm 0.16 [0.63 ; 1.00]	0.46 \pm 0.21 (0.35 - 0.46 - 0.58)	0.20 \pm 0.18 (0.17 - 0.17 - 0.25)
Winter 2016	<i>T. trachurus</i> 0.28 \pm 0.18 [0.00 ; 0.47]	<i>R. clavata</i> 0.89 \pm 0.07 [0.81 ; 1.00]	0.53 \pm 0.19 (0.40 - 0.53 - 0.67)	0.51 \pm 0.14 (0.49 - 0.53 - 0.59)

434 3.2.2. *Assemblage scale and energy fluxes*

435 The distribution of %B values in the fish assemblages differed between periods and
436 when species relative biomasses were or were not taken into account (Fig. 3).

437 Regarding trophic interactions (unweighted %B), the EEC was fueled by both benthic
438 and pelagic production at around 50% for all periods (mean %B values varied from $46 \pm 20\%$
439 in autumn 2009 and 2015 to $59 \pm 22\%$ in autumn 2014, Table 4). Regarding energy fluxes
440 (biomass-weighted %B_w), the picture was slightly different. The average benthic contribution
441 in the assemblage dropped by 50% when relative biomasses were included in autumn 2014
442 and 2015 (e.g., autumn 2014, mean %B = 59% and mean %B_w = 31%, Table 4, Fig. 3). At
443 these periods, the fish assemblages were strongly dominated by pelagic species (e.g., *T.*
444 *trachurus*) characterized by low %B values ($24 \pm 11\%$ and $14 \pm 7\%$ in autumn 2014 and
445 2015, respectively; Table 3). In contrast, a slight increase of benthic contribution was
446 observed in autumn 2009 and winter 2015 when relative biomasses were included due to the
447 dominance of benthic or demersal species.

448 3.3. *Functional indices*

449 IFRic relies on the subset of total available trophic resources actually used that varies
450 according to the studied periods. IFRic values varied between 0.21 in autumn 2014 to 0.37 in
451 winter 2016 (Fig.4, Table 2). Trophic levels ranged from 2.69 ± 0.61 for *Micromesistius*
452 *poutassou* to 4.00 ± 0.21 for *M. merlangus* in autumn 2009; from 3.82 ± 0.20 for *C. harengus*
453 to 5.07 ± 0.13 for *M. merlangus* in winter 2015 and from 3.08 ± 0.17 for *R. clavata* to $4.93 \pm$
454 0.36 for *C. lucerna* in winter 2016. Autumn 2009, winter 2015 and 2016 were periods with
455 the highest IFRic when the assemblages were composed of species of both low and high
456 trophic level but also of both low and high %B values. The assemblages thus exploited a wide
457 range of resources.

458 In autumn 2009, the polygon was mainly located at the bottom of the whole trophic
459 space. Trophic levels of species were estimated to be lower at this period. On the contrary, in
460 winter 2015 the polygon was mainly located at the top of the whole trophic space, mainly
461 reflecting the highest estimated trophic levels at this period. Lowest ranges of both %B and
462 trophic levels were found in autumn 2014, leading to the lowest value of IFRic. At this
463 period, the polygon was located at the center of the whole trophic space. The assemblage was
464 composed of intermediate trophic level species, mainly belonging to both pelagic and benthic-
465 based trophic pathways. Intermediate IFRic values were found in autumn 2015. At this
466 period, the range of %B was the highest: from 0.07 ± 0.07 for *S. scombrus* to 0.82 ± 0.16 for
467 *Scyliorhinus stellaris*. This variability reflected that species within the assemblage depended
468 on both benthic and pelagic trophic pathways.

469 Considering the trophic interactions, despite slight variation between periods, the
470 assemblages' values of the isotopic functional indices were close and no clear seasonal
471 pattern was evidenced. IFDis was moderate and always lower than 0.58, meaning that the
472 assemblages were composed of a mix of generalist and specialist species. IFEve was always
473 high and ranged between 0.71-0.81 (Table 2). Species were evenly distributed in the trophic
474 space and exploited the resources equitably. Considering the energy fluxes, IFDis_{biom} and
475 IFEve_{biom} were lower than IFDis and IFEve, respectively (Table 2). Thus, the dominant
476 species were rather generalists suggesting a higher trophic redundancy and potential
477 competition between species. However, it should be noted that despite a decrease, IFEve_{biom}
478 remained high in autumn 2014 (0.57), while IFDis_{biom} (0.23) was low, suggesting resource
479 partitioning.

480

481 **4. Discussion**

482 Our results indicate a high temporal plasticity in trophic interactions within fish
483 assemblages resulting in variable strengths of benthic-pelagic interactions and energy fluxes
484 in a temperate shallow epicontinental sea. Many species displayed trophic plasticity (*i.e.* may
485 differ in resource use over time) and were generalists (*i.e.* can predate on several trophic
486 levels and/or several food sources within a given period), supporting strong benthic-pelagic
487 couplings in the EEC. Trophic interactions differed among studied periods but assemblages
488 were always fueled by a mix of benthic and pelagic food sources. Energy fluxes revealed that
489 the contribution of benthic food sources to the assemblages differs according to the relative
490 importance of the different species at each season. Consequently, dominant species usually
491 drove overall fluxes. The shallowness of this ecosystem may allow for these trophic features.

492 ***4.1. Fish assemblages differed among studied periods***

493 A number of top-down or bottom-up forces (*e.g.*, resource availability, temperature,
494 fishing pressure) may affect the structure and diversity of fish assemblages (Auber et al.,
495 2017; Lynam et al., 2017; McLean et al., 2018; Thompson et al., 2020). Several studies have
496 demonstrated a positive relationship between diversity and ecosystem functioning (Hooper et
497 al., 2005; Tilman et al., 2014). In our study, autumn 2009 was the period with the highest
498 diversity indices (H' and J') which can be explained by the equitability of species biomass in
499 the assemblage. Autumn 2009 and winter 2016 periods were characterized by longer food
500 chains and a greater exploitation of resources. The addition of high trophic level species (*e.g.*,
501 winter 2016) or of intermediate consumers (*e.g.*, autumn 2009) may have lengthened food
502 chains at these periods (Post and Takimoto, 2007).

503 Higher trophic levels in winter may result from environmental variables such as
504 resource availability. In the EEC, there is an autumnal phytoplanktonic bloom (Breton, 2000).
505 Since phytoplankton is consumed by primary consumers, it results in a higher abundance of

506 zooplankton in autumn than in winter (Eloire et al., 2010). Due to the lower abundance of
507 zooplankton in winter, we can hypothesize that fish feed on higher trophic level preys during
508 this period, which results in the highest overall trophic levels in the fish assemblages.

509 The composition of fish assemblages varies seasonally with species migration cycles.
510 This is particularly the case for pelagic species such as *T. trachurus*, which is very abundant
511 in the EEC in summer and autumn as observed in autumn 2014 and 2015. During these
512 periods, it migrates from the North Sea to the EEC, probably due to changes in water
513 temperature (Macer, 1977). This is also the case for whiting in winter. During this period,
514 temperature has an strong influence of its spatial distribution (Loots et al., 2011; Zheng et al.,
515 2001), which explains its high biomass in winter 2015.

516 ***4.2. Trophic plasticity and trophic resource partitioning strengthen benthic-pelagic*** 517 ***couplings***

518 When considering unweighted measures, the average contribution of benthic food
519 sources %B to the fish assemblages ranged between 46% and 59% (Table 4). Species were
520 thus always feeding on both benthic and pelagic production as demonstrated for other shallow
521 marine coastal or estuarine ecosystems (Christianen et al., 2017; Griffiths et al., 2017;
522 Kiljunen et al., 2020; Ying et al., 2020). Due to the shallow depth, species can rely on both
523 benthic and pelagic sources due to physical (*e.g.*, resuspension, sedimentation) and/or
524 biological processes (*e.g.*, fish predation) (Baustian et al., 2014; Griffiths et al., 2017).

525 Many fish species displayed trophic plasticity, relying on benthic or pelagic
526 production depending on the studied period. Such plasticity may originate from changes
527 either in direct predation in relation to environmental variation such as changes in prey
528 abundance or species competition, or in indirect predation such as changes in the diet or
529 trophic level of their prey. This result confirms the hypothesis of Kopp et al. (2015) that

530 species could adapt their foraging strategy in relation to variation of the availability of their
531 trophic subsidies (*i.e.*, changes in prey abundance or prey specific composition). These
532 variations may also be due to the variation of organic matter fluxes. An increase of pelagic
533 productivity may result in an increase in pelagic-benthic coupling, whereby benthic species
534 are fueled by pelagic organic matter (Docmac et al., 2017; Hayden et al., 2019). This coupling
535 may be even more pronounced in the EEC due to the shallow depth.

536 Considering trophic interactions, functional indices (IFRic, IFEve, IFDis) revealed that
537 assemblages were composed of a mix of specialist and generalist species (IFDis between 0.38
538 and 0.58, Table 2) with little variation over time. In addition, there was low functional
539 redundancy and resources were used optimally through complementarity (IFEve \geq 0.71, Table
540 2) between species, thus evidencing niche partitioning. Complementarity between species
541 could result in reduced interspecific competition (Hooper et al., 2005). Following the niche
542 variation hypothesis, species may expand their niches due to a release of interspecific
543 competition (Costa-Pereira et al., 2019; Gajdzik et al., 2018; Van Valen, 1965). Species can
544 partition their resources through a combination of differences in trophic patterns and habitat
545 use. Many species may depend on both benthic and pelagic sources, but can also predate on
546 several trophic levels (*i.e.*, omnivory; Cury et al., 2003, Thompson et al., 2007; Vandermeer,
547 2006). A shallow depth allows pelagic species to migrate vertically and consume benthic
548 preys (Baustian et al., 2014; Griffiths et al., 2017). Stomach content analyses performed on
549 fish species of the EEC have shown that some benthic preys were found in the diet of some
550 pelagic species. For example, benthic amphipods were found in the stomach contents of
551 clupeidae and benthic fish (*e.g.* callionymidae) in the diet of *S. scombrus* (Cachera, 2013). In
552 this ecosystem, high $\delta^{13}\text{C}$ values were recorded for pelagic species probably as a result of the
553 consumption of benthic invertebrates. This behavior was observed in other shallow
554 ecosystems like the Seto Sea (mean depth of 37m, (Takai et al., 2002) or the Baltic sea mean

555 (depth of 42m, (Kiljunen et al., 2020)). Similarly, in lakes, pelagic species can derive up to
556 50-90% of their energy from benthic sources (Schindler et al., 1996; Vander Zanden and
557 Vadeboncoeur, 2002). For benthic species, the shallow depth allows them to adopt an
558 opportunistic behavior by integrating benthic production but also taking advantage of the
559 pelagic production sedimentation via the pelagic-benthic coupling (van Denderen et al.,
560 2018). Thus, depth is one of the main drivers for pelagic-benthic temporal variation in
561 shallow ecosystems, including the EEC (Cresson et al., 2020; Giraldo et al., 2017; Kopp et al.,
562 2015).

563 ***4.3. Temporal variation of benthic-pelagic couplings and energy fluxes***

564 When focusing on energy fluxes, the most dominant fish species were generalists
565 ($IFDis_{biom} \leq 0.40$, Table 2). Trophic generalism is common in marine ecosystems (Thompson
566 et al., 2007) and, in our study, it was particularly marked at all periods. In winter, the
567 dominant species was whiting, a high trophic level demersal piscivorous fish. Upper trophic
568 level species are considered as ultimate couplers. Their predatory nature allows them to
569 forage on both benthic and pelagic preys, and to stabilize food webs (Cury et al., 2003,
570 McCann, 2000; Rooney et al., 2006; Rooney and McCann, 2012; Udy et al., 2019).

571 In autumn 2014, even though the dispersion was similar to other periods (low
572 $IFDis_{biom} \leq 0.40$), evenness was the highest ($IFEve_{biom} = 0.57$, Table 2) suggesting higher
573 optimal resource use in autumn 2014 compared to other periods. According to the resource
574 diversity hypothesis (i.e. ecological opportunity), the diversity of available resources
575 promotes niche expansion and divergence among species of consumers (Araújo et al., 2011;
576 Costa-Pereira et al., 2019). Thus, we can hypothesize that at this period, resources were
577 sufficient to support assemblages leading to niche segregation to reduce competition whereas,

578 for other periods, resources were insufficient leading to some trophic redundancy ($IFEve_{biom} \leq$
579 0.41, Table 2).

580 In a similar study on a shallow ecosystem, Ying et al. (2020) suggested that high
581 functional redundancy was caused by the abundance of pelagic fish with similar traits. Our
582 results show that trophic plasticity goes beyond a replacement of dominant species by others
583 with similar traits, and that similar assemblages (in terms of species composition) can respond
584 differently depending on other biotic or abiotic factors (*e.g.*, productivity, competition, niche
585 overlap).

586 The generalist behavior of dominant species ($IFDis_{biom} \leq 0.40$) may be a way to avoid
587 competition or may also reveal the high abundance of one food source (Lefebvre et al.,
588 2009a). The broadening of resource use may improve ecosystem functioning by allowing a
589 more complete use of all available resources and promote species coexistence (Leduc et al.,
590 2015; Petchey, 2003). However, it should be noted that a generalist species can be either
591 composed of a sum of generalist individuals or a sum of specialist individuals (Bearhop et al.,
592 2004). Additional analyses at the individual level would provide a better understanding of the
593 structure and functioning of this ecosystem (Bolnick et al., 2011, 2003; Clegg et al., 2018;
594 Ingram et al., 2018).

595 **4.4. Strengths and limitations of the study**

596 This study relies on a large temporal sampling plan of a fish assemblage to decipher
597 variability in benthic-pelagic couplings at five different periods. To be comparable and
598 interpretable, isotopic values were standardized to account for the variability of the isotopic
599 baselines (Hoeinghaus and Zeug, 2008) by calculating for each period the benthic
600 contribution ($\%B$) and the trophic level (TL_C) using the same two source mixing model for
601 both metrics. A similar standardization was used by Quevedo et al. (2009) or Kiljunen et al.

602 (2020) but the originality of our study stands both in the use of the p-space for the
603 determination of the functional isotopic metrics and the use of a common mixing model for
604 both metrics. Another strength is the use of unweighted/biomass-weighted metrics that assess
605 two complementary facets of the trophic relationships in the fish assemblage. However, our
606 approach still relies on strong assumptions regarding isotope mixing models. First, the
607 isotopic values of the sources should reflect the time periods over which the consumer tissues
608 are synthesized (Phillips et al., 2014). Fortunately, isotopic values of the baseline sources in
609 our study stayed quite stable over time with the exception of higher $\delta^{15}\text{N}$ values for both
610 zooplankton and *A. opercularis* in autumn 2009 that could lead to an underestimation of fish
611 trophic levels at this period. However, we are quite confident in our results since the three
612 autumn periods displayed similar patterns in p-space. Pelagic (zooplankton) and benthic
613 (molluscs such as bivalves or gastropods) baselines are often used in marine studies (e.g.
614 Kiljunen et al., 2020; Kopp et al., 2015). *A. opercularis* is a suspension feeder and the
615 suspended particulate matter it assimilates in the deep layer originates from a mix of
616 reprocessed settling organic matter from the surface and resuspended organic matter from the
617 sediment (Rodil et al., 2020). This explains why isotopic ratios of benthic suspension feeders
618 differ significantly from zooplankton. An alternative to using primary consumers as isotopic
619 baselines would have been to use indicator fish species that rely exclusively on pelagic or
620 benthic subsidies (Duffill Telsnig et al., 2018). In our study, *S. scombrus* and *R. clavata*
621 would be the best candidates. But this approach requires isotopic values at each period and
622 invariable diet of the two fish species, both of which were not the case (Table S2). Second the
623 trophic discrimination factors should be known for each taxon, tissue and diet under study
624 (Phillips et al., 2014). Mixing models are sensitive to the values of trophic discrimination
625 factors for carbon and nitrogen (Bond and Diamond, 2011). However, changing their values
626 identically would have changed the absolute outputs of the mixing model but not their general

627 trend (Lefebvre et al., 2009b). Here, a problem arises if one considers that trophic
628 discrimination factors vary over time. Several studies showed that the trophic discrimination
629 factor of nitrogen in consumer tissues decreased when growth rate increased, both in fish
630 (Gaye-Siessegger et al., 2004) and in invertebrates (Gorokhova, 2018; Lefebvre and Dubois,
631 2016). More recently, Jacobi et al. (2020) showed that consumer length and season were
632 factors explaining the trophic level of a large river fish beyond $\delta^{15}\text{N}$ values of its prey.
633 Finally, a starvation period would increase the $\delta^{15}\text{N}$ values in consumer tissues (Doi et al.,
634 2017). Trophic level values of two fish species stretched the p-space polygons towards higher
635 trophic levels by a value of 0.5 in winter 2015 and 2016. Further, trophic level values of the
636 fish assemblage in winter 2015 were on average higher than for the other periods but still the
637 vast majority of trophic level values remained between 3 and 4.5 whatever the season.
638 Unfortunately, we do not have any evidence to support food and/or growth limitation
639 hypotheses for our fish assemblage and therefore estimations of variable trophic
640 discrimination factors are not possible. In this regard, further developments are obviously
641 needed but in the meantime, we have formulated similar assumptions as previous studies in
642 the field.

643

644 **Conclusion**

645 Couplings between benthic and pelagic realms are persistent in the EEC where most
646 species display trophic plasticity and can therefore change their food source over time
647 depending on their availability or on potential competition with other species. In addition,
648 dominant species are rather generalist: they can predate on several food sources but also on
649 prey from different trophic levels. These behaviors are permitted by the shallowness of this

650 ecosystem. Finally, accounting for fish biomass in trophic and isotopic functional metrics was
651 complementary and allowed the consideration of energy fluxes within the ecosystem.

652 **List of figures**

653

654 **Fig. 1:** Location of sampling stations in the Eastern English Channel (EEC) during the five
655 surveys: CGFS 2009 (green squares), CAMANOC 2014 (orange squares), IBTS 2015 (purple
656 circles), CGFS 2015 (blue squares) and IBTS 2016 (pink circles). Autumn and winter periods
657 were represented by squares and circles, respectively.

658

659 **Fig. 2:** Variation of benthic contributions $\%B$ (A) and trophic level TL_C (B). Green squares:
660 autumn 2009 (CGFS 2009); orange squares: autumn 2014 (CAMANOC); purple circles:
661 winter 2015 (IBTS 2015); blue squares: autumn 2015 (CGFS 2015); pink circles: winter 2016
662 (IBTS 2016).

663

664 **Fig. 3:** Comparison of violin plots of the scaled benthic contribution unweighted ($\%B$) or
665 weighted by biomass ($\%B_w$). The bottom and top edges of the boxplots represent the first and
666 third quartiles. The horizontal line is the median value. The whiskers' extremities represent
667 1.5 times the interquartile space (the distance between the first and third quartile). Larger
668 zones of each violin plot represent the benthic contribution values supporting most of the
669 biomass.

670

671 **Fig 4:** Comparison of IFRic among the five studied periods. Each point corresponds to the
672 mean trophic level (TL_C) and benthic contribution ($\%B$) of each species. The black polygon

673 corresponds to the largest IFRic space calculated for the meta-assemblage gathering the 5
674 studied periods, while the red polygon corresponds to the IFRic of each studied period. The
675 silhouettes represent the three species with the highest relative biomasses in the ecosystem for
676 each studied period. 1: *Scyliorhinus canicula*; 2: *Trisopterus luscus*; 3: *Mustelus asterias*; 4:
677 *Trachurus trachurus*; 5: *Merlangius merlangus*; 6: *Limanda limanda*; 7: *Scomber scombrus*.

678

679

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723

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