



**HAL**  
open science

## **Stomach content and stable isotope analyses provide complementary insights into the trophic ecology of coastal temperate benthic-demersal assemblages under environmental and anthropogenic pressures**

Sturbois Anthony, A Cozic, Gauthier Schaal, Nicolas Desroy, Pascal Riera, Olivier Le Pape, P Le Mao, A Ponsero, Alexandre Carpentier

### ► To cite this version:

Sturbois Anthony, A Cozic, Gauthier Schaal, Nicolas Desroy, Pascal Riera, et al.. Stomach content and stable isotope analyses provide complementary insights into the trophic ecology of coastal temperate benthic-demersal assemblages under environmental and anthropogenic pressures. *Marine Environmental Research*, 2022, 182, pp.105770. 10.1016/j.marenvres.2022.105770 . hal-03830764

**HAL Id: hal-03830764**

**<https://hal.science/hal-03830764v1>**

Submitted on 15 Feb 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 **Stomach content and stable isotope analyses provide complementary**  
2 **insights into the trophic ecology of coastal temperate benthic-demersal**  
3 **assemblages under environmental and anthropogenic pressures**

4 Sturbois A. <sup>1,2,3</sup>, Cozic A. <sup>1,2</sup>, Schaal G. <sup>3</sup>, Desroy N. <sup>4</sup>, Riera P. <sup>5</sup>, Le Pape O. <sup>6</sup>, P. Le  
5 Mao <sup>4</sup>, Ponsero A. <sup>7,2</sup>, Carpentier A. <sup>8</sup>

6  
7 <sup>1</sup> *Vivarmor Nature, 18 C rue du Sabot, 22440 Ploufragan, France*

8 <sup>2</sup> *Réserve naturelle nationale de la Baie de Saint-Brieuc, site de l'étoile, 22120*  
9 *Hillion, France*

10 <sup>3</sup> *Laboratoire des Sciences de l'Environnement Marin (LEMAR), UMR 6539*  
11 *CNRS/UBO/IRD/IFREMER, BP 70, 29280 Plouzané, France*

12 <sup>4</sup> *Ifremer, Laboratoire Environnement et Ressources Bretagne nord, 38 rue du Port*  
13 *Blanc, 35800 Dinard*

14 <sup>5</sup> *Sorbonne Université, CNRS, Station Biologique de Roscoff, UMR7144, Place*  
15 *Georges Teissier, CS90074, 29688, Roscoff Cedex, France.*

16 <sup>6</sup> *DECOD (Ecosystem Dynamics and Sustainability), Institut Agro, INRAe, Ifremer*  
17 *Rennes, France*

18 <sup>7</sup> *Saint-Brieuc Agglomération Baie d'Armor, 5 rue du 71ème RI, 22000 Saint-Brieuc,*  
19 *France*

20 <sup>8</sup> *Université de Rennes 1, BOREA, Muséum National d'Histoire Naturelle, Sorbonne*  
21 *Université, Université de Caen Normandie, Université des Antilles, Campus de*  
22 *Beaulieu, 35000 Rennes, France.*

23  
24 *Oceanic cruise: Desroy N., 2019. RESTRO 19 cruise, RV Thalía, <https://10.17600/18000934>*

25  
26 **Highlights:**

27 - Trophic ecology of fish assemblages (stomach content and stable isotopes) were  
28 studied in the bay of Saint Brieuc (France)

29 - The fish and cephalopod community was composed of 21 taxa; eight species  
30 accounted for 94.4% of the total abundance.

31 - An impoverished assemblage may reveal the impact of scallop dredging on a part  
32 of the Bay.

33 - Amphipoda was the main prey with many additional items depending on predator  
34 species.

35 - At the assemblage scale, fish and demersal fauna mostly relied on POM/SOM-  
36 based food chains.

37  
38  
39 **Abstract:**

40 Assessing organic matter fluxes and species interactions in food webs is of main

41 interest to understand the ecological functioning in bays and estuaries characterised

42 by a wide diversity of primary producers and consumers. Demersal fish and  
43 cephalopod assemblages were studied across a network of 24 shallow subtidal  
44 stations in the bay of Saint-Brieuc for their diversity, stable isotope compositions and  
45 stomach contents. The community was composed of 21 taxa, eight species  
46 accounting for 94.4% of the total abundance. Three different assemblages were  
47 identified along bathymetric gradient and spatial patterns in fish dredging. Marine  
48 POM and SOM were the most likely bases of food webs regarding  $\delta^{13}\text{C}$  range  
49 displayed by fish and cephalopod without differences among assemblages.  
50 Amphipoda was the main prey item in stomachs leading to significant diet overlaps  
51 among fish species, with some variations in additional items. *Sepia officinalis* was  
52 characterised by a singular diet and very low dietary overlap with other species.  
53 Contrasted stable isotope values and niche overlaps among species were evidenced  
54 in the  $\delta^{13}\text{C} / \delta^{15}\text{N}$  space. *Callionymus lyra* and *Buglossidium luteum*, characterised by  
55 the widest isotopic niches, encompassed those of other species, except the singular  
56  $^{13}\text{C}$ -depleted *Spondyliosoma cantharus*. Coupling taxonomic assemblages, stomach  
57 contents and stable isotope analyses help disentangling the resources uses and  
58 evidencing trophic pathways. Contrasts in fish and cephalopod demersal  
59 assemblages occurring at different depths not necessarily imply differences in the  
60 trophic resources uses in such complex shallow coastal ecosystems under  
61 anthropogenic influences.

62 **Keywords:** fish assemblages, functioning, stomach contents, stable isotope

63

64

65

## 66 **I. Introduction:**

67 Coastal areas are among the most productive marine systems in the world,

68 sustaining many ecological processes and ecosystems services (Costanza et al.,

69 1997). Worldwide, these ecosystems are suffering severe taxonomic and functional  
70 changes in response to cumulative effects of anthropogenic disturbances including  
71 overfishing, pollution, climate change, habitat degradation and introduction of non-  
72 indigenous species (Gray, 1997; Claudet & Fraschetti, 2010). Human influences  
73 induce both acute and chronic effects over various temporal and spatial scales, and  
74 can ultimately lead to broad-scale losses of productive habitats, and alteration of  
75 community structure and function (Ellis et al., 2000).

76 Bays and estuaries provide habitats to a wide range of species of potential ecological  
77 importance and commercial interest. The production in such ecosystems is  
78 supported by a wide diversity of primary producers, including phytoplankton,  
79 seaweeds, seagrass, mangroves, salt marsh plants, and benthic diatoms (Bouillon et  
80 al., 2011). The contribution of these diverse sources to estuarine and coastal food  
81 webs differs substantially across systems around the world, particularly for nekton  
82 (e.g. fishes, cephalopod), which utilize multiple sources of organic matter over space  
83 and time because of their mobility and feeding behavior (Kundu et al., 2021).

84 Individuals from many fish or cephalopod species concentrate during the juvenile  
85 stage in spatially restricted nursery areas within coastal habitats and estuaries (Beck  
86 et al., 2001; Brown et al., 2018; Seitz et al., 2014) where they feed on abundant  
87 macrobenthos, especially during biomass peaks from late spring to early fall in  
88 temperate areas (Beukema, 1974; Nicolas et al., 2007; Saulnier et al., 2020). This  
89 concentration of benthic feeding juveniles results in density-dependent regulation (Le  
90 Pape and Bonhommeau, 2015), especially related to inter-specific relationships (Post  
91 et al., 1999). Food competition may occur when individuals from one or several  
92 species share a common feeding strategy and rely on limited preys (Birch, 1957).  
93 Even if food partitioning limits competition, most benthic-demersal fish species are  
94 considered as opportunistic predators and prey on a shared pool of preys (Hunsicker

95 et al., 2011), especially at juvenile stage, leading to potential competition processes  
96 at intra and interspecific levels (Tableau et al., 2019).

97 Stomach content analysis (SCA) and stable isotope analysis (SIA) are two tools to  
98 infer basal carbon sources, trophic interactions and/or food web structure. SCA  
99 provide taxonomic information of prey items and their abundance, weight and  
100 occurrence. However, SCA represents a snapshot of recently (hours to day) ingested  
101 prey and can be biased by different digestibility among targeted items (Hyslop,  
102 1980). As predators integrate both carbon and nitrogen isotopic compositions of their  
103 preys into their own tissues, SIA provides a longer temporally integrated information  
104 on dietary habits (days to months according to tissues) reflecting actually assimilated  
105 prey (Fry, 2008). However, SIA fails to provide accurate information about the  
106 diversity and identity of prey items. Considering this complementarity, the association  
107 of SCA and SIA allows to take the best of both approaches by the calculation of  
108 complementary metrics (Cresson et al., 2014; Davis et al., 2012; Leclerc et al., 2013;  
109 Petta et al., 2020; Togashi et al., 2019).

110 In stable isotope analysis, the concept of isotopic niche is frequently analysed  
111 through different metrics used to examine food web structure, i.e., resource use and  
112 trophic positions among organisms, populations or trophic groups (Layman et al.,  
113 2007a). Trophic niche variability [*sensus* Newsome et al. (2007)] reflects the  
114 availability of food resources, habitat uses, behaviours and distributions within  
115 ecosystems (Bolnick et al., 2002; Quevedo et al., 2009). Intraspecific niche can  
116 depict opportunistic or specialist feeding behaviour within species functional diversity,  
117 while interspecific niche can reveal competition or resources partitioning strategies  
118 among populations. Interestingly, the concepts of niche variability and overlap can be  
119 tested among predator species through metrics respectively derived both from  
120 stomach contents [ $niche_{SCA}$  (Petta et al., 2020; Schoener, (1971))] and isotope

121 compositions [niche<sub>SIA</sub> (Petta et al., 2020; Cucherousset and Villéger, 2015; Layman  
122 et al., 2007a, 2012; Rigolet et al., 2015)].

123 Benthic-demersal fish and cephalopod assemblages may vary spatially in response  
124 to natural or anthropogenic factors. Variability in species richness or diversity among  
125 assemblages can also affect niches and food web structure (Wellard Kelly et al.,  
126 2021) and increase competition and specialization leading to a niche reduction for  
127 some species (Connell, 1983). The relationship between assemblage compositions  
128 and trophic complexity, including niches variability and overlap, is therefore an  
129 important aspect for these communities.

130 On the French coast of the English Channel, coastal fish and cephalopod  
131 communities and nurseries have been studied in the main coastal bays and estuaries  
132 [e.g. Rance estuary (Le Mao, 1985), bay of Seine (Day et al., 2021 ; Saulnier et al.  
133 2020), bay of Mont-Saint-Michel (Kostecki et al., 2012), bay of Morlaix (Dauvin, 1988)  
134 or Bay of Somme (Auber et al., 2017)] providing powerful information for the  
135 understanding and the conservation of coastal habitats. In the bay of Saint-Brieuc  
136 (Western English Channel), fish communities that use the intertidal area at high tide  
137 have been studied in relation to salt marsh (Laugier, 2015; Sturbois et al., 2016) and  
138 green tides (Le Luherne et al., 2016). Despite a recent update of the benthic  
139 macrofauna knowledge in the subtidal area belonging to the “Baie de Saint-Brieuc –  
140 Est” Natura 2000 site and neighbouring the National Nature Reserve of the bay of  
141 Saint-Brieuc (Sturbois et al., 2021a), data on benthic-demersal fish and cephalopods  
142 are rare and old (Gully, 1981; Le Dean and Moreau, 1981). The marine protected  
143 areas did not prevent this shallow subtidal area under a megatidal regime from  
144 different anthropogenic activities (Shellfish farming, eutrophication, invasive species)  
145 and the bay has been supporting intense bottom fishing (mostly scallop dredging) for  
146 decades. This fishing pressure has affected benthic habitats (Sturbois et al., 2021a)

147 and may have potential impacts on fish and cephalopod communities of the marine  
148 protected area.

149 In this study, we analysed fish and cephalopod communities at species and  
150 assemblages scales in the shallow soft bottom sediments of the bay of Saint-Brieuc  
151 and on the associated food web from primary producers to benthic consumers. After  
152 the analysis of the distribution of fish and cephalopods species in order to distinguish  
153 the taxonomic assemblages, our objective was to disentangle sources uses and  
154 trophic relationships among species, particularly: (1) Are taxonomic fish and  
155 cephalopod assemblages supported by different trophic sources? ; (2) How do  
156 trophic strategies of demersal fish and cephalopod species can be evidenced by  
157 crossing stomach contents and stable isotope analyses? We finally discussed results  
158 in relation with methodological benefits and caveats when crossing stomach contents  
159 and stable isotope analyses, previous information on the benthic preys production,  
160 and their implications for the understanding and the conservation of the marine  
161 protected areas.

162

## 163 **II. Material and methods**

### 164 **2.1 Study area, the bay of Saint-Brieuc (Western English Channel, France)**

165 The study area (Figure 1) encloses 11,700 ha of shallow soft-bottom sediments (0-15  
166 m) under the influence of a semi-diurnal megatidal regime. Tidal range varies from 4  
167 m at neap tides to nearly 13 m during spring tides.

168 In 2019, the benthic macrofauna was dominated by molluscs, annelids and  
169 crustaceans (Sturbois et al., 2021a). Knowledge concerning subtidal fishes in the  
170 study area are rare and old. In the last studies dating back to 1981, demersal fish  
171 communities were dominated by *Pleuronectes platessa*, *Psetta maxima*, *Solea*  
172 *lascais*, *S. vulgaris*, and *Scophthalmus rhombus*, while *Spondyliosoma cantharus*  
173 was limited to the western part of the bay, and *Limanda limanda* and *Platichthys*

174 *flesus* were scarce (Le Dean and Moreau, 1981; Gully, 1981). In the intertidal area,  
175 Le Luherne et al. (2016) evidenced the use of sandy beaches at high tide by some  
176 species; e.g. *Buglossidium luteum*, *Pleuronectes platessa*, *Pomatoschistus microps*,  
177 *Chelon spp.*, and *Dicentrarchus labrax*; these three last taxa also using the salt  
178 marsh channels (Laugier, 2015; Sturbois et al., 2016).  
179 Despite bordering the National Nature Reserve of the bay of Saint-Brieuc and  
180 partially belonging to the Natura 2000 “Baie de Saint-Brieuc-Est” site (European  
181 Union network, FR5300066), the study area is exposed to a number of  
182 anthropogenic pressures including mussel culture and scallop dredging (Sturbois et  
183 al., 2021b, 2021a). Mussels are farmed on wooden poles (312 ha; Figure 1) in the  
184 north-eastern part of the intertidal area and on ropes in the western part of the study  
185 area. The sea bed is exposed to long-term scallop dredging (Sturbois et al., 2021a).  
186 Some areas are colonized by the non-indigenous slipper limpet *Crepidula fornicata*  
187 especially in the western part of the bay (Blanchard et al., 2001; Hamon and  
188 Blanchard, 1994). The bay also suffers from eutrophication resulting in macroalgae  
189 proliferation and cyclic green tides episodes (Charlier et al., 2007; Gravier, 2012).  
190 These green tides influence the dynamics of some benthic populations of  
191 invertebrates in the intertidal area (Sturbois et al., 2021b) and impact fish nursery  
192 grounds in the upper parts of the intertidal area (Le Luherne et al., 2017, 2016).

193

## 194 **2.2 Sample collection and laboratory processes**

### 195 **2.2.1 Fish and cephalopods**

196 Fish and cephalopods were sampled in September 2019 using beam trawls (2.5/3  
197 knots) at 24 stations (Figure 1). Deeper stations (n= 14) were sampled with a 3.0 m  
198 beam trawl (1 cm mesh size, length of hauls = 1365m ± 397, mean length ± sd)  
199 towed by the RV *Thalia*. Shallower stations (n= 10) were sampled with a 1.5 m beam  
200 trawl (1 cm mesh size, length of hauls = 774m ± 8) towed by the *Emeraude Explorer*  
201 semi-rigid pneumatic boat. Fish were identified and measured (fork length, nearest



202 mm) on board before release. Some individuals were collected, euthanized with an  
203 overdosed solution of benzocaine (400 mg.L<sup>-1</sup>), and immediately frozen (-20°C) for  
204 later stable isotope (SIA) and stomach content (SCA) analyses. Note that skates  
205 (biopsy for SIA) and sea horses were systematically released.

206 In the laboratory, each fish was measured (fork length, precision: 0.01 cm) and  
207 weighted (total mass, precision: 0.0001 g) before dissection. Fish stomachs were  
208 extracted and weighted (full and without stomach content). When present, prey items  
209 were sorted under a binocular microscope into their lowest possible taxonomic group,  
210 counted and weighted (wet weight). The number of samples depends on the  
211 abundance of fish and cephalopods in the study area. To deal with a number of SCA  
212 samples < 30 individuals for some species we complemented and discussed local  
213 results with respect to a species-level review of SCA at larger scale in Europe (see  
214 section 4.3).

215 Samples for SIA consisted of individual white dorsal muscle tissues free of any bone,  
216 skin or scales fragments. All samples were rinsed, dried at 60°C for 48 h, and ground  
217 into a fine powder using a marble mortar.

### 218 **2.2.2 Benthic macrofauna**

219 Benthic macrofauna was sampled with a Rallier du Baty-dredge. Contents were  
220 gently sieved through a 5-mm square mesh sieve. Macrofauna was then sorted on  
221 board and stored at -20°C until further treatment. In the laboratory, animals were  
222 identified to the lowest possible taxonomic level and rinsed. Samples for SIA  
223 consisted of individual muscle tissues of large species (i.e. bivalves, prawns) or  
224 whole individual (for amphipods). The slipper limpet *Crepidula fornicata* containing  
225 calcium carbonates was split into two subsamples, acidified and non-acidified,  
226 respectively (Androuin et al., 2019). All samples were rinsed, dried at 60°C for 48 h,  
227 and ground into a fine powder using a marble mortar.

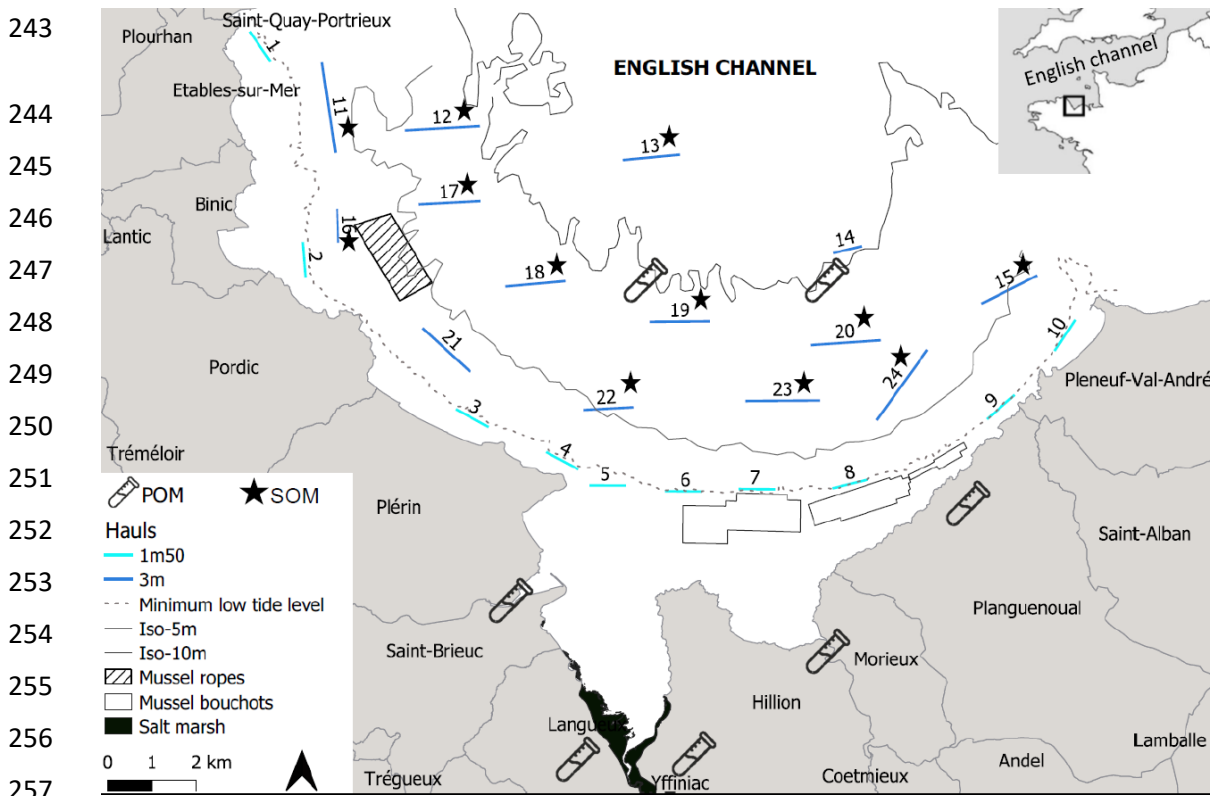
228

229

### 230 2.2.3. Trophic sources, primary producers and organic matter

231 Sedimentary organic matter (SOM) was collected at 12 stations from samples of  
232 sediment collected with the Rallier du Baty dredge (Figure 1). For each station, one  
233 subsample was acidified (10% HCl) and re-dried overnight at 60°C, whereas the  
234 other subsample remained untreated. Marine and freshwater samples collected for  
235 suspended particulate organic matter (POM) were pre-filtered through a 90- $\mu$ m-mesh  
236 to remove large detritus and then filtered on precombusted (500°C, 5h) Whatman  
237 GF/F filters (47 mm diameter). POM collected from river basins (POM\_TER, 5  
238 stations), and offshore (POM\_SEA, 2 stations) were differentiated.

239 Leaves and twigs of the most representative vascular plants colonizing salt marshes  
240 (Sturbois and Bioret, 2019, Sturbois et al. 2022) and *Ulva* spp. were also collected.  
241 Samples were rinsed in the laboratory to be cleaned from epibionts, dried at 60°C for  
242 48h, and ground into a fine powder using a marble mortar.



258 Figure 1: Location of the study area and sampling strategy: length of hauls (colored line),  
259 location of particulate organic matter (POM, test tube) and sedimentary organic matter (SOM,  
260 black stars) samples, depths (grey lines).

### 261 **2.3 Stable isotope analysis**

262 At least three replicates were analyzed per species when possible; however, for few  
263 taxa less replicates were available (Supplementary material, Appendix A). Powdered  
264 samples were packed into 5 x 8 mm ultra-clean tin capsules and analysed using an  
265 elemental analyser (EA Flash 2000 from ThermoFisher Scientific) coupled with an  
266 isotope ratio mass spectrometer (Delta V Plus from ThermoFisher Scientific) at the  
267 stable isotope facility of the Pole Spectrométrie Océan at the University of Bretagne  
268 Occidentale (Brest, France).

269 Stable isotope ratios were reported in the standard  $\delta$  notation as units of parts per mil  
270 (‰) relative to the international reference standard:

$$271 \quad \delta X = [(R_{\text{Sample}}/R_{\text{Standard}}) - 1] * 10^3$$

272 where  $X$  is  $^{13}\text{C}$  and  $^{15}\text{N}$  and  $R$  is the corresponding ratio of  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$ .

273 Reference standard used were Vienna-Pee Dee Belemnite for  $^{13}\text{C}$  and atmospheric  
274  $\text{N}_2$  for  $^{15}\text{N}$  (precision: 0.1‰).

275 Values of  $\delta^{13}\text{C}$  from acidified subsamples were combined with those of  $\delta^{15}\text{N}$  from  
276 untreated subsamples to compute both slipper limpets and SOM stable isotope  
277 values, undisturbed by calcium carbonate residues ( $\delta^{13}\text{C}$ ) and by acidification ( $\delta^{15}\text{N}$ )  
278 (Androuin et al., 2019).

### 279 **2.4 Data Analysis**

280 Data sets were investigated to analyse spatial patterns in fish and cephalopod  
281 assemblages, and in both the composition and the structure of the food web  
282 including (i) primary food resources, (ii) benthic invertebrates and (iii) fish and  
283 cephalopods. Prior to statistical analysis, abundance of fishes and cephalopods  
284 measured with the 3.0 m and 1.5 m beam trawls were standardized for 0.1 ha. SIA  
285 and SCA were used to infer on the niches variability and overlap between the most  
286 abundant fish species. All analyses were performed within the R environment.

287 **2.4.1 Fish and cephalopod assemblages**

288 A Hierarchical Cluster Analysis (HCA) was performed to distinguish fish and  
289 cephalopod assemblages (*i.e.* station groups) by using the Bray-Curtis dissimilarity  
290 (abundance raw data) between each pair of samples and by applying the Ward's  
291 clustering method.

292 Then, in order to assess the different components of  $\alpha$ -diversity at the both scales of  
293 the bay (*i.e.* including all stations) and the taxonomic assemblages derived from the  
294 HCA: the mean number per 0.1 ha and occurrence for each species, the mean total  
295 number of individuals per 0.1 ha (N), taxa richness (S), Shannon-Weaver index (H')  
296 and Pielou's species evenness (J) were calculated for each station on raw  
297 abundance data (R package BiodiversityR).

298

299 **2.4.2 Stable isotope analysis**

300 Differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of fish and cephalopod were tested with a two-way  
301 ANOVA by permutation against the factors "Species" and "Assemblages". Niche<sub>SIA</sub>  
302 were analysed through community-wide metrics (Layman et al., 2007a ; R package  
303 SIBER) calculated at species scale for the most abundant fish and cephalopod  
304 species:

- 305 -  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  range (CR and NR): Distance between the highest and the  
306 lowest  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, respectively, for a given fish or cephalopod  
307 species). CR is one representation of basal sources diversity supporting the  
308 species whereas NR is one representation of the trophic level diversity at the  
309 species level;
- 310 - *Total Area* (TA): Convex hull area encompassed by a given fish or  
311 cephalopod species in the  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  2D  $\delta$  space. This represents a measure  
312 of the total amount of niche space occupied, *i.e.*, a proxy of overall trophic  
313 strategies (specialists vs. opportunists);

- 314 - *Mean distance to centroid (CD)*: Average Euclidean distance of each  
315 individual to the  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  species centroid, where the centroid is the mean  
316  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  value for all individuals of a given fish or cephalopod species.  
317 This metric provides a measure of the average degree of variability in trophic  
318 strategy;
- 319 - *Mean nearest neighbor distance (NND)*: Mean of the Euclidean distances to  
320 each individual nearest neighbor within each fish species niche, i.e., a  
321 measure of the overall density of individual packing.

322 Four other indices (Cucherousset and Villéger, 2015 ; script `si_div`) were also  
323 calculated to analyse the niche overlap between fish and cephalopod species, and  
324 the extent of their trophic niche:

- 325 - *Isotopic similarity (ISim)*: the ratio between the isotopic niche of the  
326 intersection and of the union of the two fish or cephalopod species  
327 considered. It ranges from 0 when there is no isotopic overlap to 1 when the  
328 species with the lowest isotopic richness fills a subset of the isotopic space  
329 filled by the species with the highest one. ISim was calculated in the two  
330 dimensions of the 2D  $\delta$ -space and for each isotope (i.e. one dimension);
- 331 - *Isotopic nestedness (Ines)*: Ratio between the area of the intersection and  
332 the area filled by the species with the narrowest isotopic niche. It ranges from  
333 0 when there is no isotopic overlap to 1 when the group with the lowest  
334 isotopic richness fills a subset of the isotopic space filled by the group with the  
335 highest one;
- 336 - *Isotopic divergence (IDiv)*: Distribution of species individuals within the  
337 convexhull. IDiv is minimal (i.e. tends to 0) when most of the points are close  
338 to the centroid of the convex hull, and individuals with the most extreme  
339 stable isotope values are rare in a community. IDiv tends to 1 when all the  
340 points are located on the edges of the convex hull and individuals with  
341 extreme stable isotope value(s) dominate;

342 - *Isotopic Evenness* (IEve): Regularity in the distribution of individual of a given  
343 fish or cephalopod species along the shortest tree that links all the individuals.  
344 IEve tends to 0 when most of individuals are packed within a small region of  
345 the stable isotope space while a few others are far from this cluster. IEve  
346 tends to 1 when individuals are evenly distributed in the stable isotope space.

347

### 348 2.4.3 Stomach contents analysis

349 The importance of prey taxa in the diet of each species was assessed by the main  
350 food index (MFI) using the following equation (Rodriguez, 1996):

$$351 \quad MFI = \sqrt{W\% \frac{O\% + N\%}{2} * 100}$$

352 Where W%: weight percentage of one item to total weight of all items; O%: frequency  
353 of an item to total number of examined stomachs; N%: percentage of number of an  
354 item to total number of all preys. Prey items are considered as preferential (MFI>75),  
355 principal (50<MFI<75), secondary (25<MFI<50) or accidental (MFI<25).

356 Niche<sub>SCA</sub> breadth (Shannon–Wiener Index) was calculated from abundance  
357 (niche<sub>SCA-N</sub>) and weight (niche<sub>SCA-W</sub>) in stomach content raw data. A HCA was  
358 performed on stomach contents raw abundance data to distinguish groups of fish or  
359 cephalopod characterised by similar feeding strategies (*i.e.* same pool of preys),  
360 using the methods described for fish and cephalopod assemblages in section 2.4.1.  
361 Complementary, the Schoener index of trophic overlap (Sto) was calculated on  
362 abundance and weight of stomach raw data (Sto<sub>N</sub> and Sto<sub>W</sub>) for all pairs of fish and  
363 cephalopod species (Schoener, 1971). Using the following equation, Schoener index  
364 values distinct dietary overlap (0.3<Sto<0.6) from significant dietary overlap  
365 (Sto>0.6):

$$366 \quad Sto = 1 - 0.5 \sum_{i=1}^n (|Pxi - Pyi|)$$

367 Where  $P_{xi}$  and  $P_{yi}$ : proportion of food category  $i$  in the diet of species  $x$  and  $y$ ; and  $n$ :  
368 total number of prey.

### 369 III. Results

#### 370 3.1 General description of the fish and cephalopod community

371 A total of 558 individuals belonging to 21 species were sampled. The abundance was  
372 variable among species, eight species accounting for 94.4% of the total abundance  
373 (Table I, Figure 2-A). The northwestern part of the study area was characterised by  
374 lower abundances of fish and cephalopods (Figure 2- A&B). The common dragonet  
375 *Callionymus lyra* (232 individuals, 41.6%) and the black goby *Gobius niger* (115 ind.,  
376 20.6%) were the most abundant species while the six following ranked species were  
377 less abundant and less frequent in the study area (frequency ranging from 29 to  
378 71%, Table I). The 13 other species were rarer (frequency below 12%) and less  
379 abundant. Most individuals were observed at juvenile stages [young of the year (GO)  
380 and G1, Appendix B]

#### 381 3.2 Fish and cephalopod assemblages

382 The HCA separated three assemblages characterised by differences in abundance,  
383 richness and diversity (Table I, Figure 2-B and 2-C). Assemblage I (8 stations) mainly  
384 occurred in the shallowest stations and was dominated by *Buglossidium luteum*,  
385 *Pomatoschistus minutus* and *Alloteuthis* sp. It was characterised by a low abundance  
386 and the lowest richness and Shannon index values. Assemblages II ( $n=11$ ) and III  
387 ( $n=5$ ) were both dominated by *C. lyra*, *G. niger* and *B. luteum*. Assemblage II was  
388 characterised by higher abundances ( $13.16 \pm 2.39$  ind.), richness ( $6.09 \pm 0.74$   
389 species) and Shannon ( $1.24 \pm 0.12$ ) index compared to assemblage III. Eight species  
390 among the most abundant were common to assemblages II and III, which differed  
391 according to the presence of 9 and 4 rarer species respectively present in one of  
392 these two assemblages (Table I). Pielou indices were similar among assemblages.

393

394 Table I: Diversity metrics, abundance (mean  $\pm$  sd/se) and occurrence (occ) of species  
 395 sampled at the scale of the study area and the three assemblages identified by Hierarchical  
 396 Cluster Analysis

397		Study area (n=24)		Assemblage I (n=8)		Assemblage II (n=11)		Assemblage III (n=5)		
		mean $\pm$ sd	occ	mean. $\pm$ se	occ	mean $\pm$ se	occ	mean $\pm$ se	occ	
398	Diversity metrics	Abundance (n ind./0.1ha)		4.38 $\pm$ 1.60		13.16 $\pm$ 2.39		2.18 $\pm$ 0.64		
		4.63 $\pm$ 2.75		2.50 $\pm$ 0.42		6.09 $\pm$ 0.74		4.80 $\pm$ 2.18		
		1.03 $\pm$ 0.56		0.68 $\pm$ 0.16		1.24 $\pm$ 0.12		1.14 $\pm$ 0.36		
		0.70 $\pm$ 0.29		0.66 $\pm$ 0.15		0.73 $\pm$ 0.03		0.69 $\pm$ 0.17		
399	Abundance (n ind./0.1ha) of sampled species	<i>Callyonimus lyra</i>	<b>3.34 <math>\pm</math> 4.15</b>	<b>19</b>	0.43 $\pm$ 0.23	3	<b>6.53 <math>\pm</math> 1.29</b>	<b>11</b>	<b>0.97 <math>\pm</math> 0.17</b>	<b>5</b>
		<i>Buglossidium luteum</i>	<b>1.09 <math>\pm</math> 1.74</b>	<b>17</b>	<b>1.50 <math>\pm</math> 0.72</b>	<b>5</b>	<b>1.18 <math>\pm</math> 0.57</b>	<b>9</b>	<b>0.24 <math>\pm</math> 0.11</b>	<b>3</b>
		<i>Gobius niger</i>	<b>1.06 <math>\pm</math> 2.09</b>	<b>10</b>	0.10 $\pm$ 0.10	1	<b>2.10 <math>\pm</math> 0.84</b>	<b>6</b>	<b>0.32 <math>\pm</math> 0.15</b>	<b>3</b>
		<i>Spondylisoma cantharus</i>	0.51 $\pm$ 0.73	11	0.37 $\pm$ 0.19	3	0.81 $\pm$ 0.27	6	0.09 $\pm$ 0.06	2
400		<i>Pomatoschistus minutus</i>	0.49 $\pm$ 1.28	7	<b>0.85 <math>\pm</math> 0.74</b>	<b>2</b>	0.42 $\pm$ 0.21	4	0.05 $\pm$ 0.05	1
		<i>Arnoglossus laterna</i>	0.46 $\pm$ 0.98	10	-	0	0.92 $\pm$ 0.40	7	0.18 $\pm$ 0.09	3
		<i>Alloteuthis sp.</i>	0.37 $\pm$ 1.05	7	<b>0.88 <math>\pm</math> 0.62</b>	<b>4</b>	0.16 $\pm$ 0.09	3	-	-
		<i>Sepia officinalis</i>	0.14 $\pm$ 0.26	7	-	0	0.26 $\pm$ 0.10	5	0.09 $\pm$ 0.06	2
401		<i>Hippocampus hippocampus</i>	0.10 $\pm$ 0.35	3	-	0	0.22 $\pm$ 0.15	3	-	-
		<i>Aphia minuta</i>	0.08 $\pm$ 0.36	2	0.22 $\pm$ 0.22	1	0.02 $\pm$ 0.02	1	-	-
		<i>Mullus surmuletus</i>	0.07 $\pm$ 0.15	5	0.03 $\pm$ 0.03	1	0.11 $\pm$ 0.06	3	0.05 $\pm$ 0.05	1
402		<i>Torpedo marmorata</i>	0.06 $\pm$ 0.18	3	-	0	0.12 $\pm$ 0.08	3	-	-
		<i>Raja undulata</i>	0.05 $\pm$ 0.20	2	-	0	0.11 $\pm$ 0.09	2	-	-
		<i>Chelidonichthys lucerna</i>	0.05 $\pm$ 0.23	1	-	0	0.10 $\pm$ 0.10	1	-	-
403	<i>Symphodus bailloni</i>	0.02 $\pm$ 0.10	1	-	0	0.04 $\pm$ 0.04	1	-	-	
	<i>Eutrigla gurnardus</i>	0.01 $\pm$ 0.05	1	-	0	-	-	0.05 $\pm$ 0.05	1	
	<i>Merlangius merlangus</i>	0.01 $\pm$ 0.05	1	-	0	-	-	0.05 $\pm$ 0.05	1	
	<i>Sepiola sp.</i>	0.01 $\pm$ 0.05	1	-	0	-	-	0.05 $\pm$ 0.05	1	
404	<i>Zeus faber</i>	0.01 $\pm$ 0.05	1	-	0	-	-	0.05 $\pm$ 0.05	1	
	<i>Trachurus trachurus</i>	0.01 $\pm$ 0.04	1	-	0	0.02 $\pm$ 0.02	1	-	-	
	<i>Trigloporus lastoviza</i>	0.01 $\pm$ 0.04	1	-	0	0.02 $\pm$ 0.02	1	-	-	

405

406

407

408

409

410

411

412

413

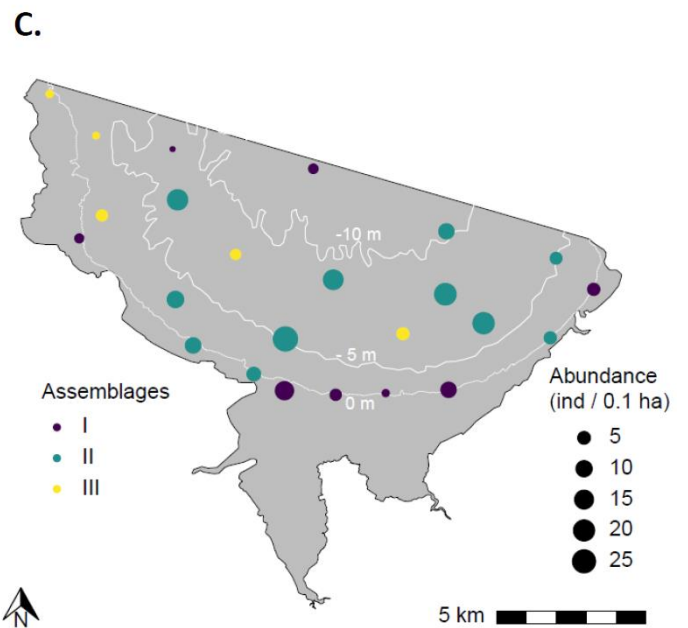
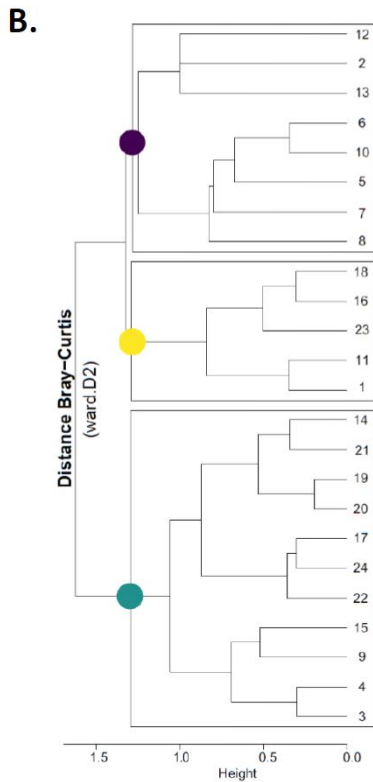
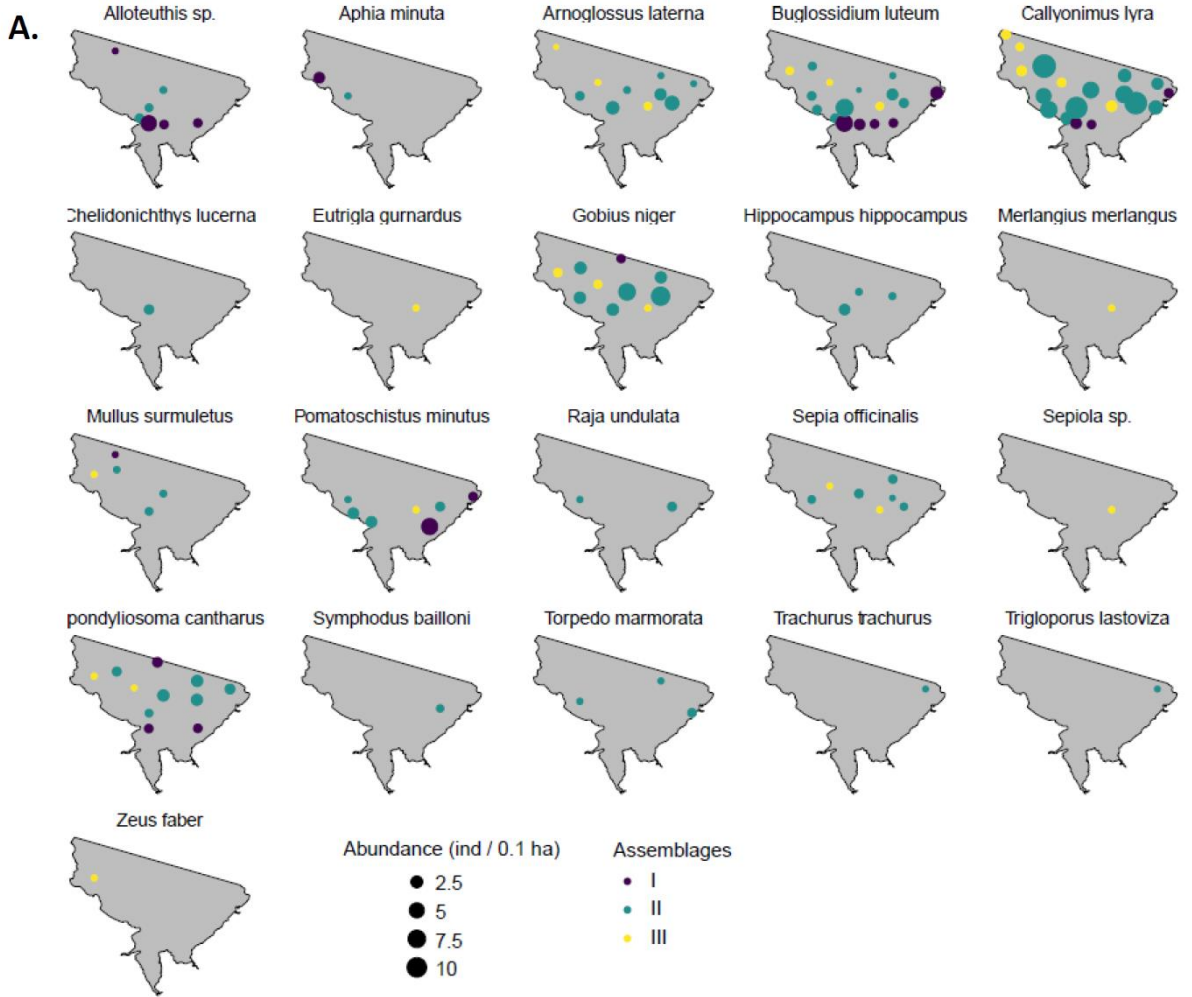
414

415

416



417  
418  
419  
420  
421  
422  
423  
424  
425  
426  
427  
428  
429  
430  
431  
432  
433  
434  
435  
436  
437  
438  
439  
440  
441  
442  
443  
444  
445  
446  
447



448 Figure 2: A. Distribution and abundance (number of individuals / 0.1 ha) of fish and  
449 cephalopod species. B. Dendrogram showing the distribution of station in the three  
450 assemblages defined by the Hierarchical Cluster Analysis. C. Spatial distribution of fish and  
451 cephalopod assemblages (white lines indicate the bathymetry).

452

### 453 **3.3 Food web**

454

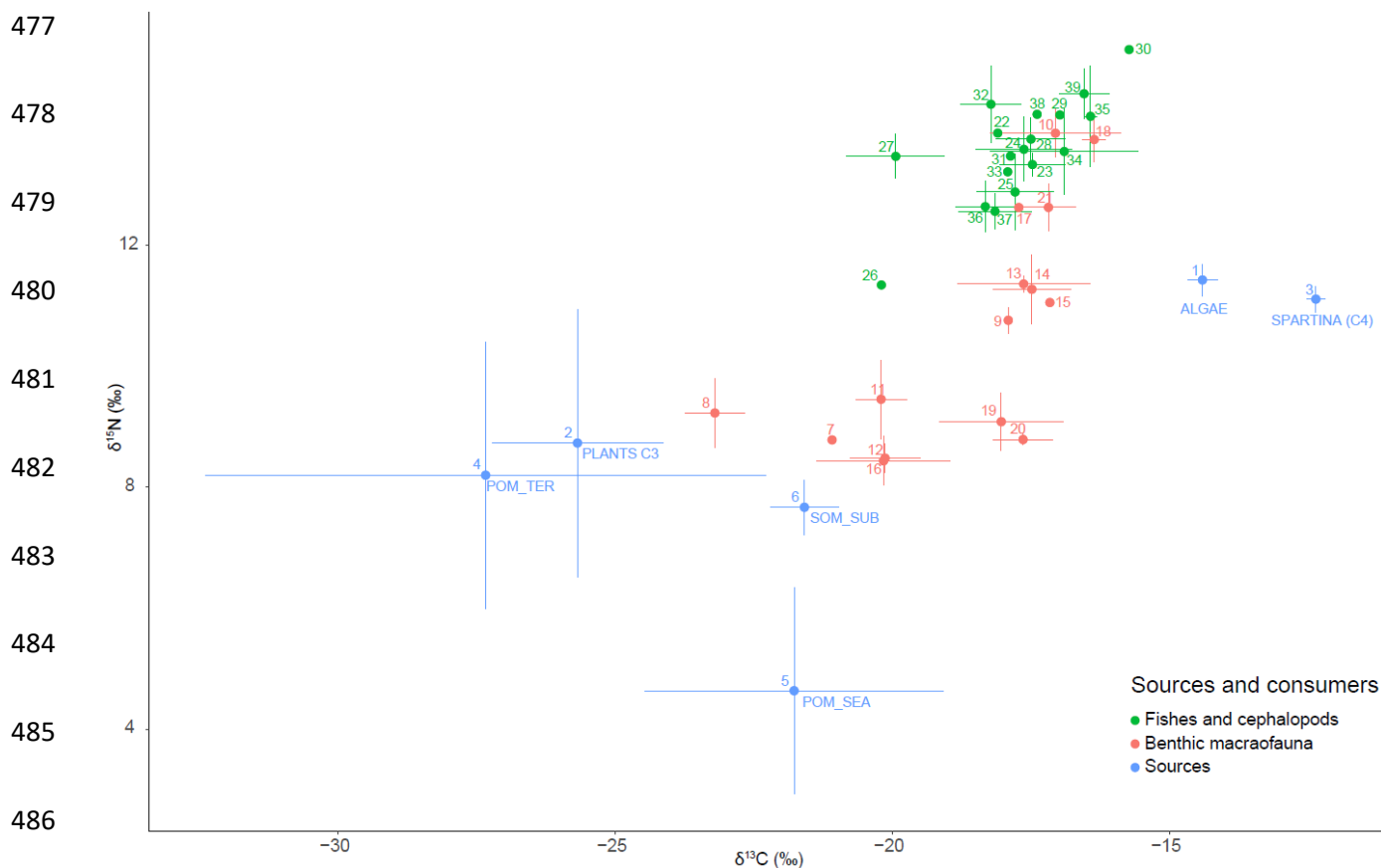
#### 455 **3.3.1 Primary food sources**

456 Contrasts were observed in primary food sources isotopic values (Figure 3, Appendix  
457 A). Values of  $\delta^{13}\text{C}$  were lower for terrestrial POM ( $-27.34 \pm 5.06 \text{ ‰}$ ) and the pool of  
458 salt marsh C3 plants ( $-25.68 \pm 1.54 \text{ ‰}$ ), while *Ulva* spp. ( $-14.41 \pm 0.27 \text{ ‰}$ ) and the  
459 C4 plant *Spartina anglica* ( $-12.36 \pm 0.17 \text{ ‰}$ ), considerably  $^{13}\text{C}$ -enriched than other  
460 sources, exhibited the highest values. The SOM and the marine POM were  
461 characterised by intermediate values. *Ulva* spp. and *Spartina anglica* were slightly  
462  $^{15}\text{N}$ -enriched compared to other potential food sources.

463

#### 464 **3.3.2 Consumers and predators: benthic invertebrates, fish and cephalopods**

465 Consumers displayed a wide range of stable isotope compositions (Figure 3,  
466 Appendix A). Fish and cephalopods exhibited higher  $\delta^{15}\text{N}$  than most benthic  
467 invertebrates. For the benthic macrofauna,  $\delta^{13}\text{C}$  mean values ranged from  $-23.21 \pm$   
468  $0.53 \text{ ‰}$  for the deposit-feeder amphipod *Ampelisca* sp. to  $-16.36 \pm 0.21 \text{ ‰}$  for the  
469 omnivorous common prawn *Palaemon serratus*.  $\delta^{15}\text{N}$  mean values ranged from  $-8.43$   
470  $\pm 0.41 \text{ ‰}$  for the suspension-feeder *C. fornicata* to  $-13.85 \pm 0.39 \text{ ‰}$  to for the  
471 omnivorous green crab *Carcinus maenas*. Most of benthic macrofauna species  
472 exhibited similar range of  $\delta^{13}\text{C}$  values to fish and cephalopods, excepted some  
473 species characterised by lower  $\delta^{13}\text{C}$  composition (e.g. *Acanthocardia echinata*,  
474 *Ampelisca* sp.). Excepted the black seabream *Spondyliosoma cantharus*, the Atlantic  
475 horse mackerel *Trachurus trachurus* and the tub gurnard *Chelidonichthys lucerna*,  
476 fish and cephalopods displayed a similar stable isotope composition.



487 Figure 3:  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of consumers and potential dietary sources of organic matter in  
 488 shallow subtidal soft bottom habitats. Colors represents groups: sources (blue), benthic  
 489 macrofauna (red) and fishes and cephalopods (green). Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are plotted with  
 490 error bars, excepted for species, which count only one individual (Supplementary material,  
 491 Appendix A). Species. Sources: 1: *Ulva spp.*; 2: Pool of C3 plants; 3: *Spartina anglica* (C4  
 492 Plant); 4: Terrestrial POM from main rivers (POM\_TER); 5: Marine POM (POM\_SEA); 6:  
 493 SOM from the subtidal area. Benthic macrofauna consumers: 7: *Acanthocardia echinata*; 8:  
 494 *Ampelisca sp.*; 9: *Buccinum undatum*; 10: *Carcinus maenas*; 11: *Varicorbula gibba*; 12:  
 495 *Crepidula fornicata*; 13: *Euspira nitida*; 14: *Pseudofusus rostratus*; 15: *Gibbula magus*; 16:  
 496 *Laevicardium crassum*; 17: *Maja brachydactyla*; 18: *Palaemon serratus*; 19: *Pecten maximus*;  
 497 20: *Politapes rhomboides*; 21: *Tritia reticulata*. Fishes and cephalopods: 22: *Aphia minuta*;  
 498 23: *Arnoglossus laterna*; 24: *Buglossidium luteum*; 25: *Callionymus lyra*; 26:  
 499 *Trachurus trachurus*; 27: *Spondyliosoma cantharus*; 28: *Gobius niger*; 29: *Eutrigla gurnardus*;  
 500 30: *Chelidonichthys lucerna*; 31: *Trigloporus lastoviza*; 32: *Alloteuthis sp.*; 33:  
 501 *Merlangius merlangus*; 34: *Pomatoschistus minutus*; 35: *Raja undulata*; 36:  
 502 *Mullus surmuletus*; 37: *Sepia officinalis*; 38: *Sepiola sp.*; 39: *Torpedo marmorata*.

503

### 504 3.4 Predators diet and isotopic niches

505 Diet composition and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were explored for seven of the most  
 506 abundant species (Table I) for which the numbers of stomach samples and stable  
 507 isotope composition were sufficient: *A. laterna*, *B. luteum*, *C. lyra*, *S. cantharus*, *G.*  
 508 *niger*, *M. surmuletus* and *S. officinalis*.

### 509 3.4.1 Niche<sub>SIA</sub>

510 Variance analyses have been performed on stable isotope values to look for  
511 differences at assemblages and species scales. The two-way permutational variance  
512 analyses did not evidenced any differences in  $\delta^{13}\text{C}$  ( $F=1.72$ ,  $p\text{-value}=0.18$ ) nor  $\delta^{15}\text{N}$   
513 ( $F=0.46$ ,  $p\text{-value}=0.63$ ) among assemblages, whereas the factor species (Appendix  
514 G) implied differences in  $\delta^{13}\text{C}$  ( $F=29.95$ ,  $p\text{-value} < 0.001$ ) and  $\delta^{15}\text{N}$  ( $F=14.46$ ,  $p\text{-value}$   
515  $< 0.001$ ) values. Pairwise Wilcoxon-tests (Appendix H) performed on  $\delta^{13}\text{C}$  values  
516 revealed significant differences between *S. cantharus* and the six other species while  
517 no difference occurred between other species, which exhibited similar carbon isotope  
518 compositions.  $\delta^{15}\text{N}$  values indicated differences between most pairs of species  
519 (Appendix H). The interaction species\*assemblages was not significant for both  
520 isotopes.

521 *C. lyra* ( $\text{TA}=6.10\text{‰}^2$ ;  $\text{CD}=0.80$ ), *B. luteum* ( $4.22\text{‰}^2$ ,  $0.92$ ) and *S. cantharus* ( $2.14\text{‰}^2$ ,  
522  $0.78$ ) (Figure 4-C, Table II), while *S. officinalis* ( $1.17\text{‰}^2$ ,  $0.63$ ), *M. surmuletus*  
523 ( $0.71\text{‰}^2$ ,  $0.60$ ) and *A. laterna* ( $0.81\text{‰}^2$ ,  $0.5$ ) displayed a lower variability. IEve values  
524 ranged from 0.62 to 0.86 pointed globally that individual of each species were evenly  
525 distributed in their respective niche<sub>SIA</sub>, with a lesser extent for *M. surmuletus*.

526 According to IDiv (min: 0.66 for *C. lyra*, max 0.79 for *M. surmuletus*), individual of  
527 each species tended to fill the whole space of their respective niche<sub>SIA</sub>.

528 Isim and Ines values associated with TA representation showed contrasted niche<sub>SIA</sub>  
529 overlaps between species (Figure 4-B, Appendix F). While most pairs of species  
530 (except pairs including *S. cantharus*) were characterised by high Isim  $\delta^{13}\text{C}$  values,  
531 the niche<sub>SIA</sub> overlap in the 2D  $\delta$ -space was limited due to the differences in  $\delta^{15}\text{N}$   
532 values and lower Isim  $\delta^{15}\text{N}$  values. Apart from *S. cantharus*, *C. lyra* and *B. luteum*,  
533 characterised by wide niches<sub>SIA</sub>, encompass at least partially the niche<sub>SIA</sub> of other  
534 benthic-demersal predators.

535

536 Table II: Stable isotope niche variability of fishes and cephalopod species. n: number of  
 537 individuals.  $\delta^{13}\text{C}$  rg and  $\delta^{15}\text{N}$  rg: range of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (‰). Cent  $\delta^{13}\text{C}$  and Cent  
 538  $\delta^{15}\text{N}$ :  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  centroids values (‰). CD: Mean distance to centroid. NND: Mean of the  
 539 Euclidean distances of each species to the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  centroids. TA: Total area (‰<sup>2</sup>). IDiv:  
 540 Isotopic divergence. IEve: Isotopic Evenness.

541		n	$\delta^{13}\text{C}$ rg	$\delta^{15}\text{N}$ rg	Cent $\delta^{13}\text{C}$	Cent $\delta^{15}\text{N}$	TA	CD	NND+SD	IDiv	IEve
542	<i>Amoglossus laterna</i>	18	2.21	0.74	-17.47	13.33	0.81	0.5	0.19 ± 0.14	0.68	0.75
	<i>Buglossidium luteum</i>	29	2.87	1.99	-17.63	13.58	4.22	0.92	0.24 ± 0.15	0.77	0.79
543	<i>Callionymus lyra</i>	46	3.31	2.82	-17.79	12.88	6.10	0.80	0.21 ± 0.16	0.66	0.74
	<i>Gobius niger</i>	22	2.6	1.14	-17.50	13.75	1.74	0.61	0.21 ± 0.15	0.69	0.76
	<i>Mullus surmuletus</i>	6	1.22	1.13	-18.33	12.64	0.71	0.60	0.34 ± 0.27	0.79	0.62
544	<i>Sepia officinalis</i>	11	2.05	0.83	-18.15	12.56	1.17	0.63	0.34 ± 0.13	0.72	0.86
	<i>Spondyliosoma cantharus</i>	22	3.49	1.24	-19.94	13.45	2.14	0.78	0.23 ± 0.13	0.67	0.78

545

### 546 3.4.2 Niche<sub>SCA</sub>

547 The vacuity was variable among species (mean ± sd ; 10.17% ± 16.08) ranging from  
 548 0% for *M. surmuletus* to 42.86% for *S. officinalis*. Individuals with empty stomach  
 549 (n=30 for all species) or unidentifiable prey items (n=12) were discarded for SCA  
 550 which included 162 stomachs for the seven species.

551 *C. lyra* was characterised by the highest richness of prey items consumed (n=9)  
 552 while *M. surmuletus* and *S. officinalis* only fed on three prey items. MFI values  
 553 revealed the importance of amphipoda for six species (Figure 5, Appendix C): main  
 554 prey for *B. luteum* (MFI= 74.6), *M. surmuletus* (62.2) and *S. cantharus* (51.9), and  
 555 secondary prey for *A. laterna* (47.4), *C. lyra* (44.2) and *G. niger* (40.8). The diet of the  
 556 cephalopod *S. officinalis* was dominated by caridea (45.7) and fishes (50.9), and was  
 557 singular with respect to the six fish species. The high consumption of annelida (36.1)  
 558 by *S. cantharus* was singular. Other items were selected by the bentho-demersal  
 559 predators, such as bivalvia for *C. lyra* and *G. niger* and caridea for *A. laterna* and *M.*  
 560 *surmuletus*.

561 No major difference was found in the niche<sub>SCA-A</sub> breadth among species (Appendix  
 562 D), except for *B. luteum* (0.50) which was characterised by lower values. The  
 563 niche<sub>SCA-W</sub> breadth values pointed out a slightly different pattern. While *B. luteum* and  
 564 *S. officinalis* were still characterised by low values (0.78 and 0.69, respectively), *C.*  
 565 *lyra* (1.44) showed the highest value.

566 The HCA performed on the abundance of preys in stomach content identified four  
567 main clusters (Appendix E), which did not follow species classification. The Schoener  
568 index values were variable (Figure 4-A, Appendix F) ranging from no overlap (>0.3)  
569 to significant (>0.6) dietary overlap among all pairs of species. In term of prey  
570 abundance, *S. officinalis* was characterised by lowest Schoener index's values. The  
571 three benthic species *A. laterna*, *B. luteum* and *C. lyra* showed significant mutual  
572 overlaps. Schoener index's values derived from the weight of preys were globally  
573 lower and more contrasted. However, the niche overlap assessed from abundance or  
574 weigh of prey items were globally congruent (Figure 4B).

575

576

577

578

579

580

581

582

583

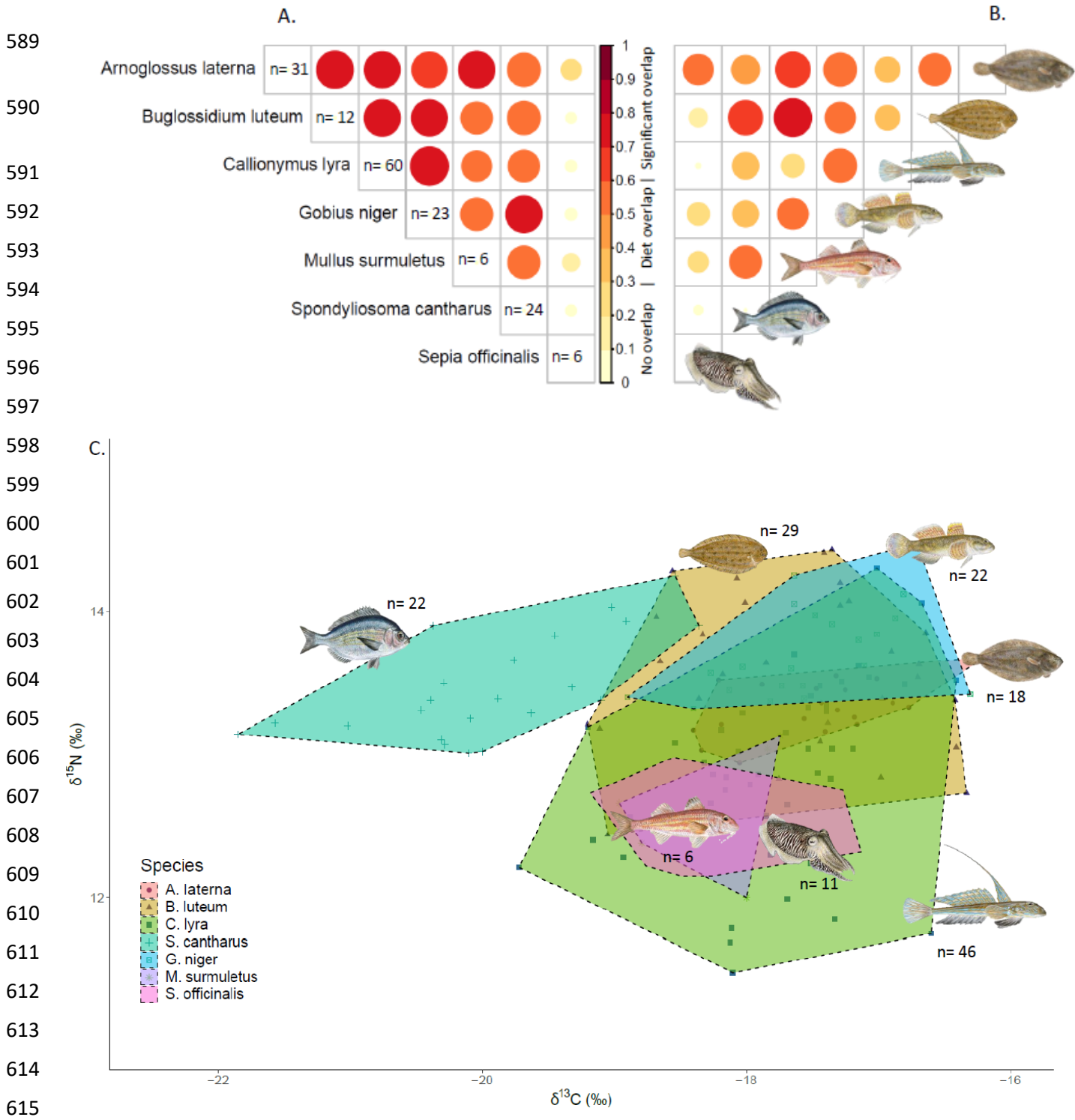
584

585

586

587

588



616 Figure 4: Overlap in fish and cephalopod's feeding strategies assessed from stomach content  
 617 (niches<sub>SCA</sub>) and stable isotope (niches<sub>SIA</sub>) analyses. Number of individuals per species is  
 618 indicated for both approaches (n). A. Plot of Shoener index's values calculated from the  
 619 abundance of preys between all pairs of fish and cephalopod species. The size and the color  
 620 gradient of circle corresponds the dietary overlap from absence (smaller yellow circles) to  
 621 significant overlap (larger red circles). B. Plot of Shoener index's values calculated from the  
 622 weight of preys. C.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope composition of fishes and cephalopods.  $\delta^{13}\text{C}$   
 623 and  $\delta^{15}\text{N}$  are plotted for each individual. Shapes represent species. Niches<sub>SIA</sub> (i.e. Total area) is  
 624 represented by convex hull polygons for each species: *Arnoglossus laterna* (red),  
 625 *Buglossidium luteum* (brown), *Callionymus lyra* (green), *Spondyliosoma cantharus* (bottle  
 626 green), *Gobius niger* (blue), *Mullus surmuletus* (purple), *Sepia officinalis* (pink).  
 627 Illustrations of species come from the © Scandinavian Fishing Year Book.

628

629

630

631

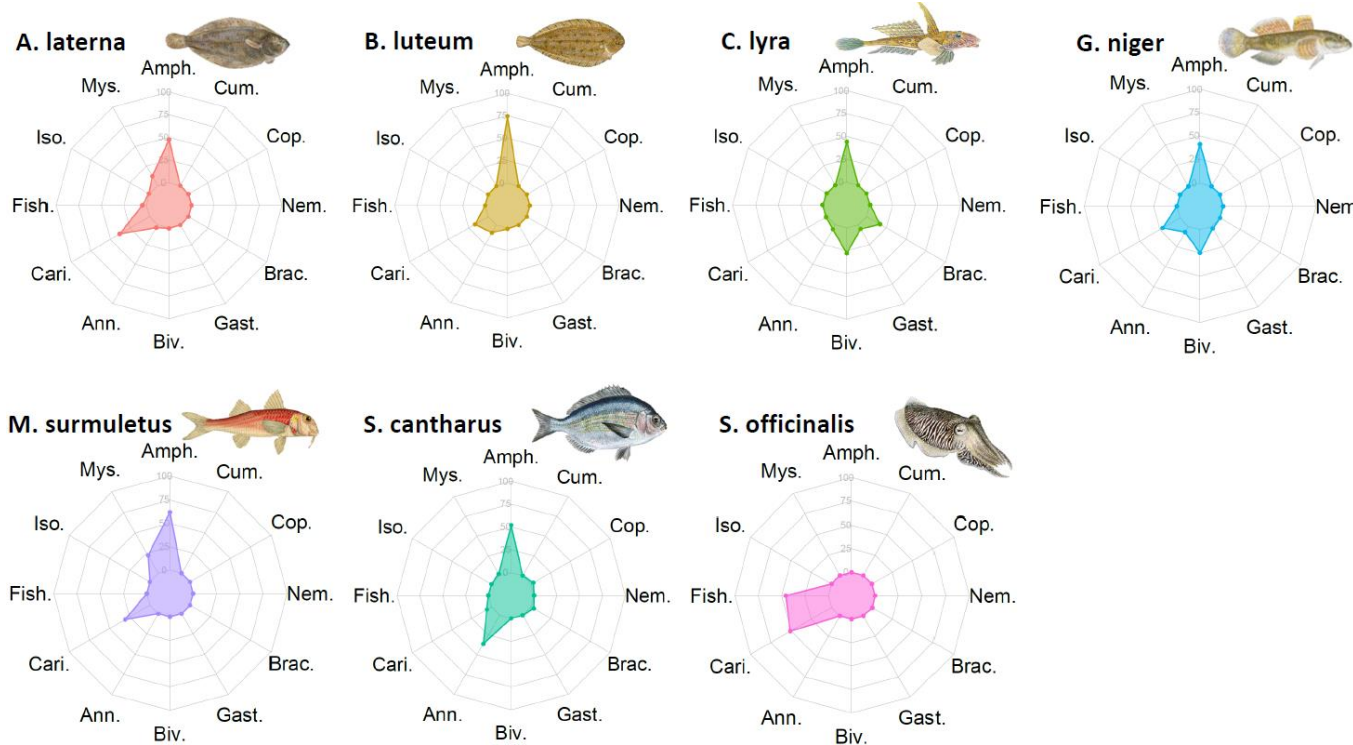
632

633

634

635

636



637

638 Figure 5: Radar plots of the main food index calculated for each fish and cephalopod species

639

640 and for each prey item. Colors correspond to species: *Arnoglossus laterna* (red),

641

642 *Buglossidium luteum* (brown), *Callionymus lyra* (green), *Spondyllosoma cantharus* (bottle

643

644 green), *Gobius niger* (blue), *Mullus surmuletus* (purple), *Sepia officinalis* (pink). The different

645

646 prey items are indicated in the periphery of the radar plot: Amph.: Amphipoda; Cum.:

647

648 Cumacea; Cop.: Copepoda; Nem.: Nemertea; Brac.: Brachyura; Gast.: Gasteropoda; Biv.:

649

650 Bivalvia; Ann.: Annelida; Cari.: Caridea; Fish; Iso.: Isopoda; Mys.: Mysida. Illustrations of

651

652 species come from the © Scandinavian Fishing Year Book.

653

654

655

656

657

## 646 IV. Discussion

647

### 647 4.1 Composition of fish and cephalopod assemblages

648

648 The fish and cephalopod community was dominated by eight species (94.4% of the

649

649 total abundance). *C. lyra* was the most abundant species in most stations, as

650

650 observed in many soft-bottoms in the English Channel (Dauvin, 1988). The diversity

651

651 of the community was rather low. Some of the species sampled in the study area

652

652 were partly or totally shared with other bays in the English Channel: e.g. *B. luteum*,

653

653 *A. laterna*, *Pomatoschistus* sp., *M. surmuletus*, *S. cantharus*; while others were

654

654 absent from our sampling: e.g. , *Dicentrarchus labrax*, *Limanda limanda*, *Chelon*

655

655 spp., *Pleuronectes platessa*, *Platichthys flesus*, *Psetta maxima*, *Scophthalmus*

656

656 *rhombus*, *Pegusa lascaris*, *Solea solea* (Auber et al., 2017; Kostecki et al., 2012; Le

657

657 Mao, 1985; Day et al., 2021; Saulnier et al., 2020). Gully (1981) observed *P.*



658 *platessa*, *Psetta maxima*, *S. solea* and *S. rhombus* in the study area, while *P.*  
659 *lascaris* was only observed further away, in the north of the bay. Most of the absent  
660 species are observed in neighbouring intertidal areas or elsewhere in the bay of  
661 Saint-Brieuc (Le Luherne et al., 2016; personal observations). Their unexpected  
662 absence in the present sampling suggests that they may be less evenly distributed  
663 than expected, especially regarding the restricted home ranges of many marine fish  
664 species at juvenile stages (Le Pape and Cognez, 2016) and/or the partial use of  
665 other habitats, as observed at low tide in intertidal channels (personal observations).  
666 Although higher sampling effort would probably have improved richness estimates in  
667 this study, we still consider that our sampling effort (6 hours of haul sampling in total)  
668 provides a reasonably robust picture of species occurring in the area.

669 Abundances were contrasted among the three assemblages. Assemblage II  
670 concentrating 3 and 6 times more fish in average than assemblages I and III  
671 respectively. Richness and specific diversity also differed among assemblages,  
672 notably due to the presence of rare species, which contributed to the distinction of  
673 clusters. The dominant species of assemblages II and III were similar (*C. lyra*, *B.*  
674 *luteum* and *G. niger*) and differed from those of assemblage I (*B. luteum*, *P. minutus*  
675 *and Alloteuthis sp.*). While assemblage I was linked to the shallowest stations located  
676 in the south of the study area, stations of assemblages II and III were more evenly  
677 distributed. While stations of assemblage I were characterised by very fine sands,  
678 assemblages II and III were associated to more heterogeneous sediments,  
679 composed of a mixture of fine sands, mud and coarser fractions (Sturbois et al.,  
680 2021a). Such contrast in the sediment, coupled with depth gradient, may explain the  
681 difference of fish and cephalopods contributions among assemblages (Le Mao,  
682 1985). Additionally, the central part of the study area was characterised by the  
683 highest benthic macrofauna abundances (Sturbois et al., 2021a), and also  
684 concentrated fish and cephalopod abundances (Figure 2).

685 Assemblage III seemed to constitute an impoverished facies of assemblage II  
686 characterised with (1) lower abundance, occurrence and evenness, and (2) absence  
687 of skates. This could be related to the degradation of benthic habitats showed by  
688 Sturbois et al. (2021a) in the study area, with significant taxonomic and functional  
689 changes. They identified scallop dredging as the main driver of these changes, as  
690 evidenced in other highly exploited systems (Fanelli et al., 2009; Rosenberg et al.,  
691 2000). Scallop dredging generates fish by-catch (Craven et al., 2013) and  
692 significantly impacts sediments properties and preys (Bradshaw et al., 2001; Morys  
693 et al., 2021). This may also directly influence fish assemblages as shown by Barletta  
694 et al. (2016) and reviewed by Wenger et al. (2017) in sediment dredging contexts.

#### 695 **4.2 Sources supporting the food web**

696 Marine POM and SOM were the most likely bases of the subtidal food webs  
697 regarding  $\delta^{13}\text{C}$  range displayed by both the benthic and fish-cephalopod community  
698 as: 1) The very singular high  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of *Ulva* spp. with respect to other  
699 primary producers evidenced that the food web did not mainly rely on *Ulva* spp.  
700 which is in accordance with Sturbois et al. (2022) who showed that the use of *Ulva*  
701 spp. by the benthic macrofauna was very limited within the neighbouring intertidal  
702 area ; and 2) The network of coastal rivers flowing in the bay is characterised by very  
703 small discharge compared to larger bays. Lower trophic levels consumers were  
704 scattered along a  $^{13}\text{C}$  enrichment gradient, which could reveal either different  
705 contributions of minor food sources, or a selective assimilation within the composite  
706 pools of POM and/or SOM. Stable isotope compositions of fish and cephalopod  
707 species were consistent with the consumption of the sampled local macrofauna. This  
708 highlights the major transfer pathway in the system, from SOM and POM to fish and  
709 cephalopod species. Interestingly, none of these predators deviated from these local  
710 sources (Figure 3). Furthermore, no difference in fish and cephalopod isotopic

711 compositions was evidenced among assemblages, suggesting that the taxonomic  
712 distinction was not supported by contrasted energy flows.

713 The local use of the salt marsh by fishes for preys supported by the vegetation or by  
714 microphytobenthos is limited to very mobile species (e.g. *D. labrax* and *Chelon spp.*)  
715 which forage in the salt marshes during high tide (Laugier, 2015; Sturbois et al.,  
716 2016) but were not represented in subtidal sampling. Most of the species sampled in  
717 the study area were not caught in the upper intertidal area (Le Luherne et al., 2016;  
718 personal observations) or in the salt marsh (Sturbois et al., 2016) suggesting that  
719 large tidal migration from subtidal to the upper limit of the large intertidal area under  
720 megatidal conditions is not a strategy retained by those species for feeding (Amara et  
721 al., 2004; Le Pape and Cognez, 2016). In this sense, the ability of tidal channels  
722 crossing sandy and muddy sediments, which constitute particular intertidal habitats,  
723 to shelter fishes in various tidal conditions need to be explored.

#### 724 **4.3 Specific diet and niches<sub>SCA</sub> variability for the seven fish and** 725 **cephalopod species compared to results observed in the bay of Saint-** 726 **Brieuc.**

727 *Arnoglossus laterna* – The diet of *A. laterna* was mainly composed of crustaceans in  
728 the study area, primarily amphipoda and caridea and in a lesser extent mysida.  
729 The scaldfish is an active predator that feed on active moving preys rather than  
730 sedentary species (Darnaude et al., 2001; De Groot, 1971). Globally, our results are  
731 congruent with the literature which points a dominance of crustaceans in the  
732 scaldfish diet across European coasts [Schücker et al., 2012) (North sea), Avşar, 1994  
733 (Turkey), Gibson and Ezzi, 1980 (Scotland), Fanelli et al., 2009 (Sicily), Cabral et al.,  
734 2002 (Portugal)]. However, while these studies pointed a relative and variable  
735 importance of fishes in the diet of *A. laterna*, fishes item were considered accidental  
736 in the study area which was in accordance with the results of Paulo-Martins et al.  
737 (2011) who found no teleost fish in the stomach content of scaldfish sampled in the

738 Cascais Bay (Portugal). Similarly, annelida was identified as a secondary prey in  
739 some of the aforementioned studies, and assessed as an accidental prey item in the  
740 bay of Saint-Brieuc.

741 *Buglossidium luteum* – The yellow sole mainly feed on amphipoda, with the highest  
742 MFI value for this item among the seven fish and cephalopod species, and in a lesser  
743 extent on caridea and annelida, which were both considered as accidental items.  
744 Schückel et al., (2012) also found a dominance of crustaceans (copepoda,  
745 amphipoda) in the diet of *B. luteum* in the North Sea but copepoda were absent of  
746 stomach in the bay of Saint-Brieuc. In several sites located on the French coast of  
747 the Eastern English Channel and the Bay of Biscay, Amara et al. (2004) observed  
748 that *B. luteum* mainly fed on crustaceans, polychaetes, and molluscs, these two last  
749 prey items being very weakly consumed in the bay of Saint-Brieuc. Cumacea,  
750 ostracoda and copepoda were the main components of crustacean's items which  
751 contrasts with the importance of amphipoda in the bay of Saint-Brieuc and the North  
752 Sea (Schückel et al., 2012). Amara et al. (2004) also showed some geographical  
753 differences with a wider range of prey items in the bay of Biscay than in the eastern  
754 English Channel confirming that this species diet may be site dependant.

755 *Callionymus lyra* – The common dragonet fed on the widest range of prey items in  
756 our study, amphipoda, bivalvia and brachyura being the main components of its diet  
757 and other constituting accidental items. Results are contrasted between studies for  
758 this species which tends to adopt a generalist feeding strategy. Our results are partly  
759 in accordance with Griffin et al. (2012) who showed that *C. lyra* mainly fed on  
760 decapods, amphipods and in a lesser extent on polychaetes in four regions from the  
761 Eastern English Channel and the Southern North Sea around the UK. López-Jamar  
762 et al. (1984) observed a similar pattern in the Northwest Spanish coast, while King et  
763 al. (1994) highlighted a dominance of polychaetes in Galway bay (Ireland), and Van  
764 Der Veer et al. (1990) and Klimpel et al. (2003) pointed the main contribution of

765 echinoderms. These different studies suggest that *C. lyra* exhibits an opportunistic  
766 feeding strategy feeding on the most available preys (Griffin et al., 2012).

767 *Gobius niger* – Amphipoda, bivalvia and caridea were the main components  
768 identified in the diet of the black goby, while annelids and gasteropods constituted  
769 accidental preys. This is congruent with the results of Filiz and Toğulga (2009) in the  
770 Aegean sea who showed that *G. niger* mainly fed on molluscs and crustaceans  
771 (90.47% of the diet), and in a lesser extent on polychaetes. These three food items  
772 belonging to the two first ranks of food items in most off studies focusing on *G. niger*  
773 diet in various area in the north and the south of Europe (De Casabianda and Kiener,  
774 1969; Filiz and Toğulga, 2009; Labropoulou and Markakis, 1998; McGrath, 1974;  
775 Vaas et al., 1975) while some studies pointed the variable importance of teleost  
776 fishes (Fjøsne, 1996; Vaas et al., 1975).

777 *Mullus surmuletus* – The red mullet mainly fed on amphipoda, caridae and mysida. In  
778 the Adriatic sea, Pavičić et al. (2018) pointed a dominance of decapods,  
779 crustaceans, bivalvia and polychaetes, with a limited contributions of amphipoda  
780 while results of Derbal et al. (2010) were more consistent with our study, finding that  
781 amphipoda and mysida were the main components in the Algerian coast.  
782 Labropoulou et al. (1997) showed that diet was dominated by crustaceans but varied  
783 seasonally: decapods were more important in summer, while amphipoda dominated  
784 in winter and spring which is congruent with our results. These three last studies also  
785 pointed a limited contribution of annelida and bivalvia. The red mullet was  
786 characterised by the lowest diversity of prey items which is consistent with the  
787 specialist feeding strategy underlined by Labropoulou et al. (1997) but the number of  
788 individual sampled (n=6) may explain this weak diversity of prey items compared to  
789 the other species.

790 *Spondyliosoma cantharus* – The black sea bream mainly fed on amphipoda and  
791 annelida in the bay of Saint-Brieuc. Five other items were identified as accidental

792 items placing the species at the second range in diversity of preys. Gonçalves and  
793 Erzini (1998) and Jakov et al. (2006) find congruent results and pointed that  
794 hydrozoans, items absent from stomachs in our study, were also an important prey in  
795 the south west coast of Portugal and in the central Eastern Central Adriatic. Quéro  
796 and Vayne (1998) found similar results but also showed an important contribution of  
797 *Enteromorpha sp.* in the diet.

798 *Sepia officinallis* – The diet of the cuttlefish mainly consisted in fishes and caridea,  
799 while few brachyura have been observed in stomachs. Alves et al. (2006) identified  
800 fishes and crustaceans as preferential items on the south coast of Portugal, as  
801 Castro and Guerra (1989) in western Spain, Le Mao (1985) in the Western English  
802 Channel, Blanc et al. (1998) in the Morbihan Gulf, and Pinczon du Sel et al. (2000) in  
803 the northern bay of Biscay. The vacuity index was important for *S. officinallis* (42%).  
804 The sampling during the daylight may explain this low proportion of full stomachs but  
805 Alves et al. (2006) found similar results in night sampling. In any case, our results  
806 should be interpreted cautiously due to the low number of cuttlefish stomachs  
807 available for SCA.

808

#### 809 **4.4 Food supply of the fish and cephalopods community, methodological** 810 **benefits and caveats**

#### 811 ***Do stomach contents mirror diet and fit with the abundance of prey in the*** 812 ***environment?***

813 In accordance with the literature (section 4.3) fish and cephalopod species exhibited  
814 a wide range of feeding strategies from opportunistic to generalist but with a close  
815 relationship between the abundance of prey in the stomach and in the environment.  
816 For instance, flatfish consume the most abundant prey resources as a result of  
817 generalist and opportunistic feeding strategies (Carter et al., 1991; Reichert, 2003;  
818 Schückel et al., 2012). Consequently, the most frequent and abundant prey in the

819 stomach contents should be among the most abundant species in the environment  
820 (Amezcuca et al., 2003; Schückel et al., 2012; Le Pape et al., 2007; Nicolas et al.,  
821 2007; Saulnier et al., 2020; Tableau et al., 2019).

822 In the benthic fauna of the study area, molluscs were the most abundant group  
823 (42.26%) ahead of annelids (38.93%) and crustaceans (15.68%) in 2019 (Sturbois et  
824 al., 2021a). SCA revealed that those three main taxa were also well represented in  
825 stomach contents, with a variable contribution depending on species. Amphipoda  
826 was the main dietary item for the six fish species (as in the bay of Morlaix,  
827 Dauvin, 1988), completed by other prey items depending on species. Despite the  
828 decrease observed in the abundance of crustaceans between 1987 and 2019  
829 (Sturbois et al., 2021a), *Amphipoda* still reach important densities and remain a  
830 major food item. The genus *Ampelisca sp.*, well represented in stomachs, is  
831 dominant. Its polyvoltine reproduction leads to more than one generation per year  
832 and contributes to the high productivity of benthic habitats. In the bay of Morlaix,  
833 three *Ampelisca* species provided 91 % of the total annual mean abundance, close to  
834 38 % of the biomass and 50 % of the net production of the total macrofauna (Dauvin,  
835 1984; Dauvin, 1989; Jeong et al., 2009). Such high densities and production rate  
836 favour the availability of prey for fishes and contribute to explain that this prey item is  
837 highly consumed.

838 Inversely, annelids were abundant in the community (Sturbois et al., 2021a) and  
839 weakly consumed by fish species, with an exception for *S. cantharus* for which it  
840 constitutes a secondary prey items. Even if they could reach locally important  
841 densities, the infaunal habitat of most annelids species may limit their availability for  
842 predators (Tableau et al., 2019). On the other hand, their high digestibility (due to the  
843 absence of hard parts) coupled to the nocturnal activity (vs daylight sampling) of  
844 most zoophagous polychaetes, have probably contributed to an underestimation of  
845 their consumption (Serrano et al., 2003). Molluscs, and particularly bivalvia have

846 been identified as secondary prey items for *C. lyra* and *G. niger*. Despite molluscs  
847 dominate the macrofauna in abundance, some bivalve and gasteropod species  
848 remain hard to digest, reaching sizes that limits their consumption by small fishes  
849 (both small species and juvenile stage), and their availability is probably limited by  
850 their infaunal position in the substrate (Tableau et al., 2019). Only juvenile molluscs  
851 were found in stomachs, their digestibility being favoured by smaller size and softer  
852 shells.

853 In the bay of Saint-Brieuc, the dominance of amphipoda in the diet of the six fish  
854 species studied suggests potential interspecific food competition which can occur  
855 when several species rely on a limiting pool of prey (Nunn et al., 2012). It also asks  
856 the question of the carrying capacity of the ecosystems to support numerous species  
857 that share a more or less common pool of prey items (Hollowed, 2000; Saulnier et al.  
858 2020). In the Bay of Seine, predator invertebrates consumed as much food as fishes  
859 and food supply may have temporarily limited the fish production (Saulnier et al.,  
860 2020). In the bay of Saint-Brieuc, regarding low abundances of fish and cephalopods,  
861 such food competition mechanisms should not constitute a main limiting factor for  
862 their populations.

863

864 ***Do stomach contents and stable isotope analyses tell same niches complexity***  
865 ***and overlap stories?***

866 No correlations were found between SCA and SIA metrics. This was somewhat  
867 expected, as SCA allows discriminating individuals feeding on different prey items,  
868 while SIA differentiate individuals feeding on different proportions of prey items, with  
869 little ability to discriminate among prey species.

870 The underlying processes influencing niche<sub>SIA</sub> are more diverse than those  
871 influencing niche<sub>SCA</sub>, as SIA metrics are influenced by far more than just diet  
872 composition (Petta et al., 2020). Caution is therefore recommended when interpreting



873 niche<sub>SIA</sub> vs niche<sub>SCA</sub> metrics in a strictly dietary niche context, especially considering  
874 the paucity of empirical information supporting the comparability of metrics derived  
875 from either methods. SIA allows for identifying the sources that support a food web  
876 and the major trophic pathways. However, in without SCA-based data, the complexity  
877 of the relation between preys and predators limits the characterisation of predator's  
878 diets and thus, the food chains to which they belong. When predators are  
879 characterised by similar SI compositions, SI analyses fail to infer on whether this  
880 signature is a consequence of a specialised diet or reflect a mean composition  
881 resulting from a generalist diet. Similarly, two predator species could be supported by  
882 a same pool of sources but not being in competition for a same pool of preys: e.g. for  
883 *M. surmuletus* and *S. officinalis* in our study. Note that a low number of stomach  
884 samples may have influenced the results for these two species as low samples  
885 number produces lower diet diversity and consequently more heterogeneous prey  
886 choice between co-occurring species.

887 Even if the link between SCA and SIA is variable, from 'no correlation' (Petta et al.,  
888 2020) to 'contrasted perception' (Cresson et al., 2014), 'complementary  
889 understanding' (Davis et al., 2012) or 'consistence' (Togashi et al., 2019), coupling  
890 SIA and SCA allows to take the best of both approaches and overpass some of their  
891 respective limits (Layman et al., 2005; Mantel et al., 2004). The relation between  
892 taxonomy and feeding modes is not straightforward, and niche<sub>SCA</sub> diversity cannot be  
893 systematically associated with dispersions patterns within the niche<sub>SIA</sub>. SIA are more  
894 relevant and informative when used in conjunction with SCA (Davis et al., 2012;  
895 Layman et al., 2005; Mantel et al., 2004). For instance, SCA are relevant to build  
896 mixing models based on actually consumed pool of preys (Phillips et al., 2014), and  
897 is a prerequisite when comparing food production with the consumption of predators  
898 (Saulnier et al., 2020; Tableau et al., 2019).

899

900 **4.5 Food supply of the fish and cephalopods community in the Bay of Saint**  
901 **Brieuc**

902 Our study evidenced species-specific feeding strategies. For instance, *S. cantharus*  
903 was  $^{13}\text{C}$ -depleted compared to other species. As with other sparids, the black sea  
904 bream is a mobile opportunistic and omnivorous feeder, able to include a wide range  
905 of organisms from rocky shore, mud and sand substrate in its diet (Gonçalves and  
906 Erzini, 1998; Jakov et al., 2006). Even if in the bay of Saint-Brieuc *S. cantharus* was  
907 an important predator of annelids, this  $^{13}\text{C}$ -depletion may reveal a higher  
908 consumption of amphipods or other pelagic sources.

909 Contrasts in niche<sub>SIA</sub> overlaps evidenced that species characterised by the largest TA  
910 (*B. luteum* and *C. lyra*) consistently exhibited the highest interspecific niche overlap  
911 while a finest trophic overlap was pointed between two pairs of species: *M.*  
912 *surmuletus* vs *S. officinalis* and *A. laterna* vs *G. niger*. These patterns of trophic  
913 range and resource partitioning have also been pointed in fish food webs of a small  
914 macrotidal estuary (Canche, English Channel; Bouaziz et al. 2021). Some trophic  
915 overlaps observed in the bay of Saint-Brieuc may result from individual level  
916 specialization as shown with the HCA performed on stomach contents, i.e., no  
917 species-dependant clusters but an intraspecific distribution of individual in different  
918 clusters. This is the case for *B. luteum* and *C. lyra*, the two species characterized by  
919 the largest trophic area.

920 Schoener indices of trophic overlap showed a consistency of diet with important  
921 overlaps among pairs of species, while values of  $\text{Sto}$  based on weight, that is a better  
922 quantification of the food potentially assimilated by predators, pointed more  
923 contrasted results. The theory of limiting similarity (Abrams, 1983; MacArthur and  
924 Levins, 1967) suggests the existence of a maximum level of niche overlap between  
925 two given species that allow their coexistence. Corollary, the concept of competitive  
926 exclusion states that two species competing for exactly the same resources cannot

927 stably coexist (Gause, 2003; Hardin, 1960; Wellard Kelly et al., 2021). However, the  
928 low abundance of fish and the large food availability may buffer such processes in  
929 the study area.

930 Except *S. cantharus* characterised by a particular niche,  $\delta^{13}\text{C}$  values strongly  
931 overlapped, pointing that the six other species were supported by a common pool of  
932 basal sources mainly composed of SOM and POM and similar pool of preys (SCA).  
933 However, the diet consistency depicted by the importance of amphipoda seems  
934 relative when compared with SIA overlaps. Accordingly, the moderate overlap in  $\delta^{15}\text{N}$   
935 values limit the trophic overlap assessed in the two dimensions of the  $\delta$ -space, a  
936 direct consequence of diet variation. Species characterised by the highest  $\delta^{15}\text{N}$   
937 values fed on prey dominated by carnivores and scavenger species of annelids  
938 enriched in  $^{15}\text{N}$ , more available than tubicolous deposit-feeder species. This  
939 predation of annelids may be more important than depicted in our study, carnivorous  
940 and scavenger species being more active at night, which favours their consumption  
941 by benthic-demersal predators (Serrano et al., 2003) and explain the higher trophic  
942 levels. On the contrary, *S. officinalis* and *M. surmuletus* were characterised by lower  
943  $\delta^{15}\text{N}$  values.

#### 944 **4.6 Understanding and conservation of such complex ecosystems**

945 As most individuals were observed at juvenile stages [young of the year (GO) and  
946 G1] and using the site for feeding, the nursery function (Beck et al., 2001) can be  
947 partially retained for a pool of main species which are common at local and regional  
948 scales. However, the fish and cephalopod community was not dominated by species  
949 of commercial interest and their low abundance, especially in the impoverished facies  
950 and the northwestern part of the study area, suggests that the nursery function was  
951 probably not optimal. The absence of some species present in other bays or in the  
952 study area suggests that they were present in low abundance and occurrence during  
953 our study, with potential seasonal patterns. They may also use limited shallow

954 habitats, within a restricted home range (Le Pape and Cognez, 2016), which have  
955 not been integrated in our subtidal sampling design. In such complex ecosystems  
956 with different habitats under megatidal conditions, an integrated sampling strategy  
957 with complementary methods may help for a better integration of habitats, from  
958 estuary and salt marshes to sandy beaches and shallow areas (Le Mao, 1985), with  
959 a seasonal dimension (Le Luherne et al., 2016; Le Mao, 1985; Sturbois et al., 2016).

960 Despite the degradation of benthic assemblages previously showed by Sturbois et al.  
961 (2021a) in the study area, most individuals were captured with full stomachs. This  
962 suggests high food availability for fish and cephalopods; however more investigations  
963 are needed to explore potential food limitation processes in the bay of Saint-Brieuc  
964 (Saulnier et al., 2020). Scallop dredging is well known to affects benthic fauna, flora  
965 and habitats by causing changes in overall biomass, species composition and size  
966 structure of demersal communities in the ecosystem (Bradshaw et al., 2001;  
967 Rosenberg et al., 2000), including fish (Craven et al., 2013). In stressed ecosystems,  
968 species with larger niches may show better performances in relation with the  
969 accessibility to a wider range of food resources (Layman et al., 2007b; Leigh, 1990;  
970 Parreira de Castro et al., 2016; Wellard Kelly et al., 2021). Species characterised by  
971 a flexible feeding strategy, such as *C. lyra*, may be favoured in variable environment  
972 in relation with natural and/or anthropogenic factors known to influence soft bottom  
973 communities and prey availability. While dredging and trawling may induce lower  
974 biodiversity on the seabed, this abundant bottom dwelling fish is able to face a  
975 changing environment (Griffin et al., 2012), which might explain why it dominates the  
976 community. In the future, coupling temporal trends in taxonomic assemblages and  
977 individual and population-level functional diversity appears as an interesting  
978 monitoring strategy for complex ecosystems characterised by interactions with  
979 anthropogenic activities.

980

981 **Acknowledgments**

982 We sincerely thank the crew of the R/V“Thalia” which participated in the  
983 oceanographic cruise RESTRO 19 and Julien Guillaudeau for the sampling of the  
984 shallower stations. Identification, biometry and diet of fish and cephalopod species  
985 was performed as part of the Master 2 intership of Amélie Cozic (Université de  
986 Bretagne Occidentale). We acknowledge Gaëtan Cormy for the help in laboratory  
987 analyses. This work was funded by Agence de l'Eau Loire-Bretagne (grant number  
988 180212501), the Région Bretagne (OSIRIS FEA621219CR0530023), the Europe for  
989 the European maritime and fisheries fund (grant number FEAMP 621-B) and the  
990 Ministère de la Transition Ecologique et Solidaire (grant number EJ N°2102930123)  
991 who fund the ResTroph Baie de Saint-Brieuc research program.

992

993 **Supplementary material**

994 **Appendix A:** Stable isotope compositions of sources and consumers ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$   
995 mean values  $\pm$  sd).

996 **Appendix B:** Size-distribution for each fish and cephalopod species.

997 **Appendix C:** Main Food Item values for the main fish and cephalopod species and  
998 each prey item.

999 **Appendix D:** Vacuity, Niche breadth and abundance/weight of preys (mean values  $\pm$   
1000 se) in stomach content for each of the main fish and cephalopod species.

1001 **Appendix E:** Hierarchical Cluster Analysis and diversity metrics performed on  
1002 stomach content.

1003 **Appendix F:** Values of Isotopic similarity, Isotopic nestedness, and Schoener index.

1004 **Appendix G:** Box plots of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  compositions for each of the main fish and  
1005 cephalopod species.

1006 **Appendix H:** Pair-wise Wilcoxon tests performed on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between  
1007 the main fish and cephalopod species.

1008

## 1009 **Reference**

- 1010 Abrams, P., 1983. The Theory of Limiting Similarity. *Annual Review of Ecology and*  
1011 *Systematics* 14, 359–376.
- 1012 Alves, D.M., Cristo, M., Sendão, J., Borges, T.C., 2006. Diet of the cuttlefish *Sepia officinalis*  
1013 (Cephalopoda: Sepiidae) off the south coast of Portugal (eastern Algarve). *J. Mar.*  
1014 *Biol. Ass.* 86, 429–436. <https://doi.org/10.1017/S0025315406013312>
- 1015 Amara, R., Mahé, K., LePape, O., Desroy, N., 2004. Growth, feeding and distribution of the  
1016 solenette *Buglossidium luteum* with particular reference to its habitat preference.  
1017 *Journal of Sea Research* 51, 211–217. <https://doi.org/10.1016/j.seares.2003.08.002>
- 1018 Amezcua, F., Nash, R.D.M., Veale, L., 2003. Feeding habits of the Order Pleuronectiformes  
1019 and its relation to the sediment type in the north Irish Sea. *J. Mar. Biol. Ass.* 83, 593–  
1020 601. <https://doi.org/10.1017/S0025315403007525h>
- 1021 Androuin, T., Dubois, S.F., Decottignies, P., Pelleter, E., Carlier, A., 2019. The dark side of soft  
1022 tissues: Unexpected inorganic carbonate in the invasive slipper limpet *CREPIDULA*  
1023 *FORNICATA* and its implications for stable isotope interpretations. *Rapid Commun*  
1024 *Mass Spectrom* 33, 107–115. <https://doi.org/10.1002/rcm.8322>
- 1025 Auber, A., Gohin, F., Goascoz, N., Schlaich, I., 2017. Decline of cold-water fish species in the  
1026 Bay of Somme (English Channel, France) in response to ocean warming. *Estuarine,*  
1027 *Coastal and Shelf Science* 189, 189–202. <https://doi.org/10.1016/j.ecss.2017.03.010>
- 1028 Avşar, D., 1994. Diel diet and feeding behaviour of Scaldfish (*Arnoglossus laterna* VALBAUM,  
1029 1792) in the Bay of Mersin. *Acta Adriatica* 34, 89–101.
- 1030 Barletta, M., Cysneiros, F.J.A., Lima, A.R.A., 2016. Effects of dredging operations on the  
1031 demersal fish fauna of a South American tropical-subtropical transition estuary:  
1032 dredging effects on fish assemblages. *J Fish Biol* 89, 890–920.  
1033 <https://doi.org/10.1111/jfb.12999>
- 1034 Beck, M.W., Heck Jr, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M.,  
1035 Halpern, B.S., Hays, C.G., Hoshino, K., Minello, T.J., 2001. The identification,  
1036 conservation, and management of estuarine and marine nurseries for fish and  
1037 invertebrates: a better understanding of the habitats that serve as nurseries for  
1038 marine species and the factors that create site-specific variability in nursery quality  
1039 will improve conservation and management of these areas. *Bioscience* 51, 633–641.
- 1040 Beukema, J.J., 1974. Seasonal changes in the biomass of the macro-benthos of a tidal flat  
1041 area in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* 8, 94–107.  
1042 [https://doi.org/10.1016/0077-7579\(74\)90028-3](https://doi.org/10.1016/0077-7579(74)90028-3)
- 1043 Birch, L.C., 1957. The Meanings of Competition. *The American Naturalist* 91, 5–18.
- 1044 Blanc, A., Du Sel, G.P., Daguzan, J., 1998. HABITAT AND DIET OF EARLY STAGES OF *SEPIA*  
1045 *OFFICINALIS* L. (CEPHALOPODA) IN MORBIHAN BAY, FRANCE. *Journal of Molluscan*  
1046 *Studies* 64, 263–274. <https://doi.org/10.1093/mollus/64.3.263>

- 1047 Blanchard, M., Blanchet, A., Gaffet, J.D., Hamon, D., 2001. Dynamique de population de la  
1048 crépidule (*Crepidula fornicata*) en baie de Saint-Brieuc (Manche-Ouest). IFREMER.  
1049 Bolnick, D.I., Yang, L.H., Fordyce, J.A., Davis, J.M., Svanbäck, R., 2002. MEASURING  
1050 INDIVIDUAL-LEVEL RESOURCE SPECIALIZATION. *Ecology* 83, 2936–2941.  
1051 [https://doi.org/10.1890/0012-9658\(2002\)083\[2936:MILRS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2936:MILRS]2.0.CO;2)  
1052 Bouaziz, R., Le Loc’h, F., Rolet, C., Veillet, G., Munaron, J.M., Rabhi, K., Djebar, A.B., Amara,  
1053 R., Ben Rais Lasram, F., 2021. Structure and seasonal variability in fish food webs in a  
1054 small macrotidal estuary (Canche estuary, Eastern English Channel) based on stable  
1055 carbon and nitrogen isotope analysis. *Regional Studies in Marine Science* 44,  
1056 101694. <https://doi.org/10.1016/j.rsma.2021.101694>  
1057 Bouillon, S., Connolly, R.M., Gillikin, D.P., 2011. Use of Stable Isotopes to Understand Food  
1058 Webs and Ecosystem Functioning in Estuaries, in: *Treatise on Estuarine and Coastal*  
1059 *Science*. Elsevier, pp. 143–173. [https://doi.org/10.1016/B978-0-12-374711-2.00711-](https://doi.org/10.1016/B978-0-12-374711-2.00711-7)  
1060 [7](https://doi.org/10.1016/B978-0-12-374711-2.00711-7)  
1061 Bradshaw, C., Veale, L.O., Hill, A.S., Brand, A.R., 2001. The effect of scallop dredging on Irish  
1062 Sea benthos: Experiments using a closed area. *Hydrobiologia* 465, 129–138.  
1063 <https://doi.org/10.1023/A:1014573731609>  
1064 Brown, E.J., Vasconcelos, R.P., Wennhage, H., Bergström, U., Støttrup, J.G., van de  
1065 Wolfshaar, K., Millisenda, G., Colloca, F., Le Pape, O., Handling editor: Emory  
1066 Anderson, 2018. Conflicts in the coastal zone: human impacts on commercially  
1067 important fish species utilizing coastal habitat. *ICES Journal of Marine Science*.  
1068 <https://doi.org/10.1093/icesjms/fsx237>  
1069 Cabral, H.N., Lopes, M., Loeper, R., 2002. Trophic niche overlap between flatfishes in a  
1070 nursery area on the Portuguese coast. *Sci. Mar.* 66, 293–300.  
1071 <https://doi.org/10.3989/scimar.2002.66n3293>  
1072 Carter, C.G., Grove, D.J., Carter, D.M., 1991. Trophic resource partitioning between two  
1073 coexisting flatfish species off the North coast of Anglesey, North Wales. *Netherlands*  
1074 *Journal of Sea Research* 27, 325–335. [https://doi.org/10.1016/0077-7579\(91\)90035-](https://doi.org/10.1016/0077-7579(91)90035-)  
1075 [Y](https://doi.org/10.1016/0077-7579(91)90035-Y)  
1076 Castro, B.G., Guerra, A., 1989. Feeding Pattern of *Sepia Officinalis* (Cephalopoda: Sepioididea)  
1077 In The Ria De Vigo (Nw Spain). *J. Mar. Biol. Ass.* 69, 545–553.  
1078 <https://doi.org/10.1017/S0025315400030952>  
1079 Charlier, R.H., Morand, P., Finkl, C.W., Thys, A., 2007. Green Tides on the Brittany Coasts.  
1080 *Environmental Research, Engineering and Management* 3, 52–59.  
1081 Claudet, J., Frascchetti, S., 2010. Human-driven impacts on marine habitats: A regional meta-  
1082 analysis in the Mediterranean Sea. *Biological Conservation* 143, 2195–2206.  
1083 <https://doi.org/10.1016/j.biocon.2010.06.004>  
1084 Connell, J.H., 1983. On the Prevalence and Relative Importance of Interspecific Competition:  
1085 Evidence from Field Experiments. *The American Naturalist* 122, 661–696.  
1086 Costanza, R., d’Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem,  
1087 S., O’Neill, R.V., Paruelo, J., 1997. The value of the world’s ecosystem services and  
1088 natural capital. *Nature* 387, 253–260.  
1089 Craven, H.R., Brand, A.R., Stewart, B.D., 2013. Patterns and impacts of fish bycatch in a  
1090 scallop dredge fishery: FISH BYCATCH IN A SCALLOP FISHERY. *Aquatic Conserv: Mar.*  
1091 *Freshw. Ecosyst.* 23, 152–170. <https://doi.org/10.1002/aqc.2289>  
1092 Cresson, P., Ruitton, S., Ourgaud, M., Harmelin-Vivien, M., 2014. Contrasting perception of  
1093 fish trophic level from stomach content and stable isotope analyses: A  
1094 Mediterranean artificial reef experience. *Journal of Experimental Marine Biology and*  
1095 *Ecology* 452, 54–62. <https://doi.org/10.1016/j.jembe.2013.11.014>

- 1096 Cucherousset, J., Villéger, S., 2015. Quantifying the multiple facets of isotopic diversity: New  
1097 metrics for stable isotope ecology. *Ecological Indicators* 56, 152–160.  
1098 <https://doi.org/10.1016/j.ecolind.2015.03.032>
- 1099 Darnaude, A.M., Harmelin-Vivien, M.L., Salen-Picard, C., 2001. Food partitioning among  
1100 flatfish (Pisces: Pleuronectiforms) juveniles in a Mediterranean coastal shallow  
1101 sandy area. *J. Mar. Biol. Ass.* 81, 119–127.  
1102 <https://doi.org/10.1017/S0025315401003460>
- 1103 Dauvin, J.-C., 1989. Life cycle, dynamics and productivity of Crustacea-Amphipoda from the  
1104 western English Channel. 5. *Ampelisca sarsi* Chevreux. *Journal of Experimental*  
1105 *Marine Biology and Ecology* 128, 31–56. [https://doi.org/10.1016/0022-](https://doi.org/10.1016/0022-0981(89)90091-9)  
1106 [0981\(89\)90091-9](https://doi.org/10.1016/0022-0981(89)90091-9)
- 1107 Dauvin, J.-C., 1988. Rôle du macrobenthos dans l'alimentation des Poissons démersaux  
1108 vivant sur les fonds de sédiments fins de la Manche occidentale. *Cahier Biologie*  
1109 *Marine* 29, 445–467.
- 1110 Dauvin, J.-C., 1984. Dynamique d'écosystèmes macrobenthiques des fonds sédimentaires de  
1111 la baie de morlaix et leur perturbation par les hydrocarbures de l'Amoco Cadiz.
- 1112 Davis, A.M., Blanchette, M.L., Pusey, B.J., Jardine, T.D., Pearson, R.G., 2012. Gut content and  
1113 stable isotope analyses provide complementary understanding of ontogenetic  
1114 dietary shifts and trophic relationships among fishes in a tropical river: Isotopic  
1115 ecology of some tropical fishes. *Freshwater Biology* 57, 2156–2172.  
1116 <https://doi.org/10.1111/j.1365-2427.2012.02858.x>
- 1117 Day, L., Brind'Amour, A., Cresson, P., Chouquet, B., Le Bris, H., 2021. Contribution of  
1118 Estuarine and Coastal Habitats Within Nursery to the Diets of Juvenile Fish in Spring  
1119 and Autumn. *Estuaries and Coasts* 44, 1100–1117. [https://doi.org/10.1007/s12237-](https://doi.org/10.1007/s12237-020-00823-z)  
1120 [020-00823-z](https://doi.org/10.1007/s12237-020-00823-z)
- 1121 De Casabianda, M.-L., Kiener, A., 1969. GOBIIDÉS DES ÉTANGS CORSES: SYSTÉMATIQUE,  
1122 ÉCOLOGIE, RÉGIME ALIMENTAIRE ET POSITION DANS LES CHAÎNES TROPHIQUES. *Vie*  
1123 *et Milieu, Observatoire Océanologique - Laboratoire Arago* 611–634.
- 1124 De Groot, S.J., 1971. On the interrelationships between morphology of the alimentary tract,  
1125 food and feeding behaviour in flatfishes (pisces: pleuronectiformes). *Netherlands*  
1126 *Journal of Sea Research* 5, 121–196. [https://doi.org/10.1016/0077-7579\(71\)90008-1](https://doi.org/10.1016/0077-7579(71)90008-1)
- 1127 Derbal, F., Slatni, S., Kara, H., 2010. Feeding variations of the striped red mullet *Mullus*  
1128 *surmuletus* (Mullidae) off eastern coast of Algeria. *Cybium* 34, 373–380.
- 1129 Desroy, N., Janson, A.-L., Denis, L., Charrier, G., Lesourd, S., Dauvin, J.-C., 2007. The intra-  
1130 annual variability of soft-bottom macrobenthos abundance patterns in the North  
1131 Channel of the Seine estuary. *Hydrobiologia* 588, 173–188.  
1132 <https://doi.org/10.1007/s10750-007-0661-2>
- 1133 Ellis, J.I., Norkko, A., Thrush, S.F., 2000. Broad-scale disturbance of intertidal and shallow  
1134 sublittoral soft-sediment habitats; effects on the benthic macrofauna. *Journal of*  
1135 *Aquatic Ecosystem Stress and Recovery* 7, 57–74.  
1136 <https://doi.org/10.1023/A:1009923530894>
- 1137 Fanelli, E., Badalamenti, F., D'Anna, G., Pipitone, C., 2009. Diet and trophic level of scaldfish  
1138 *Arnoglossus laterna* in the southern Tyrrhenian Sea (western Mediterranean):  
1139 contrasting trawled versus untrawled areas. *J. Mar. Biol. Ass.* 89, 817–828.  
1140 <https://doi.org/10.1017/S0025315409000137>
- 1141 Filiz, H., Toğulga, M., 2009. Age and growth, reproduction and diet of the black goby, (*Gobius*  
1142 *niger*) from Aegean Sea, Turkey. *JFS.com.* <https://doi.org/10.3153/jfscom.2009030>
- 1143 Fjøsne, K., 1996. Dietary composition and the potential of food competition between 0-  
1144 group cod (*Gadus morhua*L.) and some other fish species in the littoral zone. *ICES*  
1145 *Journal of Marine Science* 53, 757–770. <https://doi.org/10.1006/jmsc.1996.0097>



- 1146 Fry, B., 2008. Stable isotope ecology, Corrected as of 3rd printing. ed, Environmental science.  
1147 Springer, New York.
- 1148 Gause, G.F., 2003. The Struggle for Existence. Dover Publications.
- 1149 Gibson, R.N., Ezzi, I.A., 1980. The biology of the scaldfish, *Arnoglossus laterna* (Walbaum) on  
1150 the west coast of Scotland. *J Fish Biology* 17, 565–575.  
1151 <https://doi.org/10.1111/j.1095-8649.1980.tb02788.x>
- 1152 Gonçalves, J., Erzini, K., 1998. Feeding habits of the two-banded sea bream (*Diplodus*  
1153 *vulgaris*) and the Black Sea bream (*Spondyliosoma cantharus*) (Sparidae) from the  
1154 south-west coast of Portugal. *Cybiurn: international journal of ichthyology* 22, 245–  
1155 254.
- 1156 Gravier, D., 2012. Monitoring of green tides on the Brittany coasts (France). *Primary*  
1157 *Producers of the Sea Bio* 458, 9.
- 1158 Gray, J.S., 1997. Marine biodiversity: patterns, threats and conservation needs. *Biodiversity*  
1159 *and Conservation* 153–175.
- 1160 Griffin, R., Pearce, B., Handy, R.D., 2012. Dietary preference and feeding selectivity of  
1161 common dragonet *Callionymus lyra* in U.K. *Journal of Fish Biology* 81, 1019–1031.  
1162 <https://doi.org/10.1111/j.1095-8649.2012.03375.x>
- 1163 Gully, F., 1981. Inventaire et description des nurseries littorales de poissons du golfe  
1164 Normano-Breton. Institut Scientifique et Technique des Pêches Maritimes - Ecole  
1165 Nationale Supérieure d’Agronomie de Rennes.
- 1166 Hamon, D., Blanchard, M., 1994. Etat de la prolifération de la crépidule (*Crepidula fornicata*)  
1167 en baie de Saint-Brieuc.
- 1168 Hardin, G., 1960. The Competitive Exclusion Principle: An idea that took a century to be born  
1169 has implications in ecology, economics, and genetics. *Science* 131, 1292–1297.  
1170 <https://doi.org/10.1126/science.131.3409.1292>
- 1171 Hollowed, A., 2000. Are multispecies models an improvement on single-species models for  
1172 measuring fishing impacts on marine ecosystems? *ICES Journal of Marine Science*  
1173 57, 707–719. <https://doi.org/10.1006/jmsc.2000.0734>
- 1174 Hunsicker, M.E., Ciannelli, L., Bailey, K.M., Buckel, J.A., Wilson White, J., Link, J.S., Essington,  
1175 T.E., Gaichas, S., Anderson, T.W., Brodeur, R.D., Chan, K.-S., Chen, K., Englund, G.,  
1176 Frank, K.T., Freitas, V., Hixon, M.A., Hurst, T., Johnson, D.W., Kitchell, J.F., Reese, D.,  
1177 Rose, G.A., Sjodin, H., Sydeman, W.J., van der Veer, H.W., Vollset, K., Zador, S., 2011.  
1178 Functional responses and scaling in predator-prey interactions of marine fishes:  
1179 contemporary issues and emerging concepts: Predator-prey interactions in marine  
1180 systems. *Ecology Letters* 14, 1288–1299. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2011.01696.x)  
1181 [0248.2011.01696.x](https://doi.org/10.1111/j.1461-0248.2011.01696.x)
- 1182 Hyslop, E.J., 1980. Stomach contents analysis-a review of methods and their application. *J*  
1183 *Fish Biology* 17, 411–429. <https://doi.org/10.1111/j.1095-8649.1980.tb02775.x>
- 1184 Jakov, D., Lipej, L., Glamuzina, B., Bartulovic, V., 2006. Diet of *Spondyliosoma cantharus* and  
1185 *Diplodus puntazzo* (Sparidae) in the Eastern Central Adriatic. *Cybiurn* 30, 115–122.
- 1186 Jeong, S.J., Yu, O.H., Suh, H.-L., 2009. Reproductive patterns and secondary production of  
1187 *Gammaropsis japonicus* (Crustacea, Amphipoda) on the seagrass *Zostera marina* of  
1188 Korea. *Hydrobiologia* 623, 63–76. <https://doi.org/10.1007/s10750-008-9648-x>
- 1189 King, P.A., Fives, J.M., McGrath, D., 1994. Reproduction, growth and feeding of the dragonet,  
1190 *Callionymus lyra* (Teleostei: Callionymidae), in Galway Bay, Ireland. *J. Mar. Biol. Ass.*  
1191 74, 513–526. <https://doi.org/10.1017/S0025315400047639>
- 1192 Klimpel, S., Seehagen, A., Palm, H.W., 2003. Metazoan parasites and feeding behaviour of  
1193 four small-sized fish species from the central North Sea. *Parasitology Research* 91,  
1194 290–297. <https://doi.org/10.1007/s00436-003-0957-8>
- 1195 Kostecki, C., Roussel, J., Desroy, N., Roussel, G., Lanshere, J., Le Bris, H., Le Pape, O., 2012.  
1196 Trophic ecology of juvenile flatfish in a coastal nursery ground: contributions of

1197 intertidal primary production and freshwater particulate organic matter. *Mar. Ecol.*  
1198 *Prog. Ser.* 449, 221–232. <https://doi.org/10.3354/meps09563>  
1199 Kundu, G.K., Kim, C., Kim, D., Bibi, R., Kim, H., Kang, C.-K., 2021. Phytoplankton Fuel Fish  
1200 Food Webs in a Low-Turbidity Temperate Coastal Embayment: A Stable Isotope  
1201 Approach. *Front. Mar. Sci.* 8, 751551. <https://doi.org/10.3389/fmars.2021.751551>  
1202 Labropoulou, M., Machias, A., Tsimenides, N., Eleftheriou, A., 1997. Feeding habits and  
1203 ontogenetic diet shift of the striped red mullet, *Mullus surmuletus* Linnaeus, 1758.  
1204 *Fisheries Research* 31, 257–267. [https://doi.org/10.1016/S0165-7836\(97\)00017-9](https://doi.org/10.1016/S0165-7836(97)00017-9)  
1205 Labropoulou, M., Markakis, G., 1998. Morphological-dietary relationships within two  
1206 assemblages of marine demersal fishes. *Environmental Biology of Fishes* 51, 309–  
1207 319. <https://doi.org/10.1023/A:1007445112309>  
1208 Laugier, F., 2015. Histoires de vie et connectivité entre les habitats écologiques essentiels de  
1209 poissons des mers côtières tempérées : le cas des lançons (*Ammodytidae*) et du bar  
1210 européen (*Dicentrarchus labrax*, Linnaeus, 1758) dans le Golfe Normand Breton, une  
1211 approche par les marqueurs environnementaux. Muséum national d’Histoire  
1212 Naturelle (Paris, France).  
1213 Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R.,  
1214 Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M., Bearhop, S., 2012.  
1215 Applying stable isotopes to examine food-web structure: an overview of analytical  
1216 tools. *Biological Reviews* 87, 545–562. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-185X.2011.00208.x)  
1217 [185X.2011.00208.x](https://doi.org/10.1111/j.1469-185X.2011.00208.x)  
1218 Layman, C.A., Arrington, D.A., Montaña, C.G., Post, D.M., 2007a. CAN STABLE ISOTOPE  
1219 RATIOS PROVIDE FOR COMMUNITY-WIDE MEASURES OF TROPHIC STRUCTURE?  
1220 *Ecology* 88, 42–48. [https://doi.org/10.1890/0012-9658\(2007\)88\[42:CSIRPF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2)  
1221 Layman, C.A., Quattrochi, J.P., Peyer, C.M., Allgeier, J.E., 2007b. Niche width collapse in a  
1222 resilient top predator following ecosystem fragmentation. *Ecol Letters* 10, 937–944.  
1223 <https://doi.org/10.1111/j.1461-0248.2007.01087.x>  
1224 Layman, C.A., Winemiller, K.O., Arrington, D.A., Jepsen, D.B., 2005. BODY SIZE AND TROPHIC  
1225 POSITION IN A DIVERSE TROPICAL FOOD WEB. *Ecology* 86, 2530–2535.  
1226 <https://doi.org/10.1890/04-1098>  
1227 Le Dean, E., Moreau, Y., 1981. Nurseries littorales de la Baie de St Brieuc.  
1228 Le Luherne, E., Le Pape, O., Murillo, L., Randon, M., Lebot, C., Réveillac, E., 2017. Influence of  
1229 Green Tides in Coastal Nursery Grounds on the Habitat Selection and Individual  
1230 Performance of Juvenile Fish. *PLOS ONE* 12, e0170110.  
1231 <https://doi.org/10.1371/journal.pone.0170110>  
1232 Le Luherne, E., Réveillac, E., Ponsero, A., Sturbois, A., Ballu, S., Perdriau, M., Le Pape, O.,  
1233 2016. Fish community responses to green tides in shallow estuarine and coastal  
1234 areas. *Estuarine, Coastal and Shelf Science* 79–92.  
1235 <https://doi.org/10.1016/j.ecss.2016.03.031>  
1236 Le Mao, P., 1985. Peuplements piscicoles et teuthologiques du bassin maritime de la Rance :  
1237 impact de l’aménagement marémoteur. Université de Rennes1 / ENSA Rennes -  
1238 Ecole Nationale Supérieure Agronomique de Rennes.  
1239 Le Pape, O., Bonhommeau, S., 2015. The food limitation hypothesis for juvenile marine fish.  
1240 *Fish Fish* 16, 373–398. <https://doi.org/10.1111/faf.12063>  
1241 Le Pape, O., Cognez, N., 2016. The range of juvenile movements of estuarine and coastal  
1242 nursery dependent flatfishes: estimation from a meta-analytical approach. *Journal*  
1243 *of Sea Research* 107, 43–55. <https://doi.org/10.1016/j.seares.2015.06.001>  
1244 Le Pape, O., Gilliers, C., Riou, P., Morin, J., Amara, R., 2007. Convergent signs of degradation  
1245 of both the capacity and the quality of an essential fish habitat : synthesis on the  
1246 Seine estuary (France), an highly anthropised estuary of which flatfish nursery  
1247 function is altered. *Hydrobiologia* 225–229.

- 1248 Leclerc, J.C., Riera, P., Noël, L., Leroux, C., Andersen, A.C., 2013. Trophic ecology of  
1249 *Pomatoschistus microps* within an intertidal bay (Roscoff, France), investigated  
1250 through gut content and stable isotope analyses. *Marine Ecology*.  
1251 Leigh, E.G., 1990. Community diversity and environmental stability: A re-examination.  
1252 *Trends in Ecology & Evolution* 5, 340–344. [https://doi.org/10.1016/0169-](https://doi.org/10.1016/0169-5347(90)90183-E)  
1253 [5347\(90\)90183-E](https://doi.org/10.1016/0169-5347(90)90183-E)
- 1254 López-Jamar, E., Iglesias, J., Otero, J.J., 1984. Contribution of infauna and mussel-raft  
1255 epifauna to demersal fish diets. *Marine Ecology Progress Series* 15, 13–18.
- 1256 Macarthur, R., Levins, R., 1967. The Limiting Similarity, Convergence, and Divergence of  
1257 Coexisting Species. *The American Naturalist* 101, 377–385.
- 1258 Mantel, S.K., Salas, M., Dudgeon, D., 2004. Foodweb structure in a tropical Asian forest  
1259 stream. *Journal of the North American Benthological Society* 23, 728–755.  
1260 [https://doi.org/10.1899/0887-3593\(2004\)023<0728:FSIATA>2.0.CO;2](https://doi.org/10.1899/0887-3593(2004)023<0728:FSIATA>2.0.CO;2)
- 1261 McGrath, D., 1974. Preliminary Studies on the Feeding of *Gobius Niger* (L) and *Gobius*  
1262 *Flavescens* (Fabricius) (Pisces, Gobiidae) in the Northern Baltic Proper. Askö  
1263 Laboratory, University of Stockholm, Sweden.
- 1264 Merceron, M., Manaud, F., Guillaud, J.F., Monbert, Y., 1981. Extension du port du Légué  
1265 (Saint-Brieuc). Etude d'impact sur l'environnement marin. IFREMER.
- 1266 Morys, C., Brüchert, V., Bradshaw, C., 2021. Impacts of bottom trawling on benthic  
1267 biogeochemistry: an experimental field study. *Marine Environmental Research*  
1268 105384. <https://doi.org/10.1016/j.marenvres.2021.105384>
- 1269 Newsome, S.D., Martinez del Rio, C., Bearhop, S., Phillips, D.L., 2007. A niche for isotopic  
1270 ecology. *Frontiers in Ecology and the Environment* 5, 429–436.  
1271 <https://doi.org/10.1890/060150.1>
- 1272 Nicolas, D., Le Loc'h, F., Désaunay, Y., Hamon, D., Blanchet, A., Le Pape, O., 2007.  
1273 Relationships between benthic macrofauna and habitat suitability for juvenile  
1274 common sole (*Solea solea*, L.) in the Vilaine estuary (Bay of Biscay, France) nursery  
1275 ground. *Estuarine, Coastal and Shelf Science* 73, 639–650.  
1276 <https://doi.org/10.1016/j.ecss.2007.03.006>
- 1277 Nunn, A.D., Tewson, L.H., Cowx, I.G., 2012. The foraging ecology of larval and juvenile fishes.  
1278 *Reviews in Fish Biology and Fisheries* 22, 377–408.
- 1279 Parreira de Castro, D.M., Reis de Carvalho, D., Pompeu, P. dos S., Moreira, M.Z., Nardoto,  
1280 G.B., Callisto, M., 2016. Land Use Influences Niche Size and the Assimilation of  
1281 Resources by Benthic Macroinvertebrates in Tropical Headwater Streams. *PLoS ONE*  
1282 11, e0150527. <https://doi.org/10.1371/journal.pone.0150527>
- 1283 Paulo-Martins, C., Vinagre, C., Silva, A., Cabral, H., 2011. Variation of diet and food  
1284 consumption of the scaldfish *Arnoglossus laterna*(Walbaum, 1792): Diet of scaldfish.  
1285 *Journal of Applied Ichthyology* 27, 977–983. [https://doi.org/10.1111/j.1439-](https://doi.org/10.1111/j.1439-0426.2011.01742.x)  
1286 [0426.2011.01742.x](https://doi.org/10.1111/j.1439-0426.2011.01742.x)
- 1287 Pavičić, M., Šiljić, J., Jurica, D.B., Matić-Skoko, S., 2018. Feeding habits of the striped red  
1288 mullet, *Mullus surmuletus* in the eastern Adriatic Sea 14.
- 1289 Petta, J.C., Shipley, O.N., Wintner, S.P., Cliff, G., Dicken, M.L., Hussey, N.E., 2020. Are you  
1290 really what you eat? Stomach content analysis and stable isotope ratios do not  
1291 uniformly estimate dietary niche characteristics in three marine predators.  
1292 *Oecologia* 192, 1111–1126. <https://doi.org/10.1007/s00442-020-04628-6>
- 1293 Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens, B.X.,  
1294 Ward, E.J., 2014. Best practices for use of stable isotope mixing models in food-web  
1295 studies. *Can. J. Zool.* 92, 823–835. <https://doi.org/10.1139/cjz-2014-0127>
- 1296 Pinczon du Sel, G., Blanc, A., Daguzan, J., 2000. The diet of the cuttlefish *Sepia officinalis* L.  
1297 (mollusca: cephalopoda) during its life cycle in the Northern Bay of Biscay (France):  
1298 *Aquat. sci.* 62, 167–178. <https://doi.org/10.1007/PL00001329>

- 1299 Post, J.R., Parkinson, E.A., Johnston, N.T., 1999. DENSITY-DEPENDENT PROCESSES IN  
1300 STRUCTURED FISH POPULATIONS: INTERACTION STRENGTHS IN WHOLE-LAKE  
1301 EXPERIMENTS. *Ecological Monographs* 69, 155–175. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9615(1999)069[0155:DDPISF]2.0.CO;2)  
1302 9615(1999)069[0155:DDPISF]2.0.CO;2
- 1303 Quéro, J.C., Vayne, J.J., 1998. Les fruits de la mer et les plantes marines des pêches  
1304 françaises. Delachaux et Niestlé.
- 1305 Quevedo, M., Svanbäck, R., Eklöv, P., 2009. Intrapopulation niche partitioning in a generalist  
1306 predator limits food web connectivity. *Ecology* 90, 2263–2274.  
1307 <https://doi.org/10.1890/07-1580.1>
- 1308 Reichert, M.J.M., 2003. Diet, consumption, and growth of juvenile fringed flounder (*Etropus*  
1309 *crossotus*); a test of the ‘maximum growth/optimum food hypothesis’ in a  
1310 subtropical nursery area. *Journal of Sea Research* 50, 97–116.  
1311 [https://doi.org/10.1016/S1385-1101\(03\)00081-9](https://doi.org/10.1016/S1385-1101(03)00081-9)
- 1312 Rigolet, C., Thiébaud, E., Brind’Amour, A., Dubois, S.F., 2015. Investigating isotopic functional  
1313 indices to reveal changes in the structure and functioning of benthic communities.  
1314 *Functional Ecology* 29, 1350–1360. <https://doi.org/10.1111/1365-2435.12444>
- 1315 Rodriguez, A., 1996. Régime alimentaire de deux Soleidae, *Solea lascaris* et *Solea impar* de la  
1316 côte ouest de Bretagne. *Cybio* 20, 261–277.
- 1317 Rosenberg, A., Bigford, T., Leathery, S., Hill, R., Bickers, K., 2000. Ecosystem Approaches to  
1318 Fishery Management Through Essential Fish Habitat. *Bulletin of Marine Science* 66,  
1319 535–542.
- 1320 Saulnier, E., Le Bris, H., Tableau, A., Dauvin, J.C., Brind’Amour, A., 2020. Food limitation of  
1321 juvenile marine fish in a coastal and estuarine nursery. *Estuarine, Coastal and Shelf*  
1322 *Science* 241, 106670. <https://doi.org/10.1016/j.ecss.2020.106670>
- 1323 Schoener, T.W., 1971. Theory of Feeding Strategies. *Annu. Rev. Ecol. Syst.* 2, 369–404.  
1324 <https://doi.org/10.1146/annurev.es.02.110171.002101>
- 1325 Schückel, S., Sell, A.F., Kröncke, I., Reiss, H., 2012. Diet overlap among flatfish species in the  
1326 southern North Sea. *Journal of Fish Biology* 80, 2571–2594.  
1327 <https://doi.org/10.1111/j.1095-8649.2012.03309.x>
- 1328 Seitz, R.D., Wennhage, H., Bergström, U., Lipcius, R.N., Ysebaert, T., 2014. Ecological value of  
1329 coastal habitats for commercially and ecologically important species. *ICES Journal of*  
1330 *Marine Science* 71, 648–665. <https://doi.org/10.1093/icesjms/fst152>
- 1331 Serrano, A., Velasco, F., Olaso, I., 2003. Polychaete annelids in the diet of demersal fish from  
1332 the southern shelf of the Bay of Biscay. *J. Mar. Biol. Ass.* 83, 619–623.  
1333 <https://doi.org/10.1017/S0025315403007550h>
- 1334 Sturbois, A., Bioret, F., 2019. Le pré-salé de l’anse d’Yffiniac : historique, dynamique et  
1335 conservation. *Penn Ar Bed* 3–18.
- 1336 Sturbois, A., Cormy, G., Le Moal, A., Schaal, G., Broudin, C., Thiébaud, E., Ponsero, A., Le Mao,  
1337 P., Jones, A., Riera, P., Gauthier, O., Desroy, N., 2021a. Using ecological trajectories  
1338 to track long-term taxonomic and functional changes in benthic shallow soft-bottom  
1339 communities (Bay of Saint-Brieuc, English Channel). *Aquatic Conservation: Marine*  
1340 *and Freshwater Ecosystems* 31, 3013–3033. <https://doi.org/10.1002/aqc.3704>
- 1341 Sturbois, A., Cormy, G., Schaal, G., Gauthier, O., Ponsero, A., Le Mao, P., Riera, P., Desroy, N.,  
1342 2021b. Quantifying spatio-temporal changes in benthic communities: taxonomic and  
1343 functional trajectories of intertidal assemblages in the bay of Saint-Brieuc.
- 1344 Sturbois, A., Ponsero, A., Maire, A., Carpentier, A., Petillon, J., Riera, P., 2016. Evaluation des  
1345 fonctions écologiques des prés-salés de l’anse d’Yffiniac pour l’ichtyofaune. *Réserve*  
1346 *Naturelle Baie de Saint-Brieuc*.
- 1347 Sturbois, A., Riera, P., Desroy, N., Brébant, T., Carpentier, A., Ponsero, A., Schaal, G., 2022.  
1348 Spatio-temporal patterns in stable isotope composition of a benthic intertidal food  
1349 web reveal limited influence from salt marsh vegetation and green tide. *Marine*

1350 Environmental Research 175, 105572.  
1351 <https://doi.org/10.1016/j.marenvres.2022.105572>  
1352 Tableau, A., Le Bris, H., Saulnier, E., Le Pape, O., Brind'Amour, A., 2019. Novel approach for  
1353 testing the food limitation hypothesis in estuarine and coastal fish nurseries. *Mar.*  
1354 *Ecol. Prog. Ser.* 629, 117–131. <https://doi.org/10.3354/meps13090>  
1355 Togashi, H., Nakane, Y., Amano, Y., Kurita, Y., 2019. Estimating the Diets of Fish Using  
1356 Stomach Contents Analysis and a Bayesian Stable Isotope Mixing Models in Sendai  
1357 Bay, in: Komatsu, T., Ceccaldi, H.-J., Yoshida, J., Prouzet, P., Henocque, Y. (Eds.),  
1358 *Oceanography Challenges to Future Earth*. Springer International Publishing, Cham,  
1359 pp. 235–245. [https://doi.org/10.1007/978-3-030-00138-4\\_19](https://doi.org/10.1007/978-3-030-00138-4_19)  
1360 Vaas, K.F., Vlasblom, A.G., De Koeijer, P., 1975. Studies on the black Goby (*Gobius Niger*,  
1361 *Gobiidae*, pisces) in the veerse meer, SW Netherlands. *Netherlands Journal of Sea*  
1362 *Research* 9, 56–68. [https://doi.org/10.1016/0077-7579\(75\)90022-8](https://doi.org/10.1016/0077-7579(75)90022-8)  
1363 Van Der Veer, H.W., Creutzberg, F., Dapper, R., Duineveld, G.C.A., Fonds, M., Kuipers, B.R.,  
1364 Van Noort, G.J., Witte, J.I.J., 1990. On the ecology of the dragonet *Callionymus lyra* L.  
1365 in the southern North Sea. *Netherlands Journal of Sea Research* 26, 139–150.  
1366 [https://doi.org/10.1016/0077-7579\(90\)90063-M](https://doi.org/10.1016/0077-7579(90)90063-M)  
1367 Wellard Kelly, H.A., Kovalenko, K.E., Ahrenstorff, T.D., Bethke, B.J., Brady, V.J., Dumke, J.D.,  
1368 Hansen, G.J.A., Rantala, H.M., 2021. Trophic complexity of small fish in nearshore  
1369 food webs. *Hydrobiologia* 848, 2505–2521. [https://doi.org/10.1007/s10750-021-](https://doi.org/10.1007/s10750-021-04570-5)  
1370 [04570-5](https://doi.org/10.1007/s10750-021-04570-5)  
1371 Wenger, A.S., Harvey, E., Wilson, S., Rawson, C., Newman, S.J., Clarke, D., Saunders, B.J.,  
1372 Browne, N., Travers, M.J., Mcilwain, J.L., Erftemeijer, P.L.A., Hobbs, J.-P.A., Mclean,  
1373 D., Depczynski, M., Evans, R.D., 2017. A critical analysis of the direct effects of  
1374 dredging on fish. *Fish Fish* 18, 967–985. <https://doi.org/10.1111/faf.12218>  
1375