

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

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### Abstract :

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

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## Highlights

► Trophic ecology of fish assemblages (stomach content and stable isotopes) were studied in the bay of Saint Brieuc (France). ► The fish and cephalopod community was composed of 21 taxa; eight species accounted for 94.4% of the total abundance. ► An impoverished assemblage may reveal the impact of scallop dredging on a part of the Bay. ► Amphipoda was the main prey with many additional items depending on predator species. ► At the assemblage scale, fish and demersal fauna mostly relied on POM/SOM-based food chains.

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

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## **I. Introduction:**

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

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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 trophic  
156 strategies of demersal fish and cephalopod species can be evidenced by crossing  
157 stomach contents and stable isotope analyses? We finally discussed results in relation  
158 with methodological benefits and caveats when crossing stomach contents and stable  
159 isotope analyses, previous information on the benthic preys production, and their  
160 implications for the understanding and the conservation of the marine protected areas.

161

## 162 **II. Material and methods**

### 163 **2.1 Study area, the bay of Saint-Brieuc (Western English Channel, France)**

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

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

174 Luherne et al. (2016) evidenced the use of sandy beaches at high tide by some  
175 species; e.g. *Buglossidium luteum*, *Pleuronectes platessa*, *Pomatoschistus microps*,  
176 *Chelon spp.*, and *Dicentrarchus labrax*; these three last taxa also using the salt marsh  
177 channels (Laugier, 2015; Sturbois et al., 2016).

178 Despite bordering the National Nature Reserve of the bay of Saint-Brieuc and  
179 partially belonging to the Natura 2000 “Baie de Saint-Brieuc-Est” site (European  
180 Union network, FR5300066), the study area is exposed to a number of  
181 anthropogenic pressures including mussel culture and scallop dredging (Sturbois et  
182 al., 2021b, 2021a). Mussels are farmed on wooden poles (312 ha; Figure 1) in the  
183 north-eastern part of the intertidal area and on ropes in the western part of the study  
184 area. The sea bed is exposed to long-term scallop dredging (Sturbois et al., 2021a).  
185 Some areas are colonized by the non-indigenous slipper limpet *Crepidula fornicata*  
186 especially in the western part of the bay (Blanchard et al., 2001; Hamon and  
187 Blanchard, 1994). The bay also suffers from eutrophication resulting in macroalgae  
188 proliferation and cyclic green tides episodes (Charlier et al., 2007; Gravier, 2012).  
189 These green tides influence the dynamics of some benthic populations of  
190 invertebrates in the intertidal area (Sturbois et al., 2021b) and impact fish nursery  
191 grounds in the upper parts of the intertidal area (Le Luherne et al., 2017, 2016).

192

## 193 **2.2 Sample collection and laboratory processes**

### 194 **2.2.1 Fish and cephalopods**

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



202 overdosed solution of benzocaine (400 mg.L<sup>-1</sup>), and immediately frozen (-20°C) for  
203 later stable isotope (SIA) and stomach content (SCA) analyses. Note that skates  
204 (biopsy for SIA) and sea horses were systematically released.

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

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

### 217 **2.2.2 Benthic macrofauna**

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

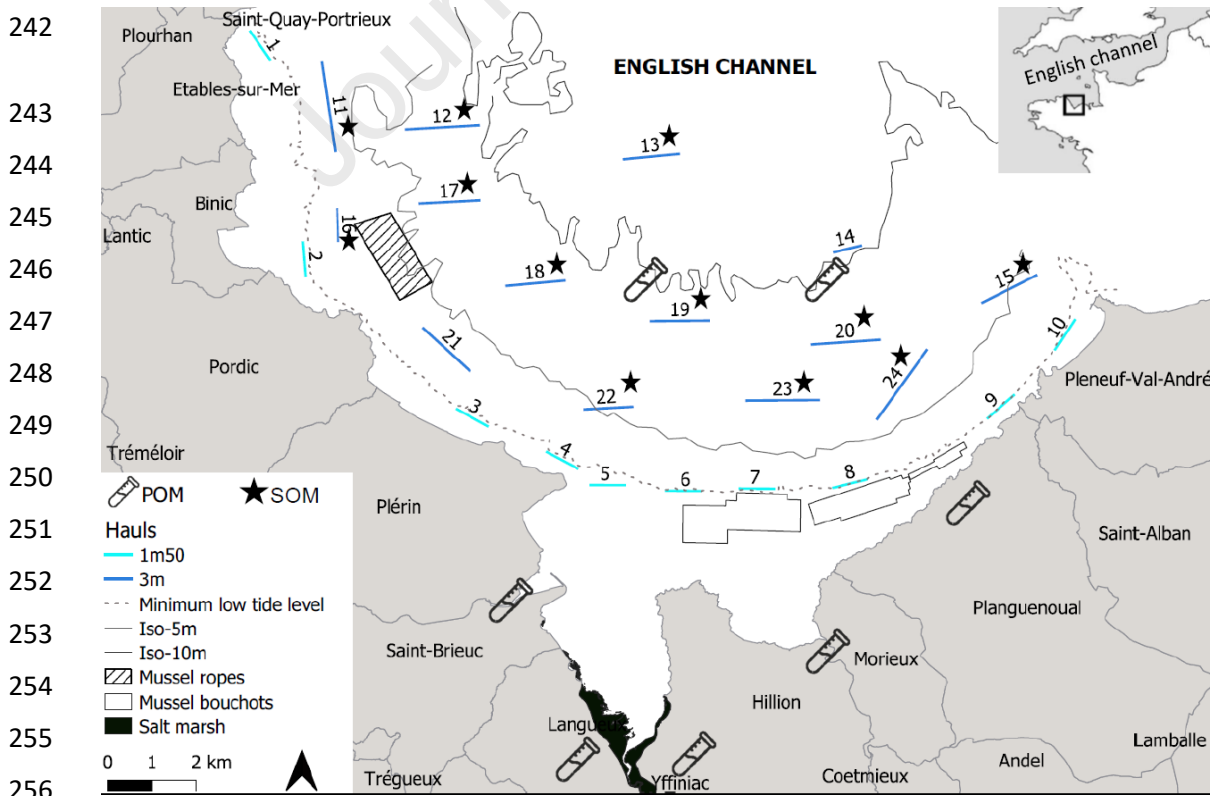
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228

229 **2.2.3. Trophic sources, primary producers and organic matter**

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

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



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

### 260 **2.3 Stable isotope analysis**

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

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

$$270 \quad \delta X = [(R_{\text{Sample}}/R_{\text{Standard}}) - 1] * 10^3$$

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

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

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

### 278 **2.4 Data Analysis**

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

286

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

297

**298 2.4.2 Stable isotope analysis**

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

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

313 - *Mean distance to centroid (CD)*: Average Euclidean distance of each  
314 individual to the  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  species centroid, where the centroid is the mean  
315  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  value for all individuals of a given fish or cephalopod species.  
316 This metric provides a measure of the average degree of variability in trophic  
317 strategy;

318 - *Mean nearest neighbor distance (NND)*: Mean of the Euclidean distances to  
319 each individual nearest neighbor within each fish species niche, i.e., a  
320 measure of the overall density of individual packing.

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

324 - *Isotopic similarity (ISim)*: the ratio between the isotopic niche of the  
325 intersection and of the union of the two fish or cephalopod species  
326 considered. It ranges from 0 when there is no isotopic overlap to 1 when the  
327 species with the lowest isotopic richness fills a subset of the isotopic space  
328 filled by the species with the highest one. ISim was calculated in the two  
329 dimensions of the 2D  $\delta$ -space and for each isotope (i.e. one dimension);

330 - *Isotopic nestedness (Ines)*: Ratio between the area of the intersection and  
331 the area filled by the species with the narrowest isotopic niche. It ranges from  
332 0 when there is no isotopic overlap to 1 when the group with the lowest  
333 isotopic richness fills a subset of the isotopic space filled by the group with the  
334 highest one;

335 - *Isotopic divergence (IDiv)*: Distribution of species individuals within the  
336 convexhull. IDiv is minimal (i.e. tends to 0) when most of the points are close  
337 to the centroid of the convex hull, and individuals with the most extreme  
338 stable isotope values are rare in a community. IDiv tends to 1 when all the  
339 points are located on the edges of the convex hull and individuals with  
340 extreme stable isotope value(s) dominate;

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

346

### 347 2.4.3 Stomach contents analysis

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

$$350 \quad MFI = \sqrt{W\% \frac{O\% + N\%}{2} * 100}$$

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

355  $Niche_{SCA}$  breadth (Shannon–Wiener Index) was calculated from abundance  
 356 ( $niche_{SCA-N}$ ) and weight ( $niche_{SCA-W}$ ) in stomach content raw data. A HCA was  
 357 performed on stomach contents raw abundance data to distinguish groups of fish or  
 358 cephalopod characterised by similar feeding strategies (*i.e.* same pool of preys),  
 359 using the methods described for fish and cephalopod assemblages in section 2.4.1.

360 Complementary, the Schoener index of trophic overlap (Sto) was calculated on  
 361 abundance and weight of stomach raw data ( $Sto_N$  and  $Sto_W$ ) for all pairs of fish and  
 362 cephalopod species (Schoener, 1971). Using the following equation, Schoener index  
 363 values distinct dietary overlap (0.3<Sto<0.6) from significant dietary overlap  
 364 (Sto>0.6):

$$365 \quad Sto = 1 - 0.5 \sum_{i=1}^n (|P_{xi} - P_{yi}|)$$

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

### 368 III. Results

#### 369 3.1 General description of the fish and cephalopod community

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

#### 380 3.2 Fish and cephalopod assemblages

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

392

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

396		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		
397	Diversity metrics	Abundance (n ind./0.1ha)		4.38 $\pm$ 1.60		13.16 $\pm$ 2.39		2.18 $\pm$ 0.64			
		Richness		2.50 $\pm$ 0.42		6.09 $\pm$ 0.74		4.80 $\pm$ 2.18			
		Shannon		0.68 $\pm$ 0.16		1.24 $\pm$ 0.12		1.14 $\pm$ 0.36			
		Pielou		0.66 $\pm$ 0.15		0.73 $\pm$ 0.03		0.69 $\pm$ 0.17			
398	Abundance (n ind./0.1 ha)	<i>Callyonimus lyra</i>		3.34 $\pm$ 4.15	19	0.43 $\pm$ 0.23	3	6.53 $\pm$ 1.29	11	0.97 $\pm$ 0.17	5
		<i>Buglossidium luteum</i>		1.09 $\pm$ 1.74	17	1.50 $\pm$ 0.72	5	1.18 $\pm$ 0.57	9	0.24 $\pm$ 0.11	3
		<i>Gobius niger</i>		1.06 $\pm$ 2.09	10	0.10 $\pm$ 0.10	1	2.10 $\pm$ 0.84	6	0.32 $\pm$ 0.15	3
399	of sampled species	<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
		<i>Pomatoschistus minutus</i>		0.49 $\pm$ 1.28	7	0.85 $\pm$ 0.74	2	0.42 $\pm$ 0.21	4	0.05 $\pm$ 0.05	1
400		<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	0.88 $\pm$ 0.62	4	0.16 $\pm$ 0.09	3	-	-
401		<i>Sepia officinalis</i>		0.14 $\pm$ 0.26	7	-	0	0.26 $\pm$ 0.10	5	0.09 $\pm$ 0.06	2
		<i>Hippocampus hippocampus</i>		0.10 $\pm$ 0.35	3	-	0	0.22 $\pm$ 0.15	3	-	-
402		<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
403		<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	-	-
404		<i>Chelidonichthys lucerna</i>		0.05 $\pm$ 0.23	1	-	0	0.10 $\pm$ 0.10	1	-	-
		<i>Symphodus bailloni</i>		0.02 $\pm$ 0.10	1	-	0	0.04 $\pm$ 0.04	1	-	-
405		<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
406		<i>Sepiola sp.</i>		0.01 $\pm$ 0.05	1	-	0	-	-	0.05 $\pm$ 0.05	1
		<i>Zeus faber</i>		0.01 $\pm$ 0.05	1	-	0	-	-	0.05 $\pm$ 0.05	1
407		<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	-	-

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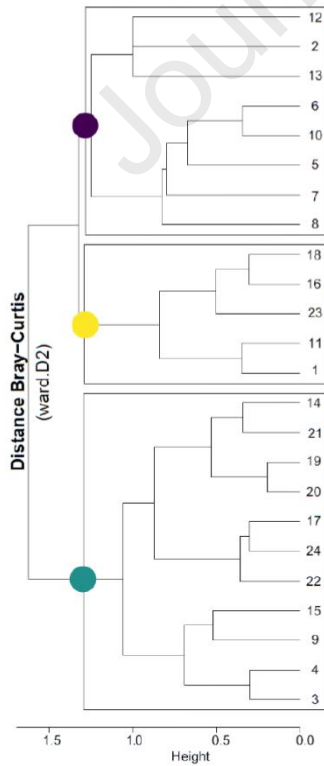
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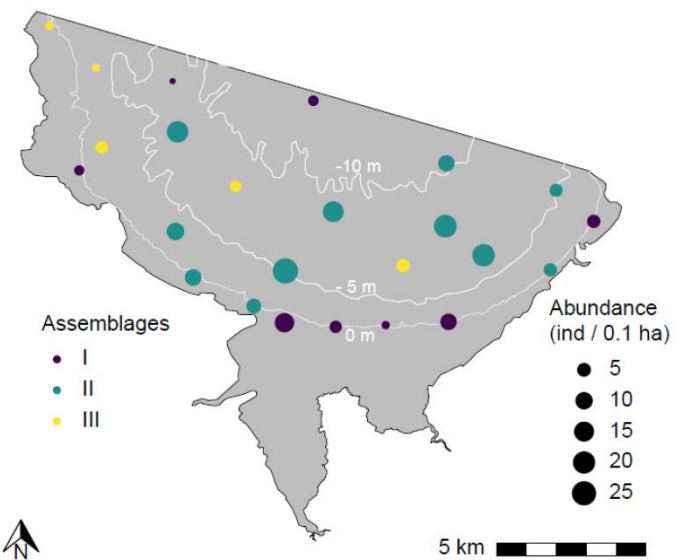
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447 Figure 2: A. Distribution and abundance (number of individuals / 0.1 ha) of fish and  
448 cephalopod species. B. Dendrogram showing the distribution of station in the three  
449 assemblages defined by the Hierarchical Cluster Analysis. C. Spatial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

451

### 452 3.3 Food web

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#### 454 3.3.1 Primary food sources

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

462

#### 463 3.3.2 Consumers and predators: benthic invertebrates, fish and cephalopods

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

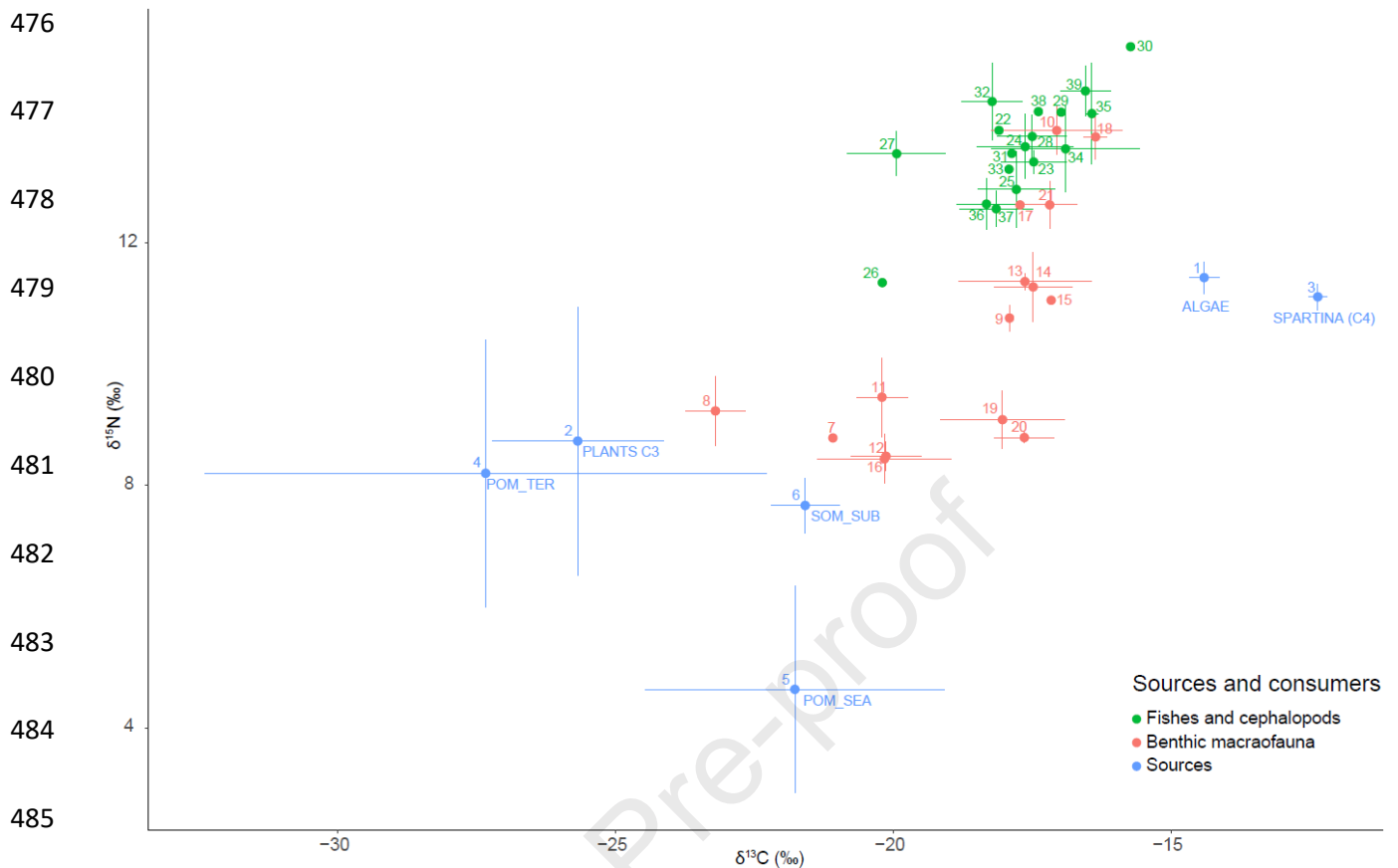


Figure 3:  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of consumers and potential dietary sources of organic matter in shallow subtidal soft bottom habitats. Colors represents groups: sources (blue), benthic macrofauna (red) and fishes and cephalopods (green). Mean  $\delta^{13}\text{C}$  and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

502

### 503 3.4 Predators diet and isotopic niches

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

508 **3.4.1 Niche<sub>SIA</sub>**

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

520 *C. lyra* ( $TA=6.10\text{‰}^2$ ;  $CD=0.80$ ), *B. luteum* ( $4.22\text{‰}^2$ ,  $0.92$ ) and *S. cantharus* ( $2.14\text{‰}^2$ ,  
521  $0.78$ ) (Figure 4-C, Table II), while *S. officinalis* ( $1.17\text{‰}^2$ ,  $0.63$ ), *M. surmuletus*  
522 ( $0.71\text{‰}^2$ ,  $0.60$ ) and *A. laterna* ( $0.81\text{‰}^2$ ,  $0.5$ ) displayed a lower variability. IEve values  
523 ranged from 0.62 to 0.86 pointed globally that individual of each species were evenly  
524 distributed in their respective niche<sub>SIA</sub>, with a lesser extent for *M. surmuletus*.  
525 According to IDiv (min: 0.66 for *C. lyra*, max 0.79 for *M. surmuletus*), individual of  
526 each species tended to fill the whole space of their respective niche<sub>SIA</sub>.

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

534

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

540		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
541	<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
542	<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
543	<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

544

### 545 3.4.2 Niche<sub>SCA</sub>

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

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

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

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

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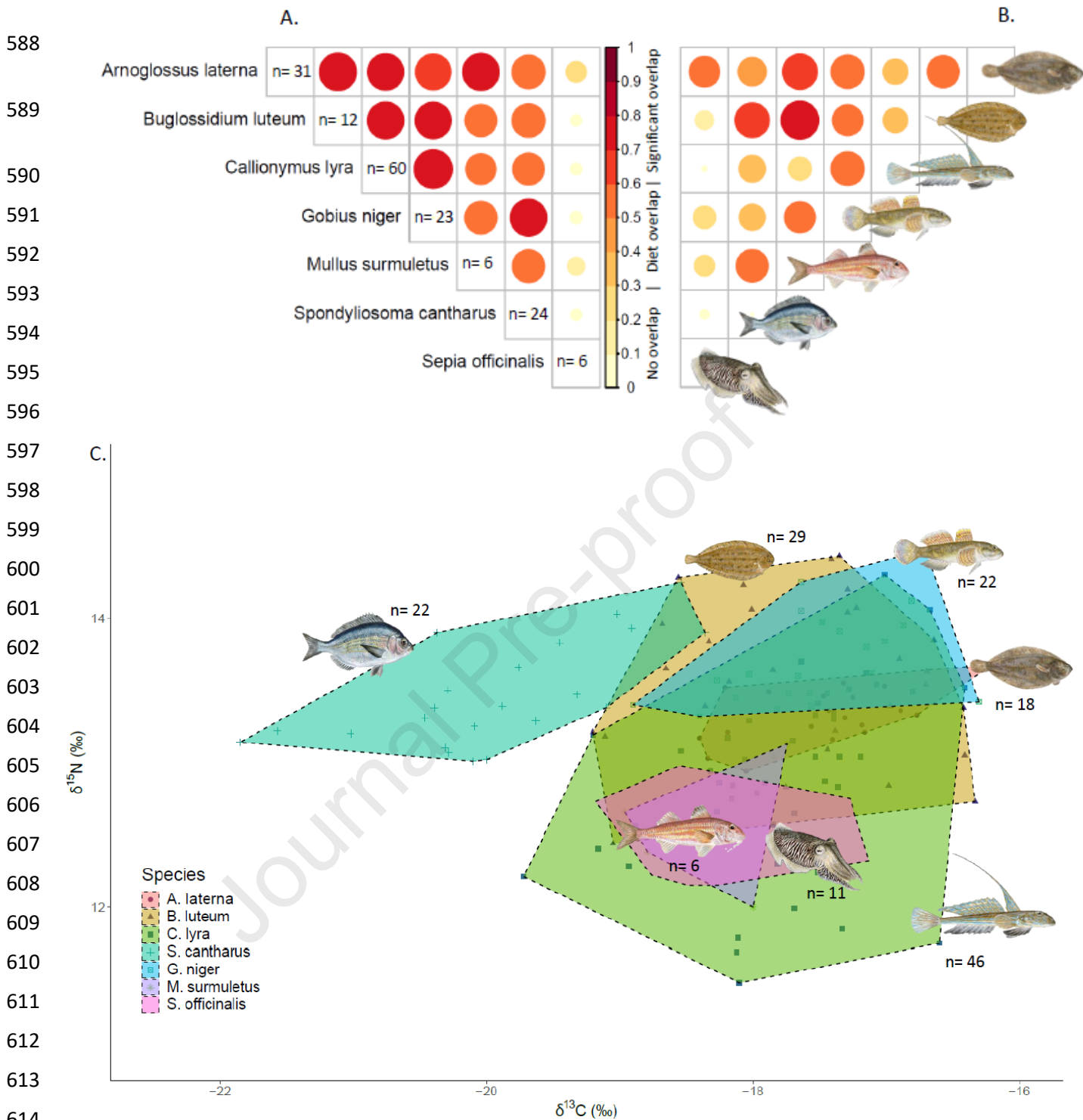
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615 Figure 4: Overlap in fish and cephalopod's feeding strategies assessed from stomach content  
 616 (niches<sub>SCA</sub>) and stable isotope (niches<sub>SIA</sub>) analyses. Number of individuals per species is  
 617 indicated for both approaches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

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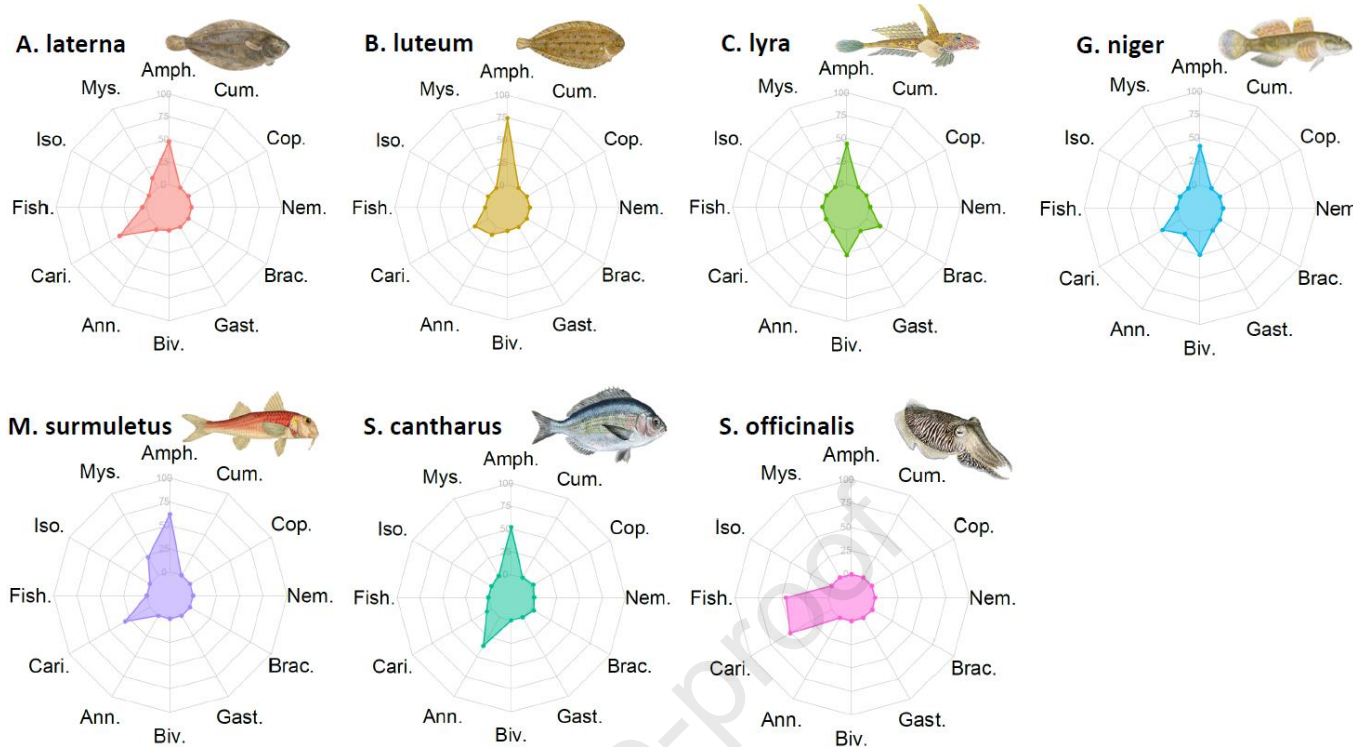
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637 Figure 5: Radar plots of the main food index calculated for each fish and cephalopod species

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

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641 *Buglossidium luteum* (brown), *Callionymus lyra* (green), *Spondylisoma cantharus* (bottle

642

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

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#### IV. Discussion

646

##### 4.1 Composition of fish and cephalopod assemblages

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

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

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

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

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

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

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

661

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

663

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

665

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



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

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

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

#### 694 **4.2 Sources supporting the food web**

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

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

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

#### 723 **4.3 Specific diet and niches<sub>SCA</sub> variability for the seven fish and** 724 **cephalopod species compared to results observed in the bay of Saint-** 725 **Brieuc.**

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

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

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

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

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

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

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

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

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

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

807

#### 808 **4.4 Food supply of the fish and cephalopods community, methodological** 809 **benefits and caveats**

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

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

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

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

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

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

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

862

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

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

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



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

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

898

#### 899 4.5 Food supply of the fish and cephalopods community in the Bay of Saint

#### 900 Brieuç

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

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

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

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

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

#### 943 **4.6 Understanding and conservation of such complex ecosystems**

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

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

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

979

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991

## 992 **Supplementary material**

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

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

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

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

1000 **Appendix E:** Hierarchical Cluster Analysis and diversity metrics performed on  
1001 stomach content.

1002 **Appendix F:** Values of Isotopic similarity, Isotopic nestedness, and Schoener index.

1003 **Appendix G:** Box plots of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  compositions for each of the main fish and  
 1004 cephalopod species.

1005 **Appendix H:** Pair-wise Wilcoxon tests performed on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between  
 1006 the main fish and cephalopod species.

1007

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1374

		Study area (n=24)		Assemblage I (n=8)		Assemblage II (n=11)		Assemblage III (n=5)	
		mean ± sd	occ	mean. ± se	occ	mean ± se	occ	mean ± se	occ
<b>Diversity metrics</b>	Abundance (n ind./0.1ha)	7.95 ± 7.65		4.38 ± 1.60		13.16 ± 2.39		2.18 ± 0.64	
	Richness	4.63 ± 2.75		2.50 ± 0.42		6.09 ± 0.74		4.80 ± 2.18	
	Shannon	1.03 ± 0.56		0.68 ± 0.16		1.24 ± 0.12		1.14 ± 0.36	
	Pielou	0.70 ± 0.29		0.66 ± 0.15		0.73 ± 0.03		0.69 ± 0.17	
<b>Abundance (n ind./0.1ha) of sampled species</b>	<i>Callyonimus lyra</i>	<b>3.34 ± 4.15</b>	<b>19</b>	0.43 ± 0.23	3	<b>6.53 ± 1.29</b>	<b>11</b>	<b>0.97 ± 0.17</b>	<b>5</b>
	<i>Buglossidium luteum</i>	<b>1.09 ± 1.74</b>	<b>17</b>	<b>1.50 ± 0.72</b>	<b>5</b>	<b>1.18 ± 0.57</b>	<b>9</b>	<b>0.24 ± 0.11</b>	<b>3</b>
	<i>Gobius niger</i>	<b>1.06 ± 2.09</b>	<b>10</b>	0.10 ± 0.10	1	<b>2.10 ± 0.84</b>	<b>6</b>	<b>0.32 ± 0.15</b>	<b>3</b>
	<i>Spondylisoma cantharus</i>	0.51 ± 0.73	11	0.37 ± 0.19	3	0.81 ± 0.27	6	0.09 ± 0.06	2
	<i>Pomatoschistus minutus</i>	0.49 ± 1.28	7	<b>0.85 ± 0.74</b>	<b>2</b>	0.42 ± 0.21	4	0.05 ± 0.05	1
	<i>Arnoglossus laterna</i>	0.46 ± 0.98	10	-	0	0.92 ± 0.40	7	0.18 ± 0.09	3
	<i>Alloteuthis sp.</i>	0.37 ± 1.05	7	<b>0.88 ± 0.62</b>	<b>4</b>	0.16 ± 0.09	3	-	
	<i>Sepia officinalis</i>	0.14 ± 0.26	7	-	0	0.26 ± 0.10	5	0.09 ± 0.06	2
	<i>Hippocampus hippocampus</i>	0.10 ± 0.35	3	-	0	0.22 ± 0.15	3	-	
	<i>Aphia minuta</i>	0.08 ± 0.36	2	0.22 ± 0.22	1	0.02 ± 0.02	1	-	
	<i>Mullus surmuletus</i>	0.07 ± 0.15	5	0.03 ± 0.03	1	0.11 ± 0.06	3	0.05 ± 0.05	1
	<i>Torpedo marmorata</i>	0.06 ± 0.18	3	-	0	0.12 ± 0.08	3	-	
	<i>Raja undulata</i>	0.05 ± 0.20	2	-	0	0.11 ± 0.09	2	-	
	<i>Chelidonichthys lucerna</i>	0.05 ± 0.23	1	-	0	0.10 ± 0.10	1	-	
	<i>Symphodus bailloni</i>	0.02 ± 0.10	1	-	0	0.04 ± 0.04	1	-	
	<i>Eutrigla gurnardus</i>	0.01 ± 0.05	1	-	0	-		0.05 ± 0.05	1
	<i>Merlangius merlangus</i>	0.01 ± 0.05	1	-	0	-		0.05 ± 0.05	1
	<i>Sepiola sp.</i>	0.01 ± 0.05	1	-	0	-		0.05 ± 0.05	1
	<i>Zeus faber</i>	0.01 ± 0.05	1	-	0	-		0.05 ± 0.05	1
	<i>Trachurus trachurus</i>	0.01 ± 0.04	1	-	0	0.02 ± 0.02	1	-	
<i>Trigloporus lastoviza</i>	0.01 ± 0.04	1	-	0	0.02 ± 0.02	1	-		

	<b>n</b>	<b><math>\delta^{13}\text{C}</math> rg</b>	<b><math>\delta^{15}\text{N}</math> rg</b>	<b>Cent <math>\delta^{13}\text{C}</math></b>	<b>Cent <math>\delta^{15}\text{N}</math></b>	<b>TA</b>	<b>CD</b>	<b>NND+SD</b>	<b>IDiv</b>	<b>IEve</b>
<i>Arnoglossus 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
<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
<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>Spondylisoma cantharus</i>	22	3.49	1.24	-19.94	13.45	2.14	0.78	0.23 ± 0.13	0.67	0.78

**Highlights:**

- Trophic ecology of fish assemblages (stomach content and stable isotopes) were studied in the bay of Saint Brieuc (France)
- The fish and cephalopod community was composed of 21 taxa; eight species accounted for 94.4% of the total abundance.
- An impoverished assemblage may reveal the impact of scallop dredging on a part of the Bay.
- Amphipoda was the main prey with many additional items depending on predator species.
- At the assemblage scale, fish and demersal fauna mostly relied on POM/SOM-based food chains.

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**CrediT authorship contribution statement**

**Anthony Sturbois:** Conceptualization, Methodology, Validation, Formal analysis, Data curation, Writing - original draft, Visualization, Project administration, Funding acquisition, Investigation. **Amélie COZIC:** Formal analysis, Investigations, Writing - review & editing. **Gauthier Schaal:** Conceptualization, Investigation, Methodology, Validation, Writing -review & editing, Supervision. **Nicolas Desroy:** Conceptualization, Methodology, Validation, Writing -review & editing, Investigation, Supervision. **Pascal Riera:** Conceptualization, Methodology, Validation, Writing - review & editing, Investigation, Supervision. **Olivier Le Pape:** Conceptualization, Methodology, Validation, Writing -review & editing, Supervision. **Patrick Le Mao:** Investigation, Writing -review & editing. **Alain Ponsero:** Investigation, Writing -review & editing. **Alexandre Carpentier:** Conceptualization, Methodology, Validation, Writing - review & editing, Supervision.

**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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