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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**

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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}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

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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_{SIA} (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⁻¹), 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.

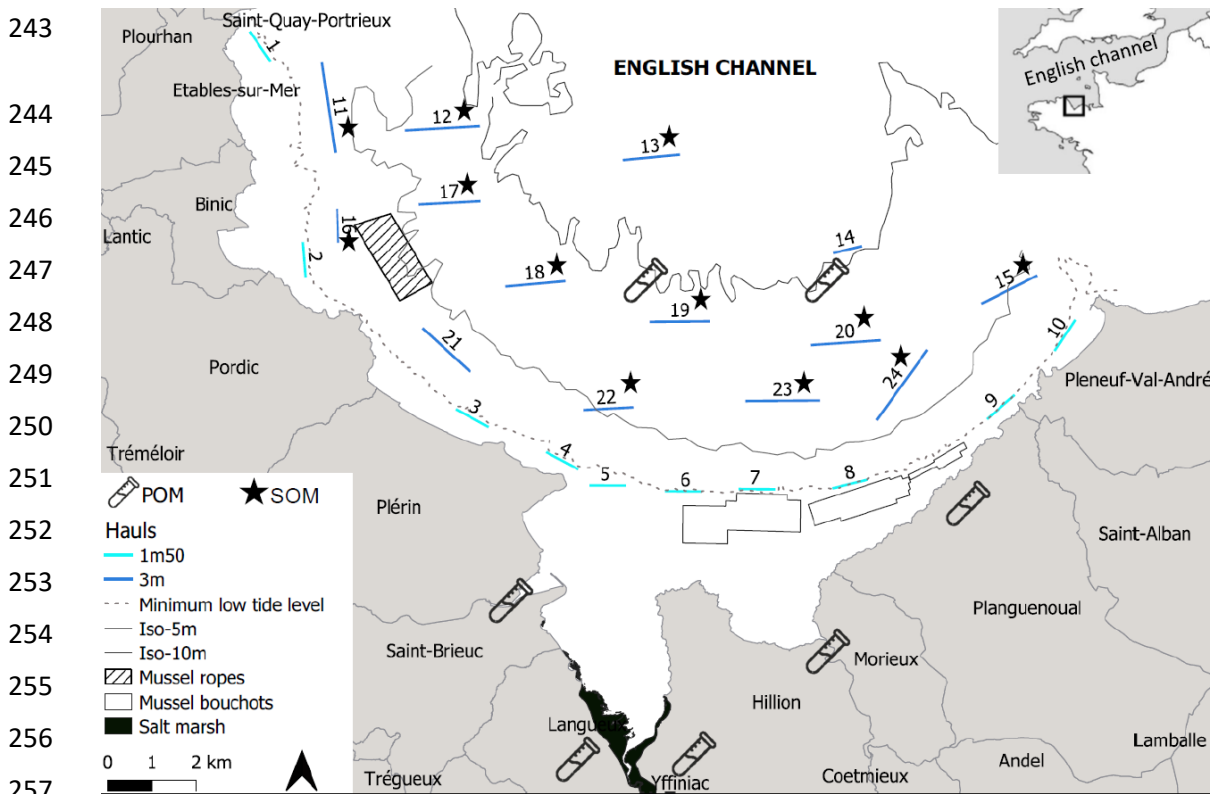
228

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- μ 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 δ 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}C and ^{15}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}C and atmospheric
274 N_2 for ^{15}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 α -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_{SIA}
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 δ 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 δ -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_{SCA} breadth (Shannon–Wiener Index) was calculated from abundance
357 (niche_{SCA-N}) and weight (niche_{SCA-W}) 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_N and Sto_W) 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 ± 2.39 ind.), richness (6.09 ± 0.74
389 species) and Shannon (1.24 ± 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>	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
		<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	0.85 \pm 0.74	2	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	0.88 \pm 0.62	4	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	-	-	

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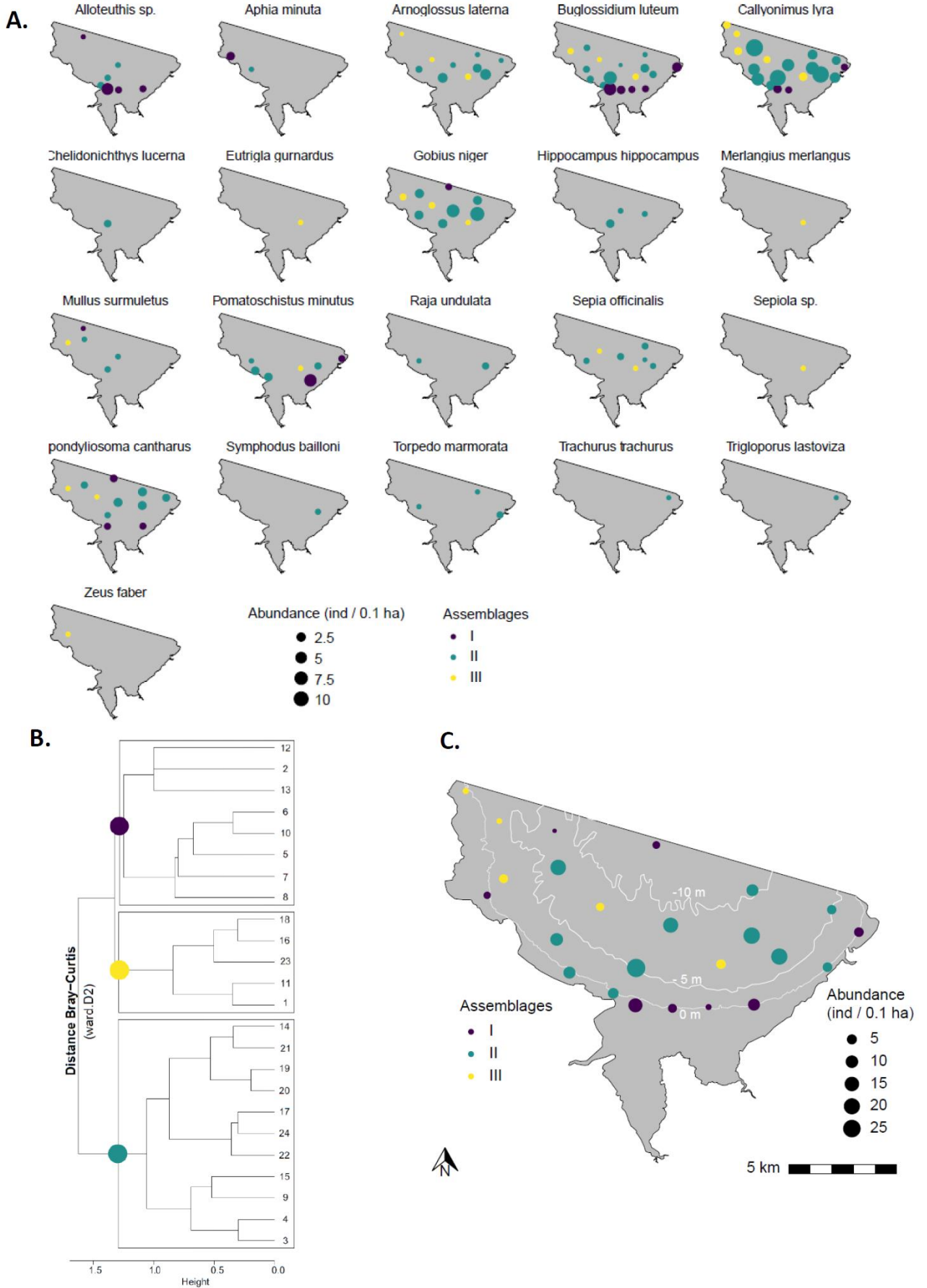
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448 Figure 2: A. Distribution and abundance (number of individuals / 0.1 ha) of fish and
449 cephalopod species. B. Dendrogram showing the distribution of station in the three
450 assemblages defined by the Hierarchical Cluster Analysis. C. Spatial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

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453 **3.3 Food web**

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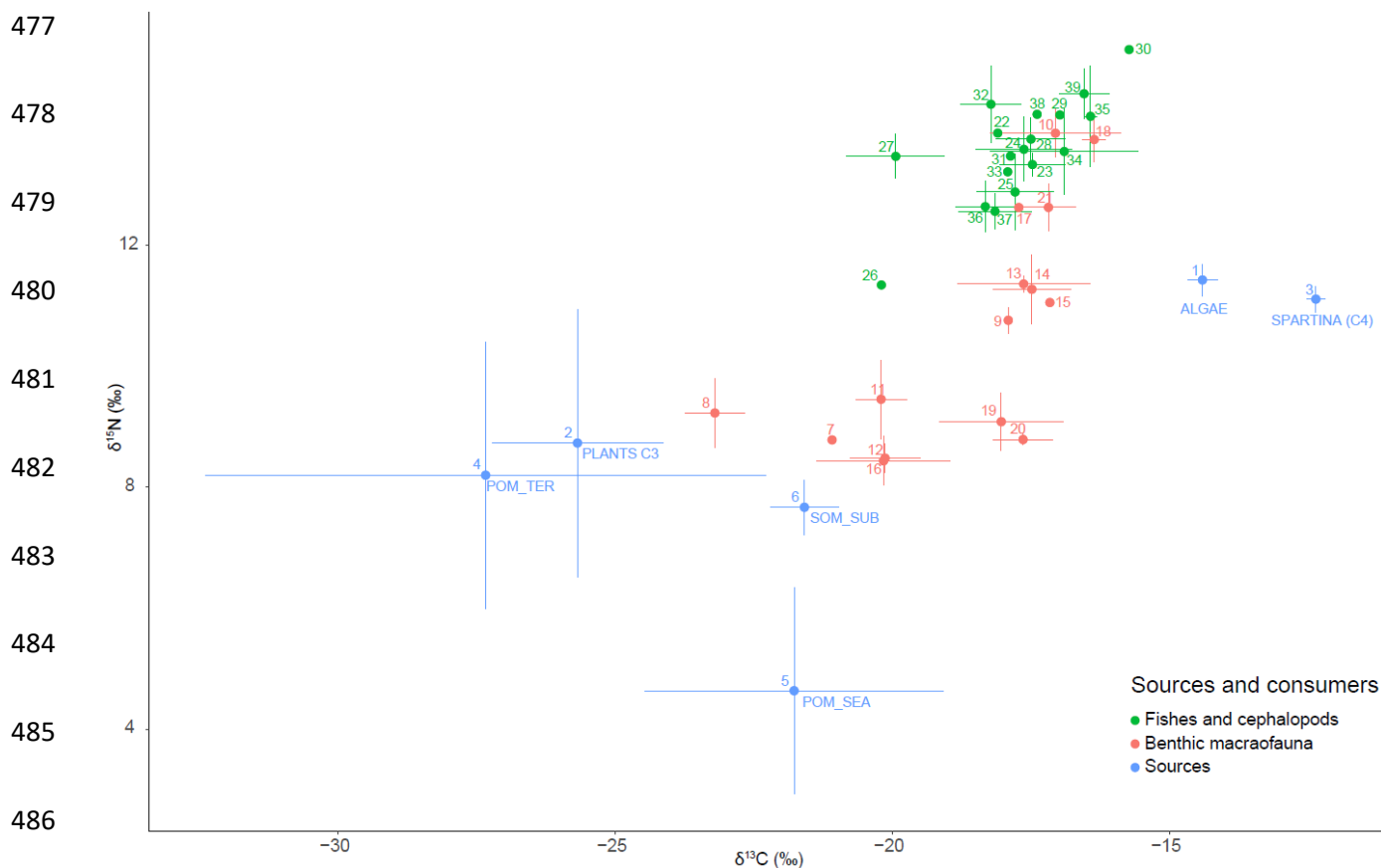
455 **3.3.1 Primary food sources**

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}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}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 ‰ 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_{SIA}

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‰^2 , 0.92) and *S. cantharus* (2.14‰^2 ,
522 0.78) (Figure 4-C, Table II), while *S. officinalis* (1.17‰^2 , 0.63), *M. surmuletus*
523 (0.71‰^2 , 0.60) and *A. laterna* (0.81‰^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_{SIA}, 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_{SIA}.

528 Isim and Ines values associated with TA representation showed contrasted niche_{SIA}
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_{SIA} overlap in the 2D δ -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_{SIA}, encompass at least partially the niche_{SIA} 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 (‰²). 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_{SCA}

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_{SCA-A} breadth among species (Appendix
 562 D), except for *B. luteum* (0.50) which was characterised by lower values. The
 563 niche_{SCA-W} 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).

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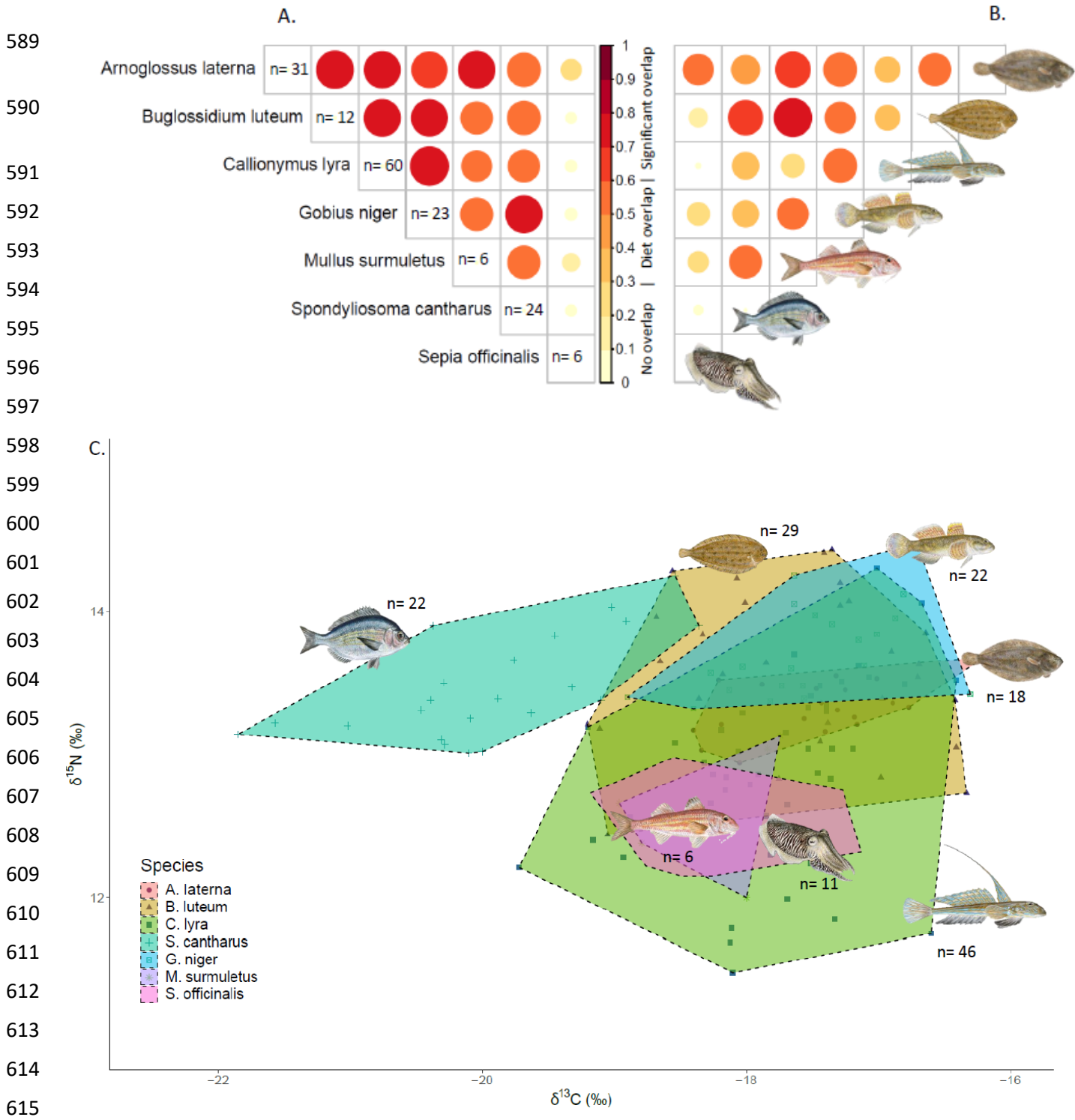
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616 Figure 4: Overlap in fish and cephalopod's feeding strategies assessed from stomach content
 617 (niches_{SCA}) and stable isotope (niches_{SIA}) analyses. Number of individuals per species is
 618 indicated for both approaches (n). A. Plot of 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_{SIA} (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.

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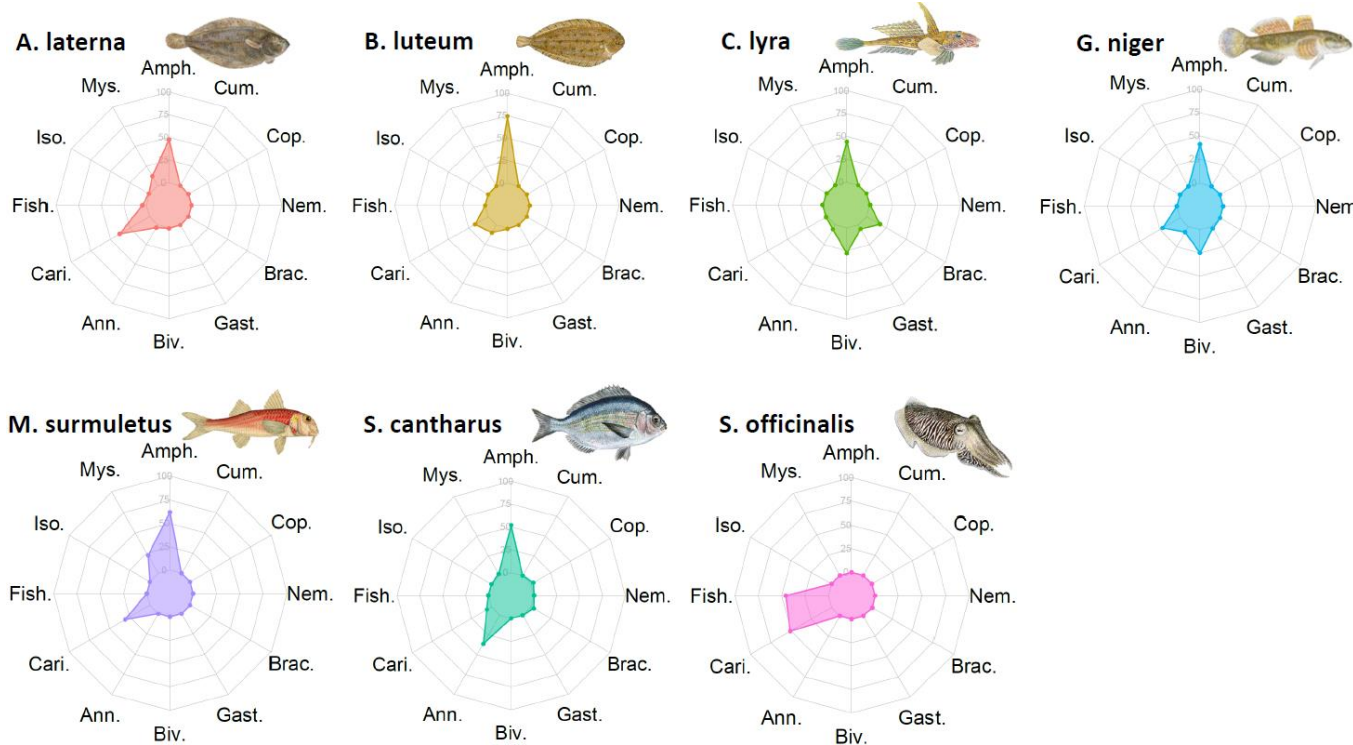
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638 Figure 5: Radar plots of the main food index calculated for each fish and cephalopod species

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

641

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

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

645

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IV. Discussion

647

4.1 Composition of fish and cephalopod assemblages

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

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

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

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

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

658

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

660

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

662

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

664

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

666

667 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}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_{SCA} 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 [Schückel 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 officinalis* – 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. officinalis* (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_{SIA} are more diverse than those
871 influencing niche_{SCA}, 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_{SIA} vs niche_{SCA} 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_{SCA} diversity cannot be
893 systematically associated with dispersions patterns within the niche_{SIA}. 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}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}C -depletion may reveal a higher
908 consumption of amphipods or other pelagic sources.

909 Contrasts in niche_{SIA} 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 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 δ -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}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

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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

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