# Stomach content and stable isotope analyses provide complementary insights into the trophic ecology of coastal temperate bentho-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 $\delta^{13}C$ 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 $\delta^{13}C/\delta^{15}N$ space. *Callionymus lyra* and *Buglossidium luteum*, characterised by the widest isotopic niches, encompassed those of other species, except the singular ^{13}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.

## 1. Introduction

Coastal areas are among the most productive marine systems in the world, sustaining many ecological processes and ecosystems services (Costanza et al., 1997). Worldwide, these ecosystems are suffering severe taxonomic and functional changes in response to cumulative effects of anthropogenic disturbances including overfishing, pollution, climate change, habitat degradation and introduction of non-indigenous species (Gray, 1997; Claudet and Fraschetti, 2010). Human influences induce both acute and chronic effects over various temporal and spatial scales, and can ultimately lead to broad-scale losses of productive habitats, and alteration of community structure and function (Ellis et al., 2000).

Bays and estuaries provide habitats to a wide range of species of potential ecological importance and commercial interest. The

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production in such ecosystems is supported by a wide diversity of primary producers, including phytoplankton, seaweeds, seagrass, mangroves, salt marsh plants, and benthic diatoms (Bouillon et al., 2011). The contribution of these diverse sources to estuarine and coastal food webs differs substantially across systems around the world, particularly for nekton (e.g. fishes, cephalopod), which utilize multiple sources of organic matter over space and time because of their mobility and feeding behavior (Kundu et al., 2021).

Individuals from many fish or cephalopod species concentrate during the juvenile stage in spatially restricted nursery areas within coastal habitats and estuaries (Beck et al., 2001; Brown et al., 2018; Seitz et al., 2014) where they feed on abundant macrobenthos, especially during biomass peaks from late spring to early fall in temperate areas (Beukema, 1974; Nicolas et al., 2007; Saulnier et al., 2020). This concentration of benthic feeding juveniles results in density-dependent regulation (Le Pape and Bonhommeau, 2015), especially related to inter-specific relationships (Post et al., 1999). Food competition may occur when individuals from one or several species share a common feeding strategy and rely on limited preys (Birch, 1957). Even if food partitioning limits competition, most bentho-demersal fish species are considered as opportunistic predators and prey on a shared pool of preys (Hunsicker et al., 2011), especially at juvenile stage, leading to potential competition processes at intra and interspecific levels (Tableau et al., 2019).

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

In stable isotope analysis, the concept of isotopic niche is frequently analysed through different metrics used to examine food web structure, i.e., resource use and trophic positions among organisms, populations or trophic groups (Layman et al., 2007a). Trophic niche variability [*sensus* Newsome et al. (2007)] reflects the availability of food resources, habitat uses, behaviours and distributions within ecosystems (Bolnick et al., 2002; Quevedo et al., 2009). Intraspecific niche can depict opportunistic or specialist feeding behaviour within species functional diversity, while interspecific niche can reveal competition or resources partitioning strategies among populations. Interestingly, the concepts of niche variability and overlap can be tested among predator species through metrics respectively derived both from stomach contents [niche$_{SCA}$ (Petta et al., 2020; Schoener (1971)] and isotope compositions [niche$_{SIA}$ (Petta et al., 2020; Cucherousset and Villéger, 2015; Layman et al., 2007a, 2012; Rigolet et al., 2015)].

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

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

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

## 2. Material and methods

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

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

In 2019, the benthic macrofauna was dominated by molluscs, annelids and crustaceans (Sturbois et al., 2021a). Knowledge concerning subtidal fishes in the study area are rare and old. In the last studies dating back to 1981, demersal fish communities were dominated by *Pleuronectes platessa, Psetta maxima, Solea lascaris, S. vulgaris*, and *Scophthalmus rhombus*, while *Spondyliosoma cantharus* was limited to the western part of the bay, and *Limanda limanda* and *Platichthys flesus* were scarce (Le Dean and Moreau, 1981; Gully, 1981). In the intertidal area, Le Luherne et al. (2016) evidenced the use of sandy beaches at high tide by some species; e.g. *Buglossidium luteum, Pleuronectes platessa, Pomatoschistus microps, Chelon* spp., *and Dicentrarchus labrax*; these three last taxa also using the salt marsh channels (Laugier, 2015; Sturbois et al., 2016).

Despite bordering the National Nature Reserve of the bay of Saint-Brieuc and partially belonging to the Natura 2000 "Baie de Saint-Brieuc-Est" site (European Union network, FR5300066), the study area is exposed to a number of anthropogenic pressures including mussel culture and scallop dredging (Sturbois et al., 2021a, 2021b). Mussels are farmed on wooden poles (312 ha; Fig. 1) in the north-eastern part of the intertidal area and on ropes in the western part of the study area. The sea bed is exposed to long-term scallop dredging (Sturbois et al., 2021a). Some areas are colonized by the non-indigenous slipper limpet *Crepidula fornicata* especially in the western part of the bay (Blanchard et al., 2001;
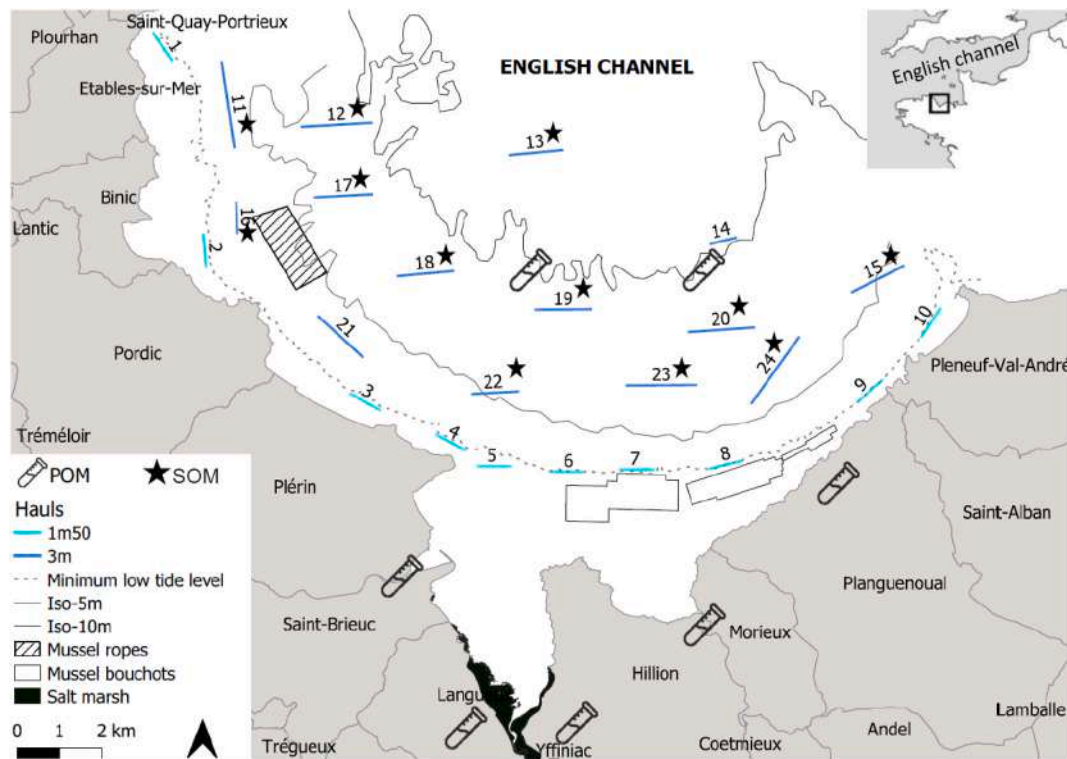
**Fig. 1.** Location of the study area and sampling strategy: length of hauls (colored line), location of particulate organic matter (POM, test tube) and sedimentary organic matter (SOM, black stars) samples, depths (grey lines).

Hamon and Blanchard, 1994). The bay also suffers from eutrophication resulting in macroalgae proliferation and cyclic green tides episodes (Charlier et al., 2007; Gravier, 2012). These green tides influence the dynamics of some benthic populations of invertebrates in the intertidal area (Sturbois et al., 2021b) and impact fish nursery grounds in the upper parts of the intertidal area (Le Luherne et al., 2016, 2017).

## 2.2. Sample collection and laboratory processes

### 2.2.1. Fish and cephalopods

Fish and cephalopods were sampled in September 2019 using beam trawls (2.5/3 knots) at 24 stations (Fig. 1). Deeper stations (n = 14) were sampled with a 3.0 m beam trawl (1 cm mesh size, length of hauls = 1365m $\pm$ 397, mean length $\pm$ sd) towed by the RV *Thalia*. Shallower stations (n = 10) were sampled with a 1.5 m beam trawl (1 cm mesh size, length of hauls = 774m $\pm$ 8) towed by the *Emeraude Explorer* semi-rigid pneumatic boat. Fish were identified and measured (fork length, nearest mm) on board before release. Some individuals were collected, euthanized with an overdosed solution of benzocaine (400 mg.L⁻1), and immediately frozen ($-20$ °C) for later stable isotope (SIA) and stomach content (SCA) analyses. Note that skates (biopsy for SIA) and sea horses were systematically released.

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

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

### 2.2.2. Benthic macrofauna

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

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

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

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

## 2.3. Stable isotope analysis

At least three replicates were analysed per species when possible; however, for few taxa less replicates were available (Supplementary material, Appendix A). Powdered samples were packed into 5 $\times$ 8 mm

ultra-clean tin capsules and analysed using an elemental analyser (EA Flash 2000 from ThermoFisher Scientific) coupled with an isotope ratio mass spectrometer (Delta V Plus from ThermoFisher Scientific) at the stable isotope facility of the Pole Spectrométrie Océan at the University of Bretagne Occidentale (Brest, France).

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

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

where $X$ is $^{13}C$ and $^{15}N$ and R is the corresponding ratio of $^{13}C/^{12}C$ and $^{15}N/^{14}N$. Reference standard used were Vienna-Pee Dee Belemnite for $^{13}C$ and atmospheric $N_2$ for $^{15}N$ (precision: 0.1‰).

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

## 2.4. Data analysis

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

### 2.4.1. Fish and cephalopod assemblages

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

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

### 2.4.2. Stable isotope analysis

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

- $\delta^{13}C$ and $\delta^{15}N$ range (CR and NR): Distance between the highest and the lowest $\delta^{13}C$ and $\delta^{15}N$ values, respectively, for a given fish or cephalopod species). CR is one representation of basal sources diversity supporting the species whereas NR is one representation of the trophic level diversity at the species level;
- *Total Area* (TA): Convex hull area encompassed by a given fish or cephalopod species in the $\delta^{13}C$-$\delta^{15}N$ 2D $\delta$ space. This represents a measure of the total amount of niche space occupied, i.e., a proxy of overall trophic strategies (specialists vs. opportunists);
- *Mean distance to centroid* (CD): Average Euclidean distance of each individual to the $\delta^{13}C$-$\delta^{15}N$ species centroid, where the centroid is the mean $\delta^{13}C$ and $\delta^{15}N$ value for all individuals of a given fish or cephalopod species. This metric provides a measure of the average degree of variability in trophic strategy;
- *Mean nearest neighbor distance* (NND): Mean of the Euclidean distances to each individual nearest neighbor within each fish species niche, i.e., a measure of the overall density of individual packing.

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

- *Isotopic similarity* (ISim): the ratio between the isotopic niche of the intersection and of the union of the two fish or cephalopod species considered. It ranges from 0 when there is no isotopic overlap to 1 when the species with the lowest isotopic richness fills a subset of the isotopic space filled by the species with the highest one. ISim was calculated in the two dimensions of the 2D $\delta$-space and for each isotope (i.e. one dimension);
- *Isotopic nestedness (Ines)*: Ratio between the area of the intersection and the area filled by the species with the narrowest isotopic niche. It ranges from 0 when there is no isotopic overlap to 1 when the group with the lowest isotopic richness fills a subset of the isotopic space filled by the group with the highest one;
- *Isotopic divergence* (IDiv): Distribution of species individuals within the convexhull. IDiv is minimal (i.e. tends to 0) when most of the points are close to the centroid of the convex hull, and individuals with the most extreme stable isotope values are rare in a community. IDiv tends to 1 when all the points are located on the edges of the convex hull and individuals with extreme stable isotope value(s) dominate;
- *Isotopic Eveness* (IEve): Regularity in the distribution of individual of a given fish or cephalopod species along the shortest tree that links all the individuals. IEve tends to 0 when most of individuals are packed within a small region of the stable isotope space while a few others are far from this cluster. IEve tends to 1 when individuals are evenly distributed in the stable isotope space.

### 2.4.3. Stomach contents analysis

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

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

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

Niche$_{SCA}$ breadth (Shannon–Wiener Index) was calculated from abundance (niche$_{SCA-N}$) and weight (niche$_{SCA-W}$) in stomach content raw data. A HCA was performed on stomach contents raw abundance data to distinguish groups of fish or cephalopod characterised by similar feeding strategies (*i.e.* same pool of preys), using the methods described for fish and cephalopod assemblages in section 2.4.1. Complementary, the Schoener index of trophic overlap (Sto) was calculated on abundance and weight of stomach raw data (Sto$_N$ and Sto$_W$) for all pairs of fish and cephalopod species (Schoener, 1971). Using the flowing equation, Schoener index values distinct dietary overlap (0.3 < Sto<0.6) from significant dietary overlap (Sto>0.6):

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

where $Pxi$ and $Pyi$: proportion of food category $i$ in the diet of species $x$ and $y$; and $n$: total number of prey.

## 3. Results

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

A total of 558 individuals belonging to 21 species were sampled. The

abundance was variable among species, eight species accounting for 94.4% of the total abundance (Table 1, Fig. 2-A). The northwestern part of the study area was characterised by lower abundances of fish and cephalopods (Fig. 2- A&B). The common dragonet *Callionymus lyra* (232 individuals, 41.6%) and the black goby *Gobius niger* (115 ind., 20.6%) were the most abundant species while the six following ranked species were less abundant and less frequent in the study area (frequency ranging from 29 to 71%, Table 1). The 13 other species were rarer (frequency below 12%) and less abundant. Most individuals were observed at juvenile stages [young of the year (GO) and G1, Appendix B].

### 3.2. Fish and cephalopod assemblages

The HCA separated three assemblages characterised by differences in abundance, richness and diversity (Table 1, Fig. 2-B and 2-C). Assemblage I (8 stations) mainly occurred in the shallowest stations and was dominated by *Buglossidium luteum*, *Pomatoschistus minutus* and *Alloteuthis* sp. It was characterised by a low abundance and the lowest richness and Shannon index values. Assemblages II (n = 11) and III (n = 5) were both dominated by *C. lyra*, *G. niger* and *B. luteum*. Assemblage II was characterised by higher abundances (13.16 ± 2.39 ind.), richness (6.09 ± 0.74 species) and Shannon (1.24 ± 0.12) index compared to assemblage III. Eight species among the most abundant were common to assemblages II and III, which differed according to the presence of 9 and 4 rarer species respectively present in one of these two assemblages (Table 1). Piélou indices were similar among assemblages.

### 3.3. Food web

#### 3.3.1. Primary food sources

Contrasts were observed in primary food sources isotopic values (Fig. 3, Appendix A). Values of $\delta^{13}C$ were lower for terrestrial POM ($-27.34 \pm 5.06‰$) and the pool of salt marsh C3 plants ($-25.68 \pm 1.54‰$), while *Ulva* spp. ($-14.41 \pm 0.27‰$) and the C4 plant *Spartina anglica* ($-12.36 \pm 0.17‰$), considerably $^{13}C$-enriched than other sources, exhibited the highest values. The SOM and the marine POM were

characterised by intermediate values. *Ulva* spp. and *Spartina anglica* were slightly $^{15}N$-enriched compared to other potential food sources.

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

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

### 3.4. Predators diet and isotopic niches

Diet composition and $\delta^{13}C$ and $\delta^{15}N$ values were explored for seven of the most abundant species (Table 1) for which the numbers of stomach samples and stable isotope composition were sufficient: *A. laterna*, *B. luteum*, *C. lyra*, *S. cantharus*, *G. niger*, *M. surmuletus* and *S. officinalis*.

#### 3.4.1. Niche$_{SIA}$

Variance analyses have been performed on stable isotope values to look for differences at assemblages and species scales. The two-way permutational variance analyses did not evidenced any differences in $\delta^{13}C$ (F = 1.72, p-value = 0.18) nor $\delta^{15}N$ (F = 0.46, p-value = 0.63) among assemblages, whereas the factor species (Appendix G) implied differences in $\delta^{13}C$ (F = 29.95, p-value <0.001) and $\delta^{15}N$ (F = 14.46, p-value <0.001) values. Pairwise Wilcoxon-tests (Appendix H) performed on $\delta^{13}C$ values revealed significant differences between *S. cantharus* and

**Table 1**
Diversity metrics, abundance (mean ± sd/se) and occurrence (occ) of species sampled at the scale of the study area and the three assemblages identified by Hierarchical Cluster Analysis.

| | | 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 |
| **Diversity metrics** | 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 | |
| | Piélou | 0.70 ± 0.29 | | 0.66 ± 0.15 | | 0.73 ± 0.03 | | 0.69 ± 0.17 | |
| **Abundance (n ind./0.1ha) of sampled species** | *Callyonimus lyra* | **3.34 ± 4.15** | **19** | 0.43 ± 0.23 | 3 | **6.53 ± 1.29** | **11** | **0.97 ± 0.17** | **5** |
| | *Buglossidium luteum* | **1.09 ± 1.74** | **17** | **1.50 ± 0.72** | **5** | **1.18 ± 0.57** | **9** | **0.24 ± 0.11** | **3** |
| | *Gobius niger* | **1.06 ± 2.09** | **10** | 0.10 ± 0.10 | 1 | **2.10 ± 0.84** | **6** | **0.32 ± 0.15** | **3** |
| | *Spondyliosoma cantharus* | 0.51 ± 0.73 | 11 | 0.37 ± 0.19 | 3 | 0.81 ± 0.27 | 6 | 0.09 ± 0.06 | 2 |
| | *Pomatoschistus minutus* | 0.49 ± 1.28 | 7 | **0.85 ± 0.74** | **2** | 0.42 ± 0.21 | 4 | 0.05 ± 0.05 | 1 |
| | *Arnoglossus laterna* | 0.46 ± 0.98 | 10 | – | 0 | 0.92 ± 0.40 | 7 | 0.18 ± 0.09 | 3 |
| | *Alloteuthis* sp. | 0.37 ± 1.05 | 7 | **0.88 ± 0.62** | **4** | 0.16 ± 0.09 | 3 | – | |
| | *Sepia officinalis* | 0.14 ± 0.26 | 7 | – | 0 | 0.26 ± 0.10 | 5 | 0.09 ± 0.06 | 2 |
| | *Hippocampus hippocampus* | 0.10 ± 0.35 | 3 | – | 0 | 0.22 ± 0.15 | 3 | – | |
| | *Aphia minuta* | 0.08 ± 0.36 | 2 | 0.22 ± 0.22 | 1 | 0.02 ± 0.02 | 1 | – | |
| | *Mullus surmuletus* | 0.07 ± 0.15 | 5 | 0.03 ± 0.03 | 1 | 0.11 ± 0.06 | 3 | 0.05 ± 0.05 | 1 |
| | *Torpedo marmorata* | 0.06 ± 0.18 | 3 | – | 0 | 0.12 ± 0.08 | 3 | – | |
| | *Raja undulata* | 0.05 ± 0.20 | 2 | – | 0 | 0.11 ± 0.09 | 2 | – | |
| | *Chelidonichthys lucerna* | 0.05 ± 0.23 | 1 | – | 0 | 0.10 ± 0.10 | 1 | – | |
| | *Symphodus bailloni* | 0.02 ± 0.10 | 1 | – | 0 | 0.04 ± 0.04 | 1 | – | |
| | *Eutrigla gurnardus* | 0.01 ± 0.05 | 1 | – | 0 | – | | 0.05 ± 0.05 | 1 |
| | *Merlangius merlangus* | 0.01 ± 0.05 | 1 | – | 0 | – | | 0.05 ± 0.05 | 1 |
| | *Sepiola* sp. | 0.01 ± 0.05 | 1 | – | 0 | – | | 0.05 ± 0.05 | 1 |
| | *Zeus faber* | 0.01 ± 0.05 | 1 | – | 0 | – | | 0.05 ± 0.05 | 1 |
| | *Trachurus trachurus* | 0.01 ± 0.04 | 1 | – | 0 | 0.02 ± 0.02 | 1 | – | |
| | *Trigloporus lastoviza* | 0.01 ± 0.04 | 1 | – | 0 | 0.02 ± 0.02 | 1 | – | |
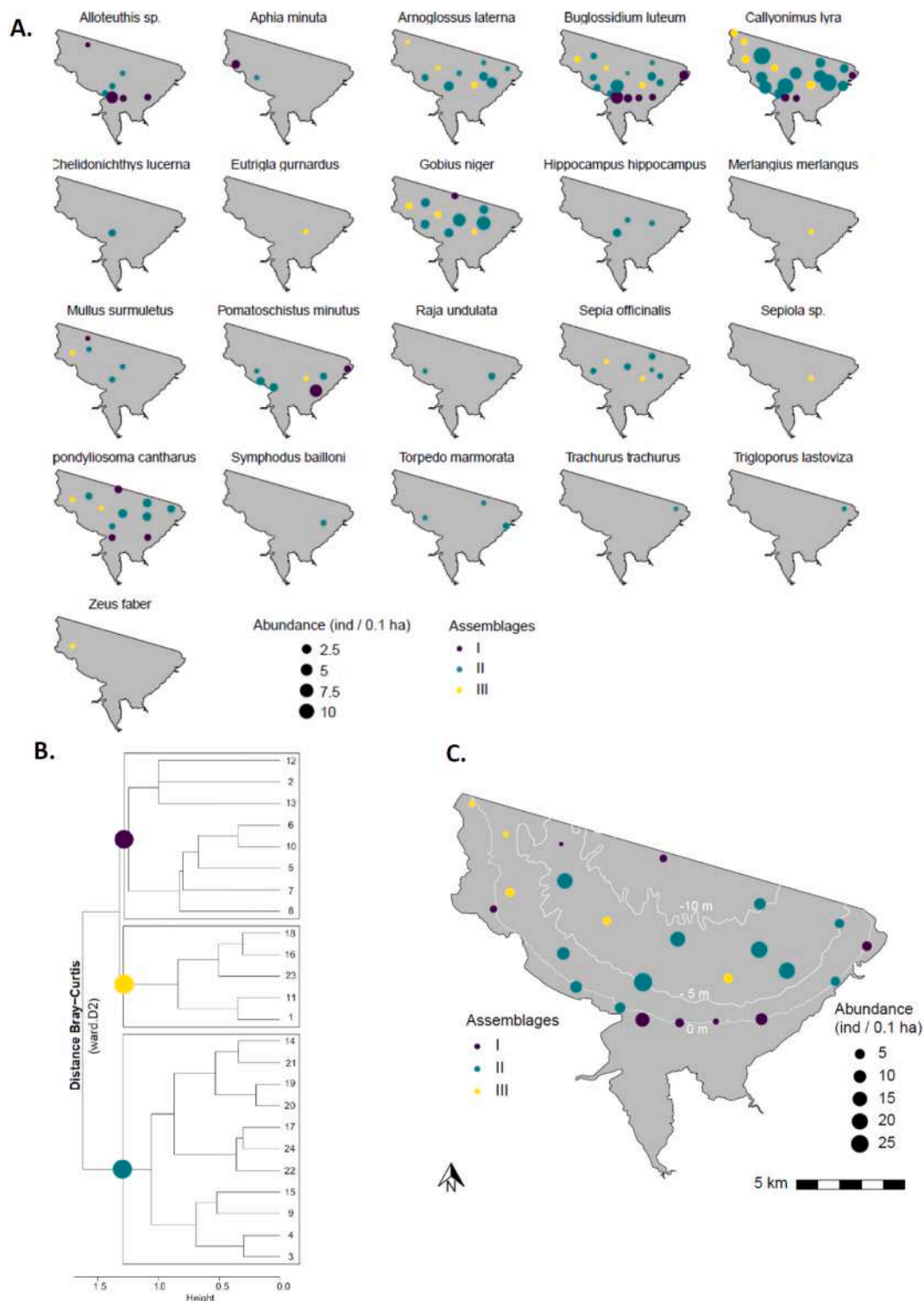
**Fig. 2.** A. Distribution and abundance (number of individuals/0.1 ha) of fish and cephalopod species. B. Dendrogram showing the distribution of station in the three assemblages defined by the Hierarchical Cluster Analysis. C. Spatial distribution of fish and cephalopod assemblages (white lines indicate the bathymetry).

the six other species while no difference occurred between other species, which exhibited similar carbon isotope compositions. $\delta^{15}N$ values indicated differences between most pairs of species (Appendix H). The interaction species*assemblages was not significant for both isotopes.

*C. lyra* (TA = 6.10‰$^2$; CD = 0.80), *B. luteum* (4.22‰$^2$, 0.92) and *S. cantharus* (2.14‰$^2$, 0.78) (Fig. 4-C, Table 2), while *S. officinalis* (1.17‰$^2$, 0.63), *M. surmuletus* (0.71‰$^2$, 0.60) and *A. laterna* (0.81‰$^2$, 0.5) displayed a lower variability. IEve values ranged from 0.62 to 0.86

pointed globally that individual of each species were evenly distributed in their respective niche$_{SIA}$, with a lesser extent for *M. surmuletus*. According to IDiv (min: 0.66 for *C. lyra,* max 0.79 for *M. surmuletus)*, individual of each species tended to fill the whole space of their respective niche$_{SIA}$.

Isim and Ines values associated with TA representation showed contrasted niche$_{SIA}$ overlaps between species (Fig. 4-B, Appendix F). While most pairs of species (except pairs including *S. cantharus*) were
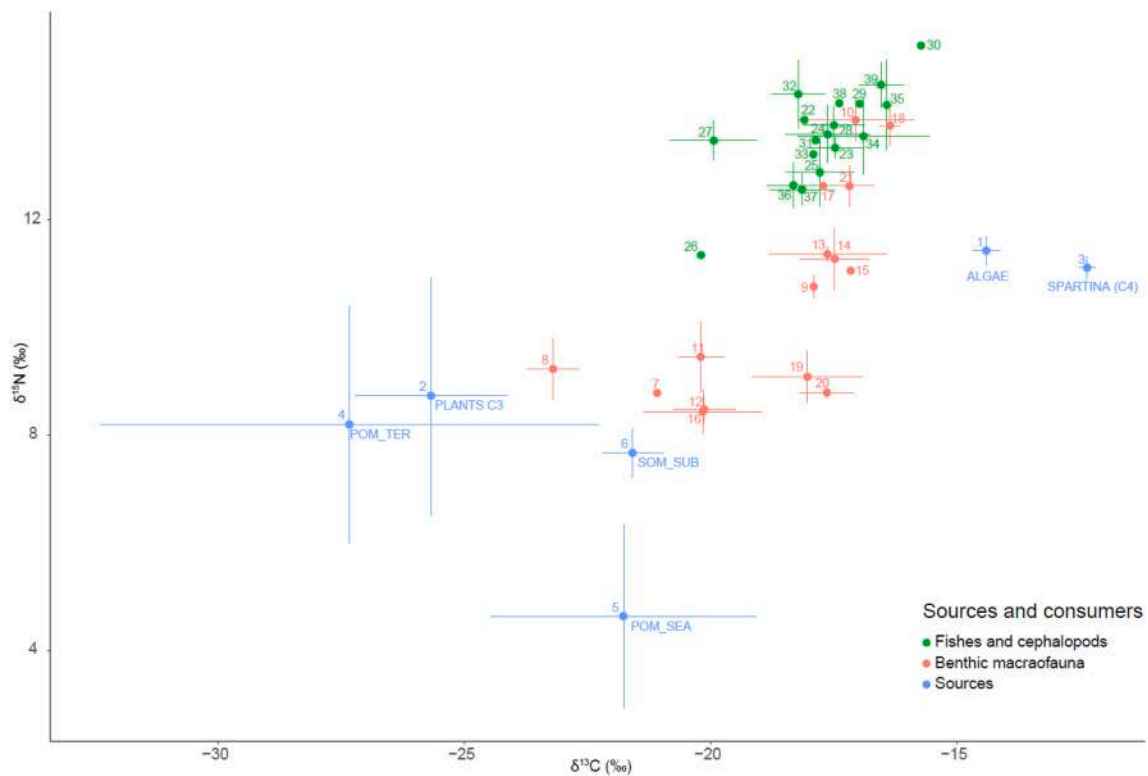
**Fig. 3.** $\delta^{13}$C and $\delta^{15}$N of consumers and potential dietary sources of organic matter in shallow subtidal soft bottom habitats. Colors represents groups: sources (blue), benthic macrofauna (red) and fishes and cephalopods (green). Mean $\delta^{13}$C and $\delta^{15}$N are plotted 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: *Polititapes 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*.

**Table 2**

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

| | n | δ13C rg | δ15N rg | Cent δ13C | Cent δ15N | TA | CD | NND + SD | IDiv | IEve |
|---|---|---|---|---|---|---|---|---|---|---|
| *Arnoglossus laterna* | 18 | 2.21 | 0.74 | −17.47 | 13.33 | 0.81 | 0.5 | 0.19 ± 0.14 | 0.68 | 0.75 |
| *Buglossidium luteum* | 29 | 2.87 | 1.99 | −17.63 | 13.58 | 4.22 | 0.92 | 0.24 ± 0.15 | 0.77 | 0.79 |
| *Callionymus lyra* | 46 | 3.31 | 2.82 | −17.79 | 12.88 | 6.10 | 0.80 | 0.21 ± 0.16 | 0.66 | 0.74 |
| *Gobius niger* | 22 | 2.6 | 1.14 | −17.50 | 13.75 | 1.74 | 0.61 | 0.21 ± 0.15 | 0.69 | 0.76 |
| *Mullus surmuletus* | 6 | 1.22 | 1.13 | −18.33 | 12.64 | 0.71 | 0.60 | 0.34 ± 0.27 | 0.79 | 0.62 |
| *Sepia officinalis* | 11 | 2.05 | 0.83 | −18.15 | 12.56 | 1.17 | 0.63 | 0.34 ± 0.13 | 0.72 | 0.86 |
| *Spondyliosoma cantharus* | 22 | 3.49 | 1.24 | −19.94 | 13.45 | 2.14 | 0.78 | 0.23 ± 0.13 | 0.67 | 0.78 |

characterised by high Isim $\delta^{13}$C values, the niche$_{SIA}$ overlap in the 2D $\delta$-space was limited due to the differences in $\delta^{15}$N values and lower Isim $\delta^{15}$N values. Apart from *S. cantharus*, *C. lyra* and *B. luteum*, characterised by wide niches$_{SIA}$, encompass at least partially the niche$_{SIA}$ of other bentho-demersal predators.

### 3.4.2. Niche$_{SCA}$

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

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

No major difference was found in the niche$_{SCA-A}$ breadth among species (Appendix D), except for *B. luteum* (0.50) which was characterised by lower values. The niche$_{SCA-W}$ breadth values pointed out a slightly different pattern. While *B. luteum* and *S. officinalis* were still characterised by low values (0.78 and 0.69, respectively), *C. lyra* (1.44)

showed the highest value.

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

## 4. Discussion

### 4.1. Composition of fish and cephalopod assemblages

The fish and cephalopod community was dominated by eight species (94.4% of the total abundance). *C. lyra* was the most abundant species in most stations, as observed in many soft-bottoms in the English Channel (Dauvin, 1988). The diversity of the community was rather low. Some of the species sampled in the study area were partly or totally shared with other bays in the English Channel: *e.g. B. luteum, A. laterna, Pomatoschistus* sp., *M. surmuletus, S. cantharus*; while others were absent from our sampling: *e.g., Dicentrarchus labrax, Limanda limanda, Chelon* spp., *Pleuronectes platessa, Platichthys flesus, Psetta maxima, Scophtalmus rhombus, Pegusa lascaris, Solea solea* (Auber et al., 2017; Kostecki et al., 2012; Le Mao, 1985; Day et al., 2021; Saulnier et al., 2020). Gully (1981)
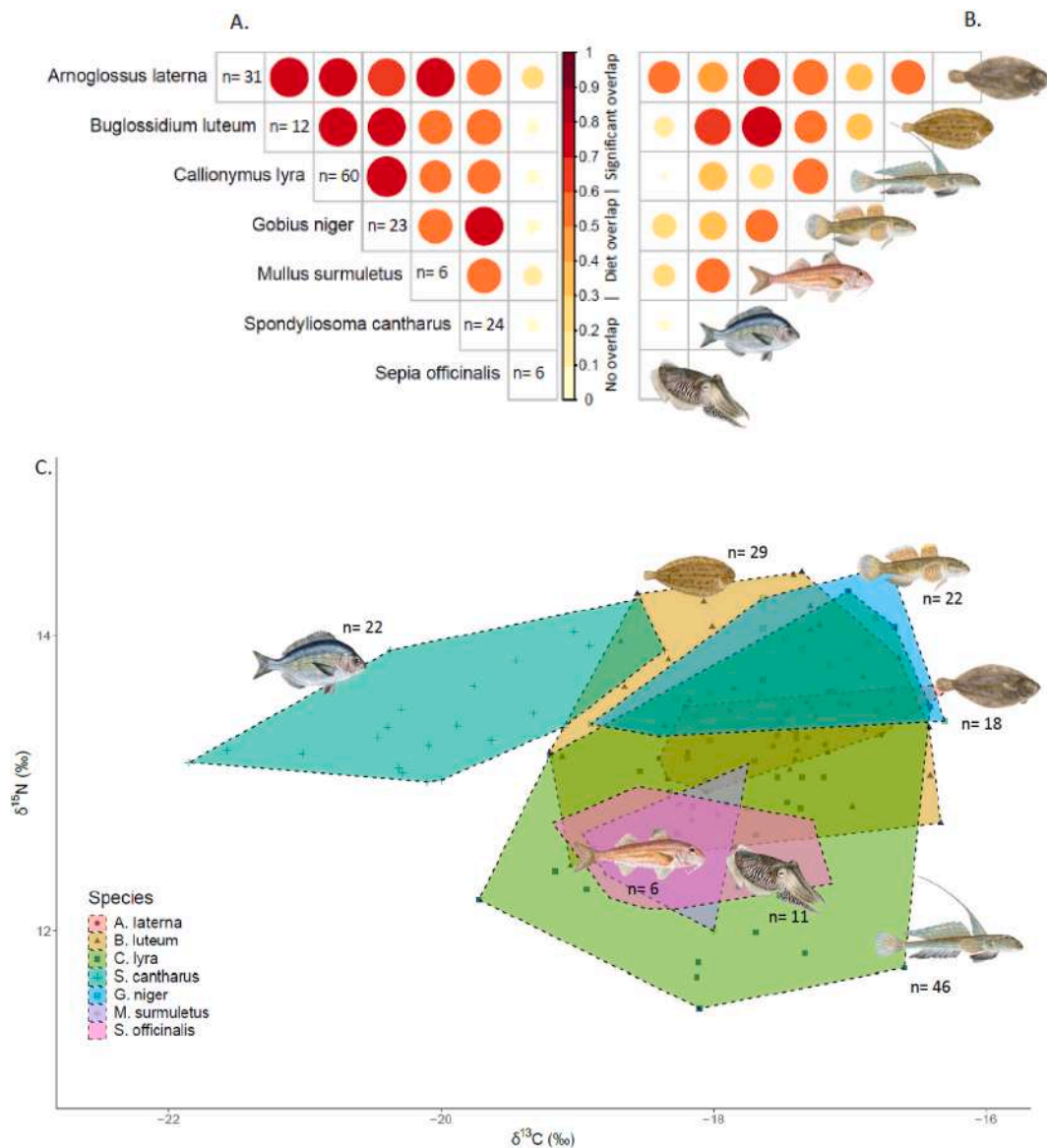


**Fig. 4.** Overlap in fish and cephalopod's feeding strategies assessed from stomach content (niche_SCA) and stable isotope (niche_SIA) analyses. Number of individuals per species is indicated for both approaches (n). A. Plot of Shoener index's values calculated from the abundance of preys between all pairs of fish and cephalopod species. The size and the color gradient of circle corresponds the dietary overlap from absence (smaller yellow circles) to significant overlap (larger red circles). B. Plot of Shoener index's values calculated from the weight of preys. C. $\delta^{13}C$ and $\delta^{15}N$ stable isotope composition of fishes and cephalopods. $\delta^{13}C$ and $\delta^{15}N$ are plotted for each individual. Shapes represent species. Niche_SIA (i.e.Total area) is represented by convex hull polygons for each species: *Arnoglossus laterna* (red), *Buglossidium luteum* (brown), *Callionymus lyra* (green), *Spondyliosoma cantharus* (bottle green), *Gobius niger* (blue), *Mullus surmuletus* (purple), *Sepia officinalis* (pink). Illustrations of species come from the © Scandinavian Fishing Year Book.
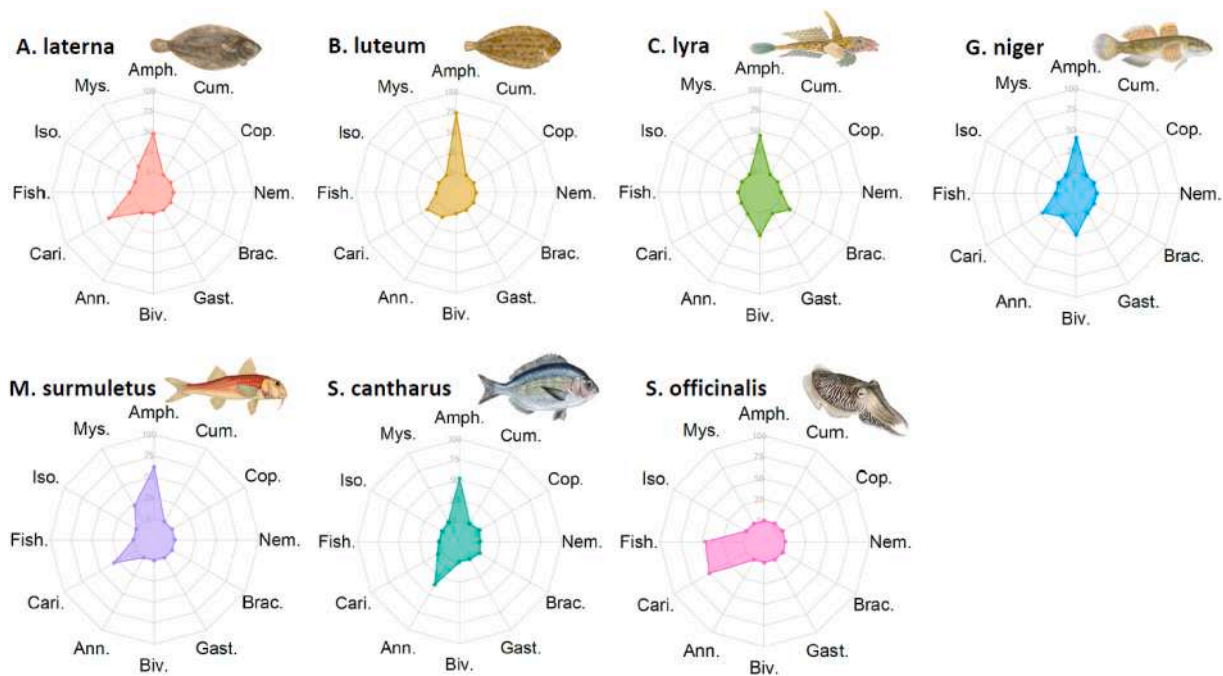
**Fig. 5.** Radar plots of the main food index calculated for each fish and cephalopod species and for each prey item. Colors correspond to species: *Arnoglossus laterna* (red), *Buglossidium luteum* (brown), *Callionymus lyra* (green), *Spondyliosoma cantharus* (bottle green), *Gobius niger* (blue), *Mullus surmuletus* (purple), *Sepia officinalis* (pink). The different prey items are indicated in the periphery of the radar plot: Amph.: Amphipoda; Cum.: Cumacea; Cop.: Copepoda; Nem.: Nemerta; Brac.: Brachyura; Gast.: Gasteropoda; Biv.: Bivalvia; Ann.: Annelida; Cari.: Caridea; Fish; Iso.:Isopoda; Mys.: Mysida. Illustrations of species come from the © Scandinavian Fishing Year Book.

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

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

Assemblage III seemed to constitute an impoverished facies of assemblage II characterised with (1) lower abundance, occurrence and eveness, and (2) absence of skates. This could be related to the degradation of benthic habitats showed by Sturbois et al. (2021a) in the study

area, with significant taxonomic and functional changes. They identified scallop dredging as the main driver of these changes, as evidenced in other highly exploited systems (Fanelli et al., 2009; Rosenberg et al., 2000). Scallop dredging generates fish by-catch (Craven et al., 2013) and significantly impacts sediments properties and preys (Bradshaw et al., 2001; Morys et al., 2021). This may also directly influence fish assemblages as shown by Barletta et al. (2016) and reviewed by Wenger et al. (2017) in sediment dredging contexts.

### 4.2. Sources supporting the food web

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

The local use of the salt marsh by fishes for preys supported by the vegetation or by microphytobenthos is limited to very mobile species (e. g. *D. labrax* and *Chelon* spp.) which forage in the salt marshes during high tide (Laugier, 2015; Sturbois et al., 2016) but were not represented

in subtidal sampling. Most of the species sampled in the study area were not caught in the upper intertidal area (Le Luherne et al., 2016; personal observations) or in the salt marsh (Sturbois et al., 2016) suggesting that large tidal migration from subtidal to the upper limit of the large intertidal area under megatidal conditions is not a strategy retained by those species for feeding (Amara et al., 2004; Le Pape and Cognez, 2016). In this sense, the ability of tidal channels crossing sandy and muddy sediments, which constitute particular intertidal habitats, to shelter fishes in various tidal conditions need to be explored.

### 4.3. Specific diet and niche_SCA variability for the seven fish and cephalopod species compared to results observed in the bay of Saint-Brieuc

*Arnoglossus laterna* – The diet of *A. laterna* was mainly composed of crustaceans in the study area, primarily amphipoda and caridea and in a lesser extent mysida. The scaldfish is an active predator that feed on active moving preys rather than sedentary species (Darnaude et al., 2001; De Groot, 1971). Globally, our results are congruent with the literature which points a dominance of crustaceans in the scaldfish diet across European coats [Schückel et al., 2012) (North sea), Avşar, 1994 (Turkey), Gibson and Ezzi, 1980 (Scotland), Fanelli et al., 2009 (Sicily), Cabral et al., 2002 (Portugal)]. However, while these studies pointed a relative and variable importance of fishes in the diet of *A. laterna*, fishes item were considered accidental in the study area which was in accordance with the results of Paulo-Martins et al. (2011) who found no teleost fish in the stomach content of scaldfish sampled in the Cascais Bay (Portugal). Similarly, annelida was identified as a secondary prey in some of the aforementioned studies, and assessed as an accidental prey item in the bay of Saint-Brieuc.

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

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

*Gobius niger* – Amphipoda, bivalvia and caridea were the main components identified in the diet of the black goby, while annelids and gasteropods constituted accidental preys. This is congruent with the results of Filiz and Toğulga (2009) in the Aegean sea who showed that *G. niger* mainly fed on molluscs and crustaceans (90.47% of the diet),

and in a lesser extent on polychaetes. These three food items belonging to the two first ranks of food items in most off studies focusing on *G. niger* diet in various area in the north and the south of Europe (De Casabianda and Kiener, 1969; Filiz and Toğulga, 2009; Labropoulou and Markakis, 1998; McGrath, 1974; Vaas et al., 1975) while some studies pointed the variable importance of teleost fishes (Fjøsne, 1996; Vaas et al., 1975).

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

*Spondyliosoma cantharus* – The black sea bream mainly fed on amphipoda and annelida in the bay of Saint-Brieuc. Five other items were identified as accidental items placing the species at the second range in diversity of preys. Gonçalves and Erzini (1998) and Jakov et al. (2006) find congruent results and pointed that hydrozoans, items absent from stomachs in our study, were also an important prey in the south west coast of Portugal and in the central Eastern Central Adriatic. Quéro and Vayne (1998) found similar results but also showed an important contribution of *Enteromorpha* sp. in the diet.

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

### 4.4. Food supply of the fish and cephalopods community, methodological benefits and caveats

#### 4.4.1. Do stomach contents mirror diet and fit with the abundance of prey in the environment?

In accordance with the literature (section 4.3) fish and cephalopod species exhibited a wide range of feeding strategies from opportunistic to generalist but with a close relationship between the abundance of prey in the stomach and in the environment. For instance, flatfish consume the most abundant prey resources as a result of generalist and opportunistic feeding strategies (Carter et al., 1991; Reichert, 2003; Schückel et al., 2012). Consequently, the most frequent and abundant prey in the stomach contents should be among the most abundant species in the environment (Amezcua et al., 2003; Schückel et al., 2012; Le Pape et al., 2007; Nicolas et al., 2007; Saulnier et al., 2020; Tableau et al., 2019).

In the benthic fauna of the study area, molluscs were the most abundant group (42.26%) ahead of annelids (38.93%) and crustaceans (15.68%) in 2019 (Sturbois et al., 2021a). SCA revealed that those three main taxa were also well represented in stomach contents, with a variable contribution depending on species. Amphipoda was the main dietary item for the six fish species (as in the bay of Morlaix, Dauvin, 1988), completed by other prey items depending on species. Despite the decrease observed in the abundance of crustaceans between 1987 and

2019 (Sturbois et al., 2021a), *Amphipoda* still reach important densities and remain a major food item. The genus *Ampelisca* sp., well represented in stomachs, is dominant. Its polyvoltine reproduction leads to more than one generation per year and contributes to the high productivity of benthic habitats. In the bay of Morlaix, three *Ampelisca* species provided 91% of the total annual mean abundance, close to 38% of the biomass and 50% of the net production of the total macrofauna (Dauvin, 1984, 1989; Jeong et al., 2009). Such high densities and production rate favour the availability of prey for fishes and contribute to explain that this prey item is highly consumed.

Inversely, annelids were abundant in the community (Sturbois et al., 2021a) and weakly consumed by fish species, with an exception for *S. cantharus* for which it constitutes a secondary prey items. Even if they could reach locally important densities, the infaunal habitat of most annelids species may limit their availability for predators (Tableau et al., 2019). On the other hand, their high digestibility (due to the absence of hard parts) coupled to the nocturnal activity (vs daylight sampling) of most zoophagous polychaetes, have probably contributed to an underestimation of their consumption (Serrano et al., 2003). Molluscs, and particularly bivalvia have been identified as secondary prey items for *C. lyra* and *G. niger*. Despite molluscs dominate the macrofauna in abundance, some bivalve and gasteropod species remain hard to digest, reaching sizes that limits their consumption by small fishes (both small species and juvenile stage), and their availability is probably limited by their infaunal position in the substrate (Tableau et al., 2019). Only juvenile molluscs were found in stomachs, their digestibility being favoured by smaller size and softer shells.

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

### 4.4.2. Do stomach contents and stable isotope analyses tell same niches complexity and overlap stories?

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

The underlying processes influencing niche$_{SIA}$ are more diverse than those influencing niche$_{SCA}$, as SIA metrics are influenced by far more than just diet composition (Petta et al., 2020). Caution is therefore recommended when interpreting niche$_{SIA}$ vs niche$_{SCA}$ metrics in a strictly dietary niche context, especially considering the paucity of empirical information supporting the comparability of metrics derived from either methods. SIA allows for identifying the sources that support a food web and the major trophic pathways. However, in without SCA-based data, the complexity of the relation between preys and predators limits the characterisation of predator's diets and thus, the food chains to which they belong. When predators are characterised by similar SI compositions, SI analyses fail to infer on whether this signature is a consequence of a specialised diet or reflect a mean composition resulting from a generalist diet. Similarly, two predator species could be supported by a same pool of sources but not being in competition for a same pool of preys: e.g. for *M. surmuletus* and *S. officinalis* in our study. Note that a low number of stomach samples may have influenced the results for these two species as low samples number produces lower diet diversity and consequently more heterogeneous prey choice between co-occurring species.

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

### 4.5. Food supply of the fish and cephalopods community in the bay of Saint Brieuc

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

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

Schoener indices of trophic overlap showed a consistency of diet with important overlaps among pairs of species, while values of Sto based on weight, that is a better quantification of the food potentially assimilated by predators, pointed more contrasted results. The theory of limiting similarity (Abrams, 1983; Macarthur and Levins, 1967) suggests the existence of a maximum level of niche overlap between two given species that allow their coexistence. Corollary, the concept of competitive exclusion states that two species competing for exactly the same resources cannot stably coexist (Gause, 2003; Hardin, 1960; Wellard Kelly et al., 2021). However, the low abundance of fish and the large food availability may buffer such processes in the study area.

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

### 4.6. Understanding and conservation of such complex ecosystems

As most individuals were observed at juvenile stages [young of the year (GO) and G1] and using the site for feeding, the nursery function (Beck et al., 2001) can be partially retained for a pool of main species which are common at local and regional scales. However, the fish and cephalopod community was not dominated by species of commercial interest and their low abundance, especially in the impoverished facies and the northwestern part of the study area, suggests that the nursery function was probably not optimal. The absence of some species present in other bays or in the study area suggests that they were present in low abundance and occurrence during our study, with potential seasonal patterns. They may also use limited shallow habitats, within a restricted home range (Le Pape and Cognez, 2016), which have not been integrated in our subtidal sampling design. In such complex ecosystems with different habitats under megatidal conditions, an integrated sampling strategy with complementary methods may help for a better integration of habitats, from estuary and salt marshes to sandy beaches and shallow areas (Le Mao, 1985), with a seasonal dimension (Le Luherne et al., 2016; Le Mao, 1985; Sturbois et al., 2016).

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

### CRediT authorship contribution statement

**A. Sturbois:** Conceptualization, Methodology, Validation, Formal analysis, Data curation, Writing – original draft, Visualization, Project administration, Funding acquisition, Investigation. **A. Cozic:** Formal analysis, Investigation, Writing – review & editing. **G. Schaal:** Conceptualization, Investigation, Methodology, Validation, Writing – review & editing, Supervision. **N. Desroy:** Conceptualization, Methodology, Validation, Writing – review & editing, Investigation, Supervision. **P. Riera:** Conceptualization, Methodology, Validation, Writing – review & editing, Investigation, Supervision. **O. Le Pape:** Conceptualization, Methodology, Validation, Writing – review & editing, Supervision. **P. Le Mao:** Investigation, Writing – review & editing. **A. Ponsero:** Investigation, Writing – review & editing. **A. Carpentier:** Conceptualization, Methodology, Validation, Writing – review & editing, Supervision.

### Declaration of competing interest

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.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2022.105770.

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