



Spatio-temporal patterns in stable isotope composition of a benthic intertidal food web reveal limited influence from salt marsh vegetation and green tide

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ABSTRACT

Assessing fluxes of matter and energy in food webs within and across benthic habitats is important to understand the ecological functioning in bays and estuaries, where the productivity is favoured by a wide diversity of primary producers. The temporal variability (March vs September 2019) in the carbon and nitrogen stable isotope composition of primary food sources and benthic invertebrates consumers was investigated in a large intertidal area (Western English-Channel, France). The study area is influenced by megatidal conditions and characterised by salt marshes in the sheltered part, and seasonal *Ulva* spp. blooms. The spatio-temporal variability in the structure of the benthic food web was analysed at the scales of both the whole bay and the different assemblages, which constitute the mosaic of habitats. Inferences on potential sources fuelling the food web were supported by spatio-temporal patterns based on covariations and stable isotope trajectory analysis. Results highlighted that phytoplankton, microphytobenthos and SOM were, most likely, the main food sources. The trophic connectivity between salt marsh and benthic habitats within the bay was limited to some macrofauna species inhabiting muddy creeks within the salt marsh. Unexpectedly, the influence of *Ulva* spp. blooms appeared also limited. Spatial patterns illustrates the constancy of the spatial variability in the benthic pelagic coupling, with a higher influence of microphytobenthos in the upper shore compared to low shore assemblages. This first attempt to characterize intertidal benthic food web constitutes a relevant baseline for the conservation of the bay of Saint-Brieuc where a national Nature Reserve has been created in 1998 for the conservation of overwintering birds. The spatial and temporal patterns of the benthic food web observed in this study (1) confirm the importance to consider food web variability at spatial and temporal scales from sampling designs to data analysis, and (2) demonstrate the ability of the stable isotope trajectory analysis framework to highlight food web dynamics.

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). The production of bays and estuaries is provided by a wide diversity of primary producers, including phytoplankton, seaweeds, seagrass, mangroves, salt marsh plants, macroalgae, and benthic diatoms (Bouillon et al., 2011). All these primary producers

contribute to an important pool of detrital organic matter, which plays a major role in the biogeochemistry and ecology of bays and estuaries ecosystems. Due to this diversity, understanding the fate of primary production within coastal ecosystems, and especially within food webs, is challenging (Mann, 1982). Furthermore, the contribution of these different producers to local food webs has been reported to vary within and among coastal systems (Chanton and Lewis, 2002; Deegan and Garritt, 1997; Domingos and Lana, 2017), leading to a lack of a

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commonly accepted paradigm for food web functioning across variable spatial and temporal scales.

Because coastal food webs depend on primary food sources which can be either sessile or mobile, assessing vertical (i.e. benthic-pelagic coupling) and horizontal (i.e. organic matter fluxes across habitats/ecosystems) trophic connectivity between adjacent habitat is crucial (Kang et al., 2015; Schaal et al., 2008). Trophic connectivity varies among systems from near total isolation to strong mixing. Water motion facilitates the movement of carbon as dissolved or particulate matter in aquatic ecosystems (Guimond and Tamborski, 2021; Polis et al., 1997).

Hydrodynamics influences coastal productivity through a variety of mechanisms (Largier, 1993). In tidal environments, the periodic movement of the tide is responsible for organic matter redistribution, enhancing trophic connectivity among different habitats and assemblages (Polis et al., 1997). Redistribution range depends on tidal amplitude across meso, macro and megatidal systems (Domingos and Lana, 2017; Ziegler et al., 2019). Resulting hydrodynamics can lead to the accumulation and/or dispersal of water column constituents, including sediment, phytoplankton, and particulate detritus (Young et al., 2021), and potentially influence production pathways and food web structure. Higher water motion increases material processing (e.g. microphytobenthos resuspension) between benthic and pelagic compartments (Ubertini et al., 2012) which can be amplified by biological factors, such as bioturbation (Rakotomalala et al., 2015).

Bay and estuaries are known to be influenced by seasonal and inter-annual variability in marine and freshwater inputs. This variability affects the abundance and distribution of resources and consumers and may drive food web dynamics (Bouillon et al., 2011). The consideration of trophic dynamics is consequently crucial to take into account the spatio-temporal variability of food sources in terms of composition and availability.

In shallow bays under the influence of mega-tidal conditions, bathymetry influences submersion/emersion time of intertidal habitats, affecting the time available for feeding. Tidal conditions coupled with sediment characteristics also have a pronounced effect on benthic macrofauna species distribution limiting for example the distribution of species requiring stable conditions to sheltered parts (Blanchet et al., 2014; França et al., 2009). Such a broad spatial-pattern in the distribution of intertidal benthic species can be strongly consistent over time, leading to the persistence of contrasting benthic assemblages along inshore/offshore and sheltered/exposed gradients in intertidal soft bottom-habitats (Sturbois et al., 2021a).

Organic matter inputs (e.g. detrital plants or algae) from vegetated systems may diversify food webs structure and energy pathways (Hyndes and Lavery, 2005; Nordström et al., 2015; Quillien et al., 2016; Schaal et al., 2008). Such additional food resources may originate from close productive habitats such as salt marshes (Nordström et al., 2014). It may also result from seasonal eutrophication with the proliferation of green algae, which may have important consequences on the structure of benthic food webs (Quillien et al., 2016) and fish assemblages (Jones et al., 2020).

For decades, stable isotope analysis has been widely used in trophic ecology studies to understand feeding behaviour, trophic relationship and organic matter flow within and across marine food webs (Fry, 2008; Peterson, B.J., 1999). Carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) are the most commonly used stable isotope in trophic studies. The carbon isotope ratio, expressed as $\delta^{13}\text{C}$, is particularly relevant to determine the origin of organic matter supporting consumers (e.g. benthic vs pelagic or freshwater vs marine), while the nitrogen isotope ratio ($\delta^{15}\text{N}$) allow the estimation of trophic positions (Fry, 2008). More recently, the development of numerous isotopic metrics has allowed to better assess stable isotope measurements at the community scale, providing relevant information about ecosystems structure and functioning (Chucherousset and Villéger, 2015; Layman et al., 2007, 2012; Rigolet et al., 2015).

In this study, we focused on the structure and the dominant sources that support the food web in an intertidal sandflat influenced by mega-

tidal conditions and characterised by a variety of primary producers. We specifically explored $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from sources to benthic invertebrates consumers at the scale of the entire sandflat and for benthic assemblages which constitute the mosaic of habitat within the bay. Classical analyses ($\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ raw values, graphical inference, indices of structure) were coupled with distance- and direction-based metrics of the new Stable Isotope Trajectory Analysis (SITA) framework (Sturbois et al., 2021b). This new method provides an assessment of stable isotope data at different levels of biological organization, from individuals to ecosystems to derive structural and functional trajectories. We hypothesized that: (1) due to the aforementioned characteristics of the bay, spatial gradients and temporal variability would drive the sources supporting the food web, (2) the variability would induces spatial and temporal difference in the food web structure among habitats. Implications in sampling strategy and conservation processes were finally discussed.

2. Material and methods

2.1. Study area and sampling design

Fieldwork was conducted in the bay of Saint-Brieuc, France (Fig. 1), a 2900 ha tidal flat divided in two coves (Yffiniac and Morieux coves). The area is mainly dominated by fine to medium sands, while the most sheltered parts are characterised by muddy sands. The bay is under the influence of a semi-diurnal megatidal regime. Tidal range varies between 4 m at neap tides and nearly 13 m during spring tides, generating strong tide currents rising between 0.3 and 0.5 m/s in this part of the bay.

The upper shore is dominated by salt marshes (125 ha) characterised by a current dynamic of extension and a good conservation status (Sturbois and Bioret, 2019).

The bay suffers from eutrophication, resulting in strong ephemeral macroalgae proliferation and cyclic green tides episodes (Charlier et al., 2007; Gravier, 2012) (Supplementary material, Appendix A). The national Nature Reserve of Saint-Brieuc was created in 1998 for the protection of shore birds. Because overwintering and migratory waders forage on macrofauna (Ponsero et al., 2016; Ponsero and Le Mao, 2011; Sturbois et al., 2015), their protection required the conservation of marine habitats and benthic resources.

The bathymetry and hydrodynamics strongly influence the structure of benthic assemblages on the study area: from muddy sands assemblage, on the upper shore, to medium sands. Following the main benthic assemblages characterized by Sturbois et al. (2021a), sampling of macrofauna was carried out on four soft-bottom habitats in the bay of Saint-Brieuc from the top to the low flat: salt marsh muddy creeks (2 stations), and muddy (5 stations), fine (9 stations) and medium sands (6 stations, Fig. 1). The bathymetric gradient among habitats leads to differences in mean daily submersion time: salt marsh (2:07 h per 24 h), muddy sands (4:59 ± 3:09), fine sands (12:21 ± 6:05) and medium sands (20:35 ± 3:31).

2.2. Sample collection and laboratory processes

Sources – Samples were collected in early March and September 2019. Sedimentary organic matter (SOM) was collected at each station by scraping the upper 1 cm of the sediment during the low tide. For each station, one subsample was acidified (10% HCl) and re-dried overnight at 60 °C, whereas the other subsample remained untreated. Values of $\delta^{13}\text{C}$ from acidified subsamples were combined with those of $\delta^{15}\text{N}$ from untreated subsamples to compute the SOM isotope values undisturbed by calcium carbonate residues ($\delta^{13}\text{C}$) and by acidification ($\delta^{15}\text{N}$) (Androuin et al., 2019). Benthic diatoms (Microphytobenthos, MPB), abundant in the muddy/sandy sediments of the area at the end of spring/early summer, were collected in June 2019 and July 2020 by scraping the surface of the sediment and extracted according to a

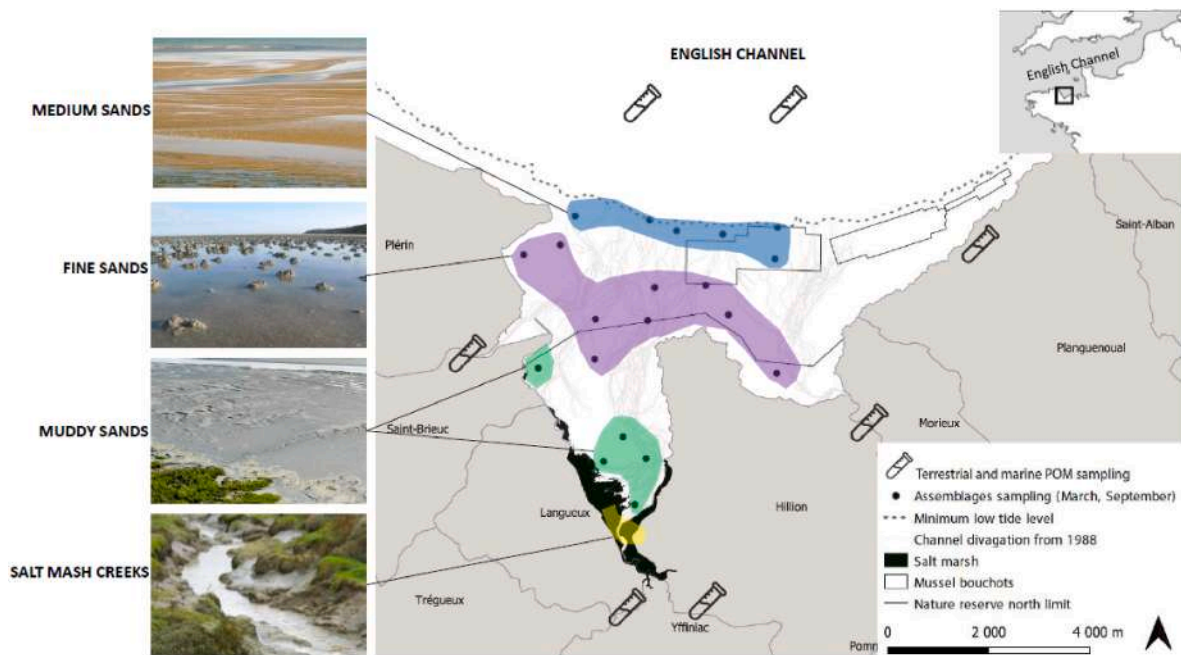


Fig. 1. Location of the study area and sampling stations. Dots correspond to the stations sampled in the different habitats. Colors of polygons correspond to the four assemblages (i.e. habitats) sampled: salt marsh creeks (yellow), muddy sands (green), fine sands (purple) and medium sands (blue).

method of Couch (1989), modified by Riera et al. (1999). The diatoms were collected on previously combusted glass fiber filters, briefly washed with 10% HCl and rinsed with Milli-Q water and kept frozen (-20°C) until analysis. Stable isotope compositions of 2019 and 2020 were averaged.

Marine and freshwater samples collected for suspended particulate organic matter (POM) were pre-filtered through a $90\text{-}\mu\text{m}$ -mesh to remove large detritus and then filtered on precombusted (500°C , 5 h) Whatman GF/F filters. POM collected from river basins (POM_TER, 5 stations), and offshore (POM_SEA, 2 stations) were differentiated in further analysis.

Leaves and twigs of the most representative vascular plants colonizing salt marshes (Sturbois and Bioret, 2019) were sampled by hand at low tide, as well as fresh stranded algae (*Ulva* spp.) whenever present on the flat (fine and medium sand habitats). Samples were rinsed at the laboratory to be cleaned from epibionts, dried at 60°C for 48 h, and ground into a fine powder using a marble mortar.

Consumers - Benthic macrofauna was sampled in March and September 2019 from the four assemblages using a $1/32\text{ m}^2$ hand corer (diameter: 20 cm), at a depth of 25 cm (Supplementary material, Appendix B). Sampling was coupled with spade prospection for over-dispersed megafauna, or for species typically difficult to sample using hand corers (e.g. the lugworm *Arenicola marina*). The content of the cores was gently sieved through a 1-mm square mesh sieve. Macrofauna was then sorted on the field and preserved in plastic vials. The beach-hopper *Orchestia gammarellus* was captured by hand in the vegetation bordering salt marsh creeks. In the laboratory, animals were identified to the lowest possible taxonomic level, rinsed and stored at -20°C until further treatment. Samples consisted of individual muscle tissues of large species (bivalves, annelids, echinoderms) or, whenever necessary for small species, pooled individuals (for the small gastropod *Peringia ulvae*) and whole individual (for amphipods species). Species containing calcium carbonates (e.g. the burrowing brittle-star *Acrocnida spatulispina* or the slippershell snail *Crepidula fornicata*) were split into two acidified and non-acidified subsamples. Values of $\delta^{13}\text{C}$ from acidified subsamples and $\delta^{15}\text{N}$ and from untreated subsamples were combined. All samples were rinsed, dried at 60°C for 48 h, and ground into fine powder using a marble mortar.

At least three replicates were analysed per species when possible, but for several taxa less replicates were available (Supplementary material, Appendix B). As much as possible, the different replicates were chosen among available samples to cover the widest part of each assemblage.

2.3. Stable isotope analysis

Ground samples were packed into $5 \times 8\text{ mm}$ 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 platform of the Pole Spectrométrie Océan at the University of Bretagne Occidentale (Brest, France). Stable isotope ratios were reported in the standard δ notation as units of parts per thousands (‰) relative to the international reference standard: $\delta X = [(R_{\text{Sample}}/R_{\text{Standard}})-1] \times 10^3$ where X is ^{13}C and ^{15}N and R is the corresponding ratio of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$. Reference standard used were Vienna-Pee Dee Belemnite for ^{13}C and atmospheric N_2 for ^{15}N (precision: 0.1).

2.4. Data analysis

Data sets were investigated to analyse spatial patterns and temporal variability of the intertidal benthic food web between March and September. Analyses were conducted in terms of composition and structure at the bay scale (i.e. entire community), and at the finer scale of the different benthic assemblages. Each species has been assigned to a trophic group: carnivores, deposit-feeders, deposit-suspension-feeders, suspension-feeders, grazers, omnivores. This assignation was performed with respect to primary literature on specific taxa, expert knowledge and three publicly available databases: polytraits (<http://polytraits.lifewatchgreece.eu>), the World Register of Marine Species (WoRMS Editorial Board, 2020), and Biological Trait Information Catalogue (BIOTIC, <http://www.marlin.ac.uk/biotic/>). Trajectory analysis was performed to quantify and characterize the magnitude (distance) and the nature (direction) of temporal shift in the $\delta^{13}\text{C}/\delta^{15}\text{N}$ -space for trophic groups. All analyses were performed within the R environment.

Spatial differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were tested with a one-way ANOVA against the factor 'Assemblages'. The food web structure was

analysed through community-wide metrics (Layman et al., 2007):

- $\delta^{13}\text{C}$ range (CR): Distance between the highest and the lowest $\delta^{13}\text{C}$ values of the community (i.e., maximum $\delta^{13}\text{C}$ - minimum $\delta^{13}\text{C}$). CR is one representation of basal source diversity within a food web;
- $\delta^{15}\text{N}$ Range (NR): Distance between highest and the lowest $\delta^{15}\text{N}$ values of the community (i.e., maximum $\delta^{15}\text{N}$ - minimum $\delta^{15}\text{N}$). NR is one representation of the total length (i.e. total number of trophic levels) within a food web;
- Total Area (TA): Convex hull area encompassed by all species in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ 2D δ space. This represents a measure of the total amount of niche space occupied, and thus a proxy for the total extent of trophic diversity within a food web;
- Mean distance to centroid (CD): Average Euclidean distance of each species to the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ centroid, where the centroid is the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value for all species in the food web. This metric provides a measure of the average degree of trophic diversity within a food web;
- Mean nearest neighbor distance (NND): Mean of the Euclidean distances to each species' nearest neighbor in bi-plot space, and thus a measure of the overall density of species packing.

Three other indices from Cucherousset and Villéger (2015) were also calculated to analyse the similarity between March and September and among assemblages:

- Isotopic similarity (ISim): Overlap in the total isotopic niches as the ratio between the isotopic niche of the intersection and of the union off the two groups considered. 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 isotopic richness;
- Isotopic divergence (IDiv): Distribution of points (close to the centroid or edges) within the convexhull. IDiv is minimal (i.e. tends to 0) when most of the points are close to the centre of gravity of the convex hull, and organisms 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 organisms with the most extreme stable isotope value(s) dominate the foodweb;
- Isotopic Evenness (IEve): Regularity in the distribution of organisms along the shortest tree that links all the points. IEve tends to 0 when most of organisms 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 organisms are evenly distributed in the stable isotope space.

The new Stable isotope trajectory analysis (SITA) framework was used to measure shifts in stable isotope values for sources and trophic groups (Sturbois et al., 2021b). The quantitative analysis of stable isotope dynamics in response to ecological and environmental changes has been explored in the past through the comparative analysis of temporal trajectories in a two-dimensional (usually $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) isotopic space (δ space). For instance, Schmidt et al. (2007) and Wantzen et al. (2002) quantified the direction and magnitude of temporal changes in food web structure based on the geometric properties of trajectories in the δ space. Schmidt et al. (2007) used specifically circular statistics and charts to represent and test direction shifts in the δ space. Turner et al. (2010) characterized attributes of path trajectories (size, direction and shape) over data sets containing more than two temporal samples to provide a quantitative description and tested changes in stable isotope compositions change in response to spatial and temporal gradients. Building on these previous works and on the recent Community trajectory analysis framework (De Cáceres et al., 2019; Sturbois et al., 2021c), the SITA framework goes further in the explicit quantitative description, analysis and representation of the magnitude and the nature of changes in stable isotope composition.

Length- and direction-based SITA metrics were calculated. The net change (Euclidian distance between March and September for a given group) and the angle α (0–360° direction in the δ -space considering the Y axis, $\delta^{15}\text{N}$, as the North, i.e. 0°) were calculated to assess the magnitude and the nature of change in the $\delta^{13}\text{C}/\delta^{15}\text{N}$ -space, respectively. Net changes and angle α were represented through trajectory diagrams and trajectory roses (Sturbois et al., 2021b) and temporal differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean values for sources and trophic groups were represented through bar plots and tested with permutation Student's t-tests (package 'RVAAMemoire', 'perm.t.test' function, 999 permutations).

3. Results

3.1. Primary food sources

3.1.1. Bay scale

Contrasts were observed in primary food sources stable isotope values (Fig. 2, Table 1). Values of $\delta^{13}\text{C}$ were lower for terrestrial POM ($-30.13 \pm 0.98\text{‰}$). Salt marsh plants exhibited among the lowest $\delta^{13}\text{C}$ values, excepted the common cord-grass *Spartina anglica* characterised by the highest $\delta^{13}\text{C}$ ($-12.89 \pm 0.20\text{‰}$) typical of C4 plants (Currin et al., 1995). Higher $\delta^{15}\text{N}$ values were observed for the sea purslane *Halimione portulacoides* in March ($12.98 \pm 1.74\text{‰}$), and September ($11.94 \pm 0.44\text{‰}$).

3.1.2. Temporal variability

The SOM samples of all assemblages were characterized by the lowest variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fig. 3, Table 1). The stable isotope composition of *Ulva* spp. was characterized by an increase in both isotopes in September (angle α : 50.57° , trajectory length: 6.49), although this variation was not significant for $\delta^{13}\text{C}$ ($p = 0.094$, Supplementary material, Appendix C). POMs followed an inverse pattern (243.49° , 7.41). Significant $\delta^{13}\text{C}$ shifts between March and September were observed, with a decrease for POM_SEA ($p = 0.004$), and an increase for terrestrial POM ($p = 0.032$).

3.2. Consumers

3.2.1. Bay scale

Benthic consumers displayed a wide range of stable isotope compositions in both months (Table 2). In March, mean $\delta^{13}\text{C}$ values ranged from $-21.90 \pm 0.30\text{‰}$ in the grazer *O. gammarellus* to $-12.58 \pm 0.94\text{‰}$ in the deposit-feeder *P. ulvae* (Fig. 2, A.). Mean $\delta^{15}\text{N}$ values ranged from $8.81 \pm 0.50\text{‰}$ in the deposit-feeder *Bathyporeia sarsi* to $13.46 \pm 0.73\text{‰}$ in the carnivore *Sigalion mathildae*. In September, $\delta^{13}\text{C}$ mean values ranged from $-21.39 \pm 0.93\text{‰}$ still for *O. gammarellus*, to $-11.88 \pm 0.94\text{‰}$ in the deposit-feeder *Bathyporeia pilosa* (Fig. 2, B.). $\delta^{15}\text{N}$ mean values ranged from $9.08 \pm 0.50\text{‰}$ in the deposit-feeder *Bathyporeia pilosa*, $14.37 \pm 0.29\text{‰}$ in the omnivore *Hediste diversicolor*. Omnivores and carnivores exhibited among the highest $\delta^{15}\text{N}$ values, while deposit-feeders and suspension-feeders among the lowest with an important variability (Fig. 2).

Shifts in the stable isotope compositions of sources helped with the identification of potential food sources for different consumers. POM_SEA was characterised by an important depletion in $\delta^{13}\text{C}$ values between March and September, as observed in the suspension-feeders (Fig. 2). SOM $\delta^{13}\text{C}$ values were quite similar among assemblages in March, while a $\delta^{13}\text{C}$ -depletion was observed in the SOM measured from muddy salt marsh creeks. SOM collected in fine and medium sands also were likely to support deposit-feeders in these assemblages (Fig. 2).

Total areas were similar in March (43.46‰^2) and September (46.64‰^2) (Table 3, Fig. 4). The food web centroid was characterized by a $\delta^{13}\text{C}$ decrease (-0.95‰) but the food web still strongly overlapped in March and September (Isotopic Similarity = 0.728). CD remained similar over time (1.99 vs 2.02) revealing a stable trophic diversity. In September, species were more evenly distributed, decreasing the trophic

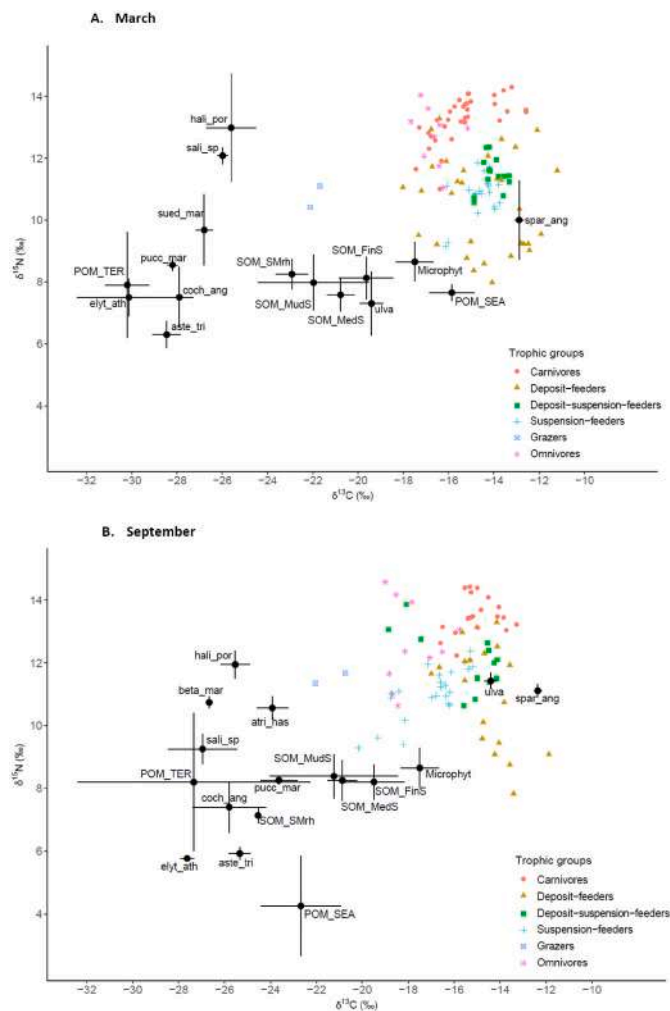


Fig. 2. Stable isotope composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of consumers and potential dietary sources of organic matter in March (A) and September (B) from intertidal soft-bottom sediments of the bay of Saint-Brieuc. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are plotted for each individual consumer. Colors and shapes represent trophic groups. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of potential dietary sources are represented with black dots with error bars (size proportional to sd values). Marine and terrestrial particulate organic matter (POM_SEA, POM_TER). Sedimentary organic matter in the different habitat from salt marsh to muddy, fine and medium sands (SOM_SMrh, SOM_MudS, SOM_FinS, SOM_MedS). Microphytobenthos (Microphyt). C3 plants: *Halimione protulacoides* (hali_por), *Beta maritima* (beta_mar), *Atriplex hastata* (atri_has), *Salicornia* sp. (salic), *Puccinellia maritima* (pucc_mar), *Cochlearia anglica* (coch_ang), *Elytrigia atherica* (Elyt_ath), *Aster Tripolium* (aste_tri). C4 plant: *Spartina anglica* (spar_ang). Algae: *Ulva* sp. (ulva).

redundancy as shown by the increase in NND (0.28 vs 0.36), SDNND (0.24 vs 0.31), and IEve (0.61 vs 0.80).

3.2.2. Assemblage scale

3.2.2.1. Stable isotope composition. Species sampled in the salt marsh were characterised by the lowest $\delta^{13}\text{C}$ values at both months and were excluded to fulfil the normality assumption and perform ANOVA across the three sands assemblages. Excluding salt marshes, $\delta^{13}\text{C}$ values showed significant spatio-temporal variability characterised by a $\delta^{13}\text{C}$ depletion gradient from muddy to medium sands (F: 54.38, p-value < 0.0001) which was consistent over time (Supplementary material, Appendix D), and followed the previously mentioned emersion time gradient. CR increased between March and September (2.74 vs 5.20) in medium sands and remained stable in other assemblages (Table 3). $\delta^{15}\text{N}$

were significantly different between assemblages (F: 5.16, p-value < 0.01).

Some spatial patterns in the stable isotope composition of trophic groups were also identified at the scale of trophic groups and correlated with emersion time. Deposit-suspension-feeder $\delta^{13}\text{C}$ values were negatively correlated with emersion time in March (-0.674 , $p < 0.01$, Pearson), while suspension-feeders (0.720 , $p < 0.001$), deposit-feeders (0.635 , $p < 0.01$), and carnivores (0.588 , $p < 0.01$) showed a positive correlation in September.

3.2.2.2. Structure. TA was higher in March for muddy (21.92%) and fine sands (23.16%) compared to medium sands (9.12%) and salt marsh (9.59%) (Table 3, Fig. 5). In September, the TA of the different sand assemblages were equivalent, following a decrease in muddy and fine sands and an increase in medium sands.

Little convex hull overlap was observed between the salt marsh and other assemblages. An overall decreasing $\delta^{13}\text{C}$ gradient from muddy ($\delta^{13}\text{C}$ centroids in March: -13.93% , September: -14.46%), to fine (-15.01% , -15.08%) and medium (-16.41% , -17.34%) sands assemblages led to a partial convex hull overlap. The lowest isotopic similarity among sand assemblages were observed between muddy and medium sands in both months (March: 0.139, September: 0.149). In March, fine sands were more similar to muddy sands (0.607) than medium sands (0.351). In September, overlap became more balanced (0.401 vs 0.441, respectively), revealing more similarity in isotopic niche between assemblages. More specifically, dissimilarity at the lower levels of the food web increased in September between muddy and medium sands indicating some differences in stable isotopes values mainly implying suspension-feeders (Fig. 5B).

In sand assemblages, CD ranged from 1.40 to 1.76 in March, and from 1.50 to 1.91 in September. Species sampled in muddy and medium sands were more evenly distributed in the δ -space in September as shown by the increase in NND, SDNND, IDiv and IEve values (Table 3).

3.2.2.3. Trajectories of trophic groups. Significant decreases in $\delta^{13}\text{C}$ value between March and September were observed in muddy sands in suspension-feeders ($p = 0.012$, Supplementary material, Appendix C) and deposit-suspension-feeders ($p = 0.020$), and for suspension-feeders from fine ($p = 0.002$) and medium sands ($p = 0.002$) (Figs. 3 and 6, A & B). A moderate increase in $\delta^{13}\text{C}$ value was observed in carnivores from medium sands ($p = 0.022$). Contrasts among assemblages were observed in trophic groups stable isotope compositions between March and September. Medium sands suspension-feeders exhibited the longest trajectory (Euclidean distance = 3.12), while muddy sand deposit-feeders were characterized by the lower shift (0.16) (Table 4, Fig. 6A and B). Trophic groups stable isotope compositions of consumers remained contrasted between assemblages but the temporal shifts of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, were similar for some trophic groups among assemblages. Suspension-feeders exhibited very similar directions ($283.90 \pm 3.70^\circ$) and among the highest changes (2.27 ± 0.68 , Euclidean distance), characterized by a ^{13}C -depletion and a moderate increase in $\delta^{15}\text{N}$. Similar temporal patterns across assemblages were also observed in deposit/suspension-feeders from muddy (0.95 , 297.24°) and fine (0.81 , 294.95°) sands, and in omnivores and carnivores from fine and medium sands respectively. Inversely, deposit-feeders exhibited contrasting trajectories in muddy (0.16 , 221.10°), fine (1.19 , 359.20°) and medium sands (0.63 , 182.00°) mainly influenced by shifts in $\delta^{15}\text{N}$. In salt marsh creeks, omnivores and grazers both exhibited singular trajectories.

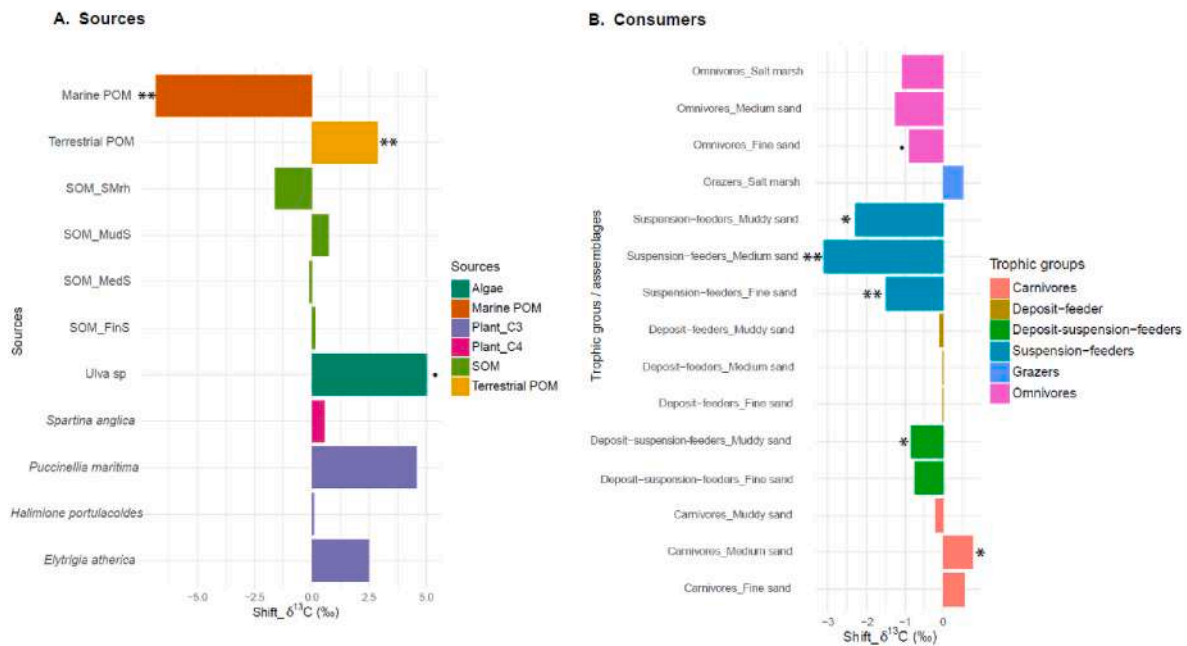


Fig. 3. Temporal variation of $\delta^{13}\text{C}$ between March and September. Sources (A): main primary food sources are represented by colors: marine POM, terrestrial POM, SOM for the four assemblages (Salt marsh creeks (SOM_SMrh), and muddy (SOM_MudS), fine (SOM_FinS), and medium (SOM_MedS) sands), *Ulva* sp, and the four main C3 (*Puccinellia maritima*, *Halimione portulacoides*, *Elytrigia atherica*) and C4 salt marsh plants (*Spartina anglica*). Consumers (B): consumers are represented by colors and temporal shift in $\delta^{13}\text{C}$ values is provided for each habitat. Mean significant differences tested with Permutation Student's t-tests are summarized as *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$). Mean differences near the significant level are also represented (., $P < 0.1$).

Table 1

Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean \pm sd) of the various food sources collected in March and September 2019. n: number of samples. Marine and terrestrial particulate organic matter (POM_SEA, POM_TER). Sedimentary organic matter in the different assemblages from salt marsh to muddy, fine and medium sands (SOM_SMrh, SOM_MudS, SOM_FinS, SOM_MedS).

| Sources | Types | March | | | September | | |
|--------------------------------|------------------------------------|-------|-----------------------|-----------------------|-----------|-----------------------|-----------------------|
| | | n | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | n | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ |
| <i>Atriplex hastata</i> | Plant C3 | | | | 3 | -23.92 \pm 0.68 | 10.56 \pm 0.36 |
| <i>Beta maritima</i> | Plant C3 | | | | 3 | -26.66 \pm 0.11 | 10.74 \pm 0.19 |
| <i>Elytrigia atherica</i> | Plant C3 | 3 | -30.13 \pm 2.28 | 7.50 \pm 0.62 | 3 | -27.63 \pm 0.29 | 5.77 \pm 0.08 |
| <i>Cochlaearia anglica</i> | Plant C3 | 3 | -27.90 \pm 0.60 | 7.51 \pm 0.97 | 3 | -25.80 \pm 1.59 | 7.40 \pm 0.86 |
| <i>Halimione portulacoides</i> | Plant C3 | 3 | -25.61 \pm 1.08 | 12.98 \pm 1.74 | 3 | -25.53 \pm 0.63 | 11.94 \pm 0.44 |
| <i>Puccinellia maritima</i> | Plant C3 | 3 | -28.20 \pm 0.23 | 8.55 \pm 0.19 | 3 | -23.63 \pm 0.79 | 8.26 \pm 0.14 |
| <i>Salicornia</i> sp. | Plant C3 | 3 | -25.98 \pm 0.23 | 12.08 \pm 0.27 | 3 | -26.96 \pm 1.50 | 9.25 \pm 0.47 |
| <i>Sueda maritima</i> | Plant C3 | 3 | -26.80 \pm 0.37 | 9.67 \pm 1.15 | | | |
| <i>Spartina anglica</i> | Plant C4 | 3 | -12.89 \pm 0.20 | 10.00 \pm 1.28 | 3 | -12.36 \pm 0.16 | 11.11 \pm 0.21 |
| <i>Ulva</i> spp. | Algae | 3 | -19.41 \pm 0.52 | 7.30 \pm 1.03 | 3 | -14.40 \pm 0.27 | 11.42 \pm 0.26 |
| POM_TER | Terrestrial POM | 15 | -30.20 \pm 0.98 | 7.90 \pm 1.71 | 15 | -27.34 \pm 5.06 | 8.20 \pm 2.20 |
| POM_SEA | Marine POM | 6 | -15.86 \pm 0.99 | 7.65 \pm 0.27 | 5 | -22.68 \pm 1.73 | 4.26 \pm 1.59 |
| SOM_INTER_FinS | SOM | 10 | -19.64 \pm 1.19 | 8.13 \pm 0.68 | 10 | -19.49 \pm 1.31 | 8.20 \pm 0.56 |
| SOM_INTER_MedS | SOM | 4 | -20.78 \pm 0.61 | 7.58 \pm 0.54 | 6 | -20.87 \pm 0.64 | 8.25 \pm 0.64 |
| SOM_INTER_MudS | SOM | 5 | -21.97 \pm 2.44 | 7.97 \pm 0.90 | 7 | -21.24 \pm 2.79 | 8.39 \pm 0.70 |
| SOM_SMrh | SOM | 2 | -22.93 \pm 0.69 | 8.25 \pm 0.49 | 3 | -24.54 \pm 0.12 | 7.14 \pm 0.25 |
| Microphythobenthos | MPB (mean June 2019 and July 2020) | 5 | -17.50 \pm 0.83 | 8.65 \pm 0.63 | 5 | -17.50 \pm 0.83 | 8.65 \pm 0.63 |

4. Discussion

4.1. Spatio-temporal patterns as a potential alternative to track trophic links

Consumers and their food sources stable isotope compositions are commonly used to determine the composition diet. The use of isotopic mixing models is a way to convert isotopic data into estimates of food source contributions from the various components of a consumer's diet (Phillips et al., 2014). The use of source pools characterized by distinct isotope values allows for the full exploitation of the mixing model analysis. Inversely, a multiplicity of sources or strong similarity in their stable isotope composition may decrease the relevance of mixing models

in answering questions about trophic relationships (Fry, 2013; Layman et al., 2012). When mixing models are not correctly applied or when the data sets do not allow their proper application (Fry, 2013; Phillips et al., 2014), conclusions may lead to an incomplete picture. It may mislead the description of functioning and dynamics with potential overstating conservation progress or misdirecting conservation actions.

The source pools described in this study were highly diversified and characterised by strong overlap and high dynamics, potentially limiting the relevance of mixing models and claiming for an alternative approach. The present study therefore focused on stable isotope trajectories of sources and consumers to infer trophic relationships. Spatial and temporal covariation of stable isotope composition between sources and consumers has previously proven to be very useful in identifying the

Table 2Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean \pm sd) of consumers in March and September. n: number of samples.

| Species | Trophic groups | March | | | September | | |
|-------------------------------|----------------------------|-------|-----------------------|-----------------------|-----------|-----------------------|-----------------------|
| | | n | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | n | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ |
| <i>Euspira catena</i> | Carnivores | 2 | -16.50 \pm 0.15 | 11.79 \pm 1.11 | | | |
| <i>Nephtys hombergii</i> | Carnivores | 17 | -14.68 \pm 1.40 | 13.39 \pm 0.68 | 10 | -14.71 \pm 0.92 | 13.19 \pm 0.65 |
| <i>Sigalion mathildae</i> | Carnivores | 9 | -15.56 \pm 0.76 | 13.46 \pm 0.73 | 9 | -15.09 \pm 0.50 | 13.81 \pm 0.53 |
| <i>Tritia reticulata</i> | Carnivores | 6 | -16.40 \pm 0.65 | 13.08 \pm 0.17 | 2 | -16.56 \pm 0.07 | 12.88 \pm 0.36 |
| <i>Arenicola marina</i> | Deposit-feeders | 4 | -13.91 \pm 1.38 | 11.88 \pm 0.78 | 4 | -14.50 \pm 0.44 | 12.81 \pm 0.48 |
| <i>Bathyporeia sarsi</i> | Deposit-feeders | 7 | -13.41 \pm 1.03 | 8.81 \pm 0.50 | | | |
| <i>Bathyporeia pilosa</i> | Deposit-feeders | | | | 1 | -11.88 | 9.09 |
| <i>Corophium arenarium</i> | Deposit-feeders | 5 | -15.39 \pm 1.70 | 9.43 \pm 0.59 | 3 | -13.60 \pm 0.21 | 9.11 \pm 1.49 |
| <i>Maldanidae</i> sp. | Deposit-feeders | | | | 1 | -14.74 | 10.10 |
| <i>Peringia ulvae</i> | Deposit-feeders | 2 | -12.58 \pm 0.94 | 9.19 \pm 0.50 | 3 | -14.35 \pm 0.38 | 9.37 \pm 0.26 |
| <i>Scoloplos armiger</i> | Deposit-feeders | 9 | -16.46 \pm 0.84 | 11.73 \pm 0.86 | 6 | -15.95 \pm 0.70 | 12.00 \pm 0.53 |
| <i>Urothoe poseidonis</i> | Deposit-feeders | 4 | -12.90 \pm 1.17 | 11.96 \pm 0.62 | 1 | -13.57 | 11.93 \pm |
| <i>Limicola balthica</i> | Deposit-Suspension-feeders | 7 | -13.91 \pm 0.46 | 11.79 \pm 0.46 | 4 | -14.36 \pm 0.20 | 12.28 \pm 0.29 |
| <i>Macomangulus tenuis</i> | Deposit-Suspension-feeders | 4 | -14.05 \pm 0.62 | 11.13 \pm 0.44 | 5 | -14.84 \pm 0.55 | 11.31 \pm 0.38 |
| <i>Scrobicularia plana</i> | Deposit-Suspension-feeders | 3 | -14.46 \pm 0.36 | 11.17 \pm 0.55 | 4 | -17.37 \pm 1.62 | 12.63 \pm 1.28 |
| <i>Cerastoderma edule</i> | Suspension-feeders | 19 | -14.50 \pm 0.54 | 10.98 \pm 0.44 | 16 | -16.23 \pm 0.60 | 11.40 \pm 0.52 |
| <i>Pecten maximus</i> | Suspension-feeders | 2 | -16.09 \pm 0.07 | 9.27 \pm 0.08 | 2 | -18.77 \pm 0.79 | 9.50 \pm 0.15 |
| <i>Donax vittatus</i> | Suspension-feeders | | | | 1 | -18.14 | 10.16 |
| <i>Mactra stultorum</i> | Suspension-feeders | | | | 3 | -18.63 \pm 0.20 | 10.99 \pm 0.11 |
| <i>Crepidula fornicata</i> | Suspension-feeders | | | | 1 | -20.17 | 9.29 |
| <i>Orchestia gammarellus</i> | Grazers | 2 | -21.92 \pm 0.30 | 10.76 \pm 0.49 | 2 | -21.39 \pm 0.93 | 11.51 \pm 0.23 |
| <i>Hediste diversicolor</i> | Omnivores | 3 | -16.05 \pm 1.41 | 13.10 \pm 0.12 | 2 | -18.77 \pm 0.34 | 14.37 \pm 0.29 |
| <i>Acrocnida spatulispina</i> | Omnivores | 7 | -16.70 \pm 0.38 | 12.60 \pm 1.06 | 8 | -17.66 \pm 1.10 | 12.14 \pm 1.07 |

Table 3Food web structure properties at site (whole bay) and assemblage scale in March and September. $\delta^{13}\text{C}_{\text{rg}}$ and $\delta^{15}\text{N}_{\text{rg}}$: range in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰). $\delta^{13}\text{C}_{\text{ctr}}$ and $\delta^{15}\text{N}_{\text{ctr}}$: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ centroids values (‰). CD: Mean distance to centroid. NND: Mean of the Euclidean distances to each species to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ centroids. SDNND: Standard deviation of nearest neighbor distance. TA: Total area. IDiv: Isotopic divergence. IEve: Isotopic Evenness.

| | | $\delta^{13}\text{C}_{\text{rg}}$ | $\delta^{15}\text{N}_{\text{rg}}$ | $\delta^{13}\text{C}_{\text{ctr}}$ | $\delta^{15}\text{N}_{\text{ctr}}$ | CD | NND | SDNND | TA | IDiv | IEve |
|-----------|-------------|-----------------------------------|-----------------------------------|------------------------------------|------------------------------------|------|-------|-------|-------|------|------|
| March | Whole bay | 10.92 | 6.31 | -15.30 | 11.41 | 1.99 | 0.284 | 0.24 | 43.46 | 0.73 | 0.61 |
| | Muddy sand | 5.32 | 6.31 | -13.93 | 11.21 | 1.58 | 0.416 | 0.36 | 21.92 | 0.67 | 0.67 |
| | Fine sand | 5.59 | 5.71 | -15.01 | 11.79 | 1.76 | 0.34 | 0.39 | 23.16 | 0.82 | 0.81 |
| | Medium sand | 2.74 | 4.87 | -16.41 | 12.07 | 1.40 | 0.492 | 0.27 | 9.12 | 0.66 | 0.52 |
| | Salt marsh | 4.80 | 3.67 | -18.97 | 11.15 | 2.25 | 2.25 | 1.66 | 9.59 | 0.91 | 0.87 |
| September | Whole bay | 10.16 | 6.74 | -16.25 | 11.42 | 2.02 | 0.36 | 0.32 | 46.64 | 0.73 | 0.80 |
| | Muddy sand | 5.58 | 5.95 | -14.46 | 11.28 | 1.80 | 0.53 | 0.42 | 16.25 | 0.78 | 0.73 |
| | Fine sand | 5.40 | 4.31 | -15.08 | 12.16 | 1.50 | 0.36 | 0.25 | 15.08 | 0.74 | 0.90 |
| | Medium sand | 5.21 | 5.09 | -17.34 | 11.38 | 1.91 | 0.622 | 0.38 | 15.80 | 0.73 | 0.89 |
| | Salt marsh | 3.96 | 3.23 | -19.54 | 13.11 | 1.71 | 0.92 | 0.39 | 3.79 | 0.77 | 0.43 |

sources at the base of food webs (Leclerc et al., 2013; Melville and Connolly, 2003; Vanderklift and Wernberg, 2010).

4.2. Saltmarsh influence on the sandflat food web

The productivity of salt marshes during summer is high, reaching 30 tonnes of dry matter per ha per year (Lefevre et al., 2000). The outwelling hypothesis states that salt marshes export organic matter, dissolved carbon and nutrients to tidal adjacent habitats from tidal channels to estuaries and coastal ocean (Odum, 1968; Teal, 1962). The influence of salt marsh vegetation on food webs is highly variable, ranging from almost insignificant (Christianen et al., 2017), to very important, and reflected in the stable isotope composition of marshes inhabiting consumers (Nordström et al., 2014; Riera et al., 1999), or adjacent habitats assemblages (Conway-Cranos et al., 2015).

In the study area, salt marshes are characterised by good conservation status but only cover a limited area [125 ha, Sturbois and Bioret (2019)], compared to other comparable coastal bays of the French Atlantic coast, such as the bay of Mont-Saint-Michel [4000 ha, Lafage et al. (2021)], the bay of Seine [1200 ha, Lafage et al., 2021], or the bay of Aiguillon [1100 ha, Joyeux et al. (2017)]. Trophic connectivity relies on the relative proportion of allochthonous and autochthonous resources rather than only on asymmetric production among habitats, especially when the nutritional value of allochthonous sources (i.e. salt

marsh detritus) is lower than local, fresh sources (Mann, 1982). Differences in the proportion of resources result from interaction among productivity, permeability, and transport vectors that lead to many states of trophic connectivity (Domingos and Lana, 2017).

The influence of C3 plants was limited to the grazer *O. gammarellus*, the omnivore *H. diversicolor* and the deposit-suspension-feeder *Scrobicularia plana* inhabiting the muddy salt marsh creeks. *O. gammarellus* is a known consumer of salt marsh detritus [*H. portulacoides* in particular (Joyeux et al., 2017; Laffaille et al., 2001)]. *H. diversicolor* is a very generalistic omnivore able to: feed on sediment, microphytobenthos, macroalgae, detritus and plant material; predate small invertebrates; suspension feed by secreting and using a mucobag as a filter when drawing down particles in its burrow; and garden by sprouting seeds (Durou et al., 2007; Scaps, 2002; Zhu et al., 2016).

Only a few evidences have been reported in the use of salt marsh vegetation in the study area: juveniles of *Dicentrachus labrax* were proven to feed on ^{13}C -depleted preys inhabiting salt marshes (Sturbois et al., 2016), or *Branta bernicla*, on *Puccinellia maritima* (Ponsoero et al., 2009b). As no benthic species displayed such a ^{13}C depletion, which would be consistent with the significant assimilation of such sources further on the shore, no evidence was found that salt marsh plants support the benthic food webs in unvegetated sandy habitats. The influence of the C4 plant *S. anglica* was also discarded according to its ^{13}C enriched values. The capacity of salt marsh plants to fuel intertidal

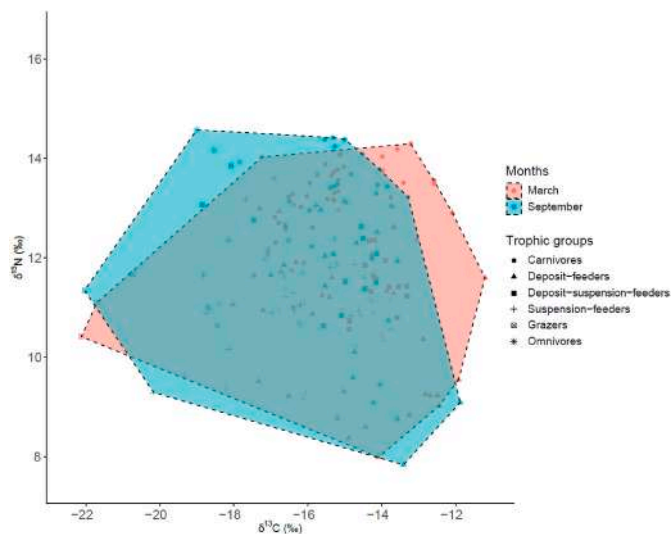


Fig. 4. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the sampled species in March (red) and September (green) in intertidal soft-bottom sediments of the bay of Saint-Brieuc. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are plotted for each individual consumer. Shapes represent trophic groups. Isotopic niche (total area) is represented by convex hull polygons for March (green) and September (red).

benthic habitat seems limited, especially for macrofauna species which exhibit limited mobility in a large flat characterised by megatidal and dispersive conditions.

Consequently, we believe that salt marsh organic matter is either transferred into coastal food webs through highly mobile consumers (fish, shorebirds), thereby overpassing the intertidal benthic food web, or exported over spatial scales which exceed the bay, contributing to the overall detrital pool. It results in a strong dilution and the impossibility to assess its influence through stable isotopes. In further studies, fatty acid analysis might be useful in this regard.

Salt marsh muddy creeks are characterized by a large production of benthic diatoms. Mulletts (*Chelon* spp.) feeding on biofilm and associated meiofauna contribute to the exportation pathway of the biofilm (Carpentier et al., 2014). Regularly reach by the tide at high tide, salt marshes are submerged when water height exceeds 10.70 m, which

represents 45% of the tide cycles (76% for associated creeks) (Sturbois et al., 2016). Megatidal conditions associated with strong currents may also contribute to the effective resuspension of sediments and microphytobenthos (personal observation), exporting benthic diatoms in the water column and further away in the bay. The importance of resuspended microphytobenthos as a major food source for macrobenthos in mudflat environments is a long known mechanism (De Jonge and Van Beuselom, 1992; Riera and Richard, 1996).

4.3. Sources supporting the food web: limited influence of seasonal *Ulva* spp. Blooms

The year 2019 was characterised by important *Ulva* spp. biomass which progressively accumulated during summer (Supplementary materials, Appendix A). In the close bay of Douarnenez, Quillien et al. (2016) found evidence of a direct consumption of *Ulva* spp. fragments by a few species (*Owenia fusiformis*, *Acrocnida spatulispina*), and an indirect influence on the whole food web through the isotopic modification of SOM and POM due to *Ulva* spp. presence. On the western coast of Korea, Park et al. (2016) showed that blooming green macroalgae support an intertidal macrobenthic food web with a certain variability depending on both feeding strategies of consumers and resource availability. From field experiments with varying macroalgal mat thickness (0.5, 1.5 and 4 cm) over eight weeks, Green and Fong (2016) quantified the effects on macrofauna on a Californian lagoon mudflat. They found that the predominant mechanism triggering negative effects on macrofauna for the highest macroalgal biomasses was the development of anoxic conditions. Sulfide accumulation for the 4 cm treatment reduced ecosystem functioning, favouring subsurface deposit feeding such as capitellids.

Ulva spp. was ^{13}C - and ^{15}N -enriched in September compared to March, which provided an opportunity to investigate the potential role of *Ulva* spp. in the food web. Our results reveal that the influence of *Ulva* spp. on the entire food web can be considered as low, regarding the limited area concerned by stranded *Ulva* spp. in February (12 ha), and the absence of such isotopic enrichment at the community scale in September. For example, *A. spatulispina* sampled in September were ^{13}C -depleted, suggesting no *Ulva* spp. influence and contrasting with the results of Quillien et al. (2016). The moderate ^{13}C - and ^{15}N -enrichment observed for carnivores may reveal accidental ingestion of *Ulva* spp. fragments when hunting and feeding on preys, but the low magnitude of the trophic trajectory suggest a very limited influence. Such a low

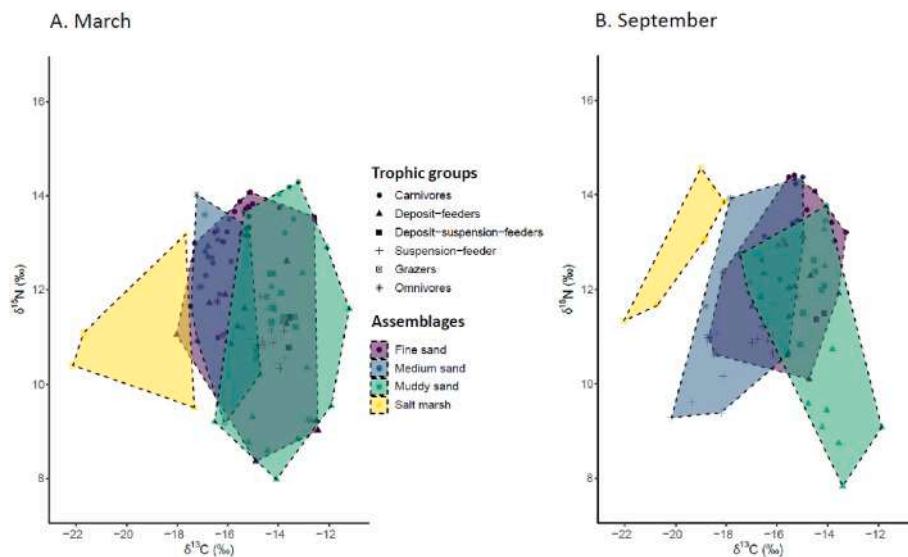


Fig. 5. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope composition of the sampled species in March (A) and September (B) in the four assemblages. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are plotted for each individual of consumers. Shapes represent trophic groups. Isotopic niche (Total area) is represented by convex hull polygons for each habitat: salt marsh creeks (yellow), muddy sands (green), fine sands (purple) and medium sands (blue).

Table 4
 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean \pm sd) of trophic groups in March and September. n: number of samples.

| Trophic groups | Assemblages | March | | | September | | | Trajectory metrics | |
|----------------------------|-------------------|-------|-----------------------|-----------------------|-----------|-----------------------|-----------------------|--------------------|----------------|
| | | n | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | N | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | N. changes | Angle α |
| Grazers | Salt marsh creeks | 2 | -21.92 \pm 0.30 | 10.75 \pm 0.49 | 2 | -21.39 \pm 0.93 | 11.51 \pm 0.23 | 0.92 | 35.13 |
| Omnivores | Salt marsh creeks | 1 | -17.68 \pm | 13.18 | 2 | -18.77 \pm 0.34 | 14.37 \pm 0.29 | 1.61 | 317.46 |
| Carnivores | Muddy sands | 6 | -13.88 \pm 0.77 | 13.82 \pm 0.42 | 2 | -14.09 \pm 0.04 | 13.62 \pm 0.22 | 0.28 | 225.93 |
| Deposit-feeders | Muddy sands | 16 | -13.67 \pm 1.44 | 10.16 \pm 1.53 | 9 | -13.78 \pm 0.81 | 10.04 \pm 1.81 | 0.16 | 221.11 |
| Deposit-Suspension-feeders | Muddy sands | 12 | -14.15 \pm 0.50 | 11.53 \pm 0.56 | 8 | -15.00 \pm 1.06 | 11.97 \pm 0.65 | 0.95 | 297.24 |
| Suspension-feeders | Muddy sands | 6 | -14.16 \pm 0.26 | 11.13 \pm 0.53 | 3 | -16.44 \pm 0.82 | 11.87 \pm 0.22 | 2.40 | 287.95 |
| Carnivores | Fine sands | 19 | -15.25 \pm 1.18 | 13.40 \pm 0.67 | 10 | -14.69 \pm 0.80 | 13.74 \pm 0.50 | 0.66 | 58.44 |
| Deposit-feeders | Fine sands | 11 | -14.99 \pm 1.76 | 10.81 \pm 1.34 | 8 | -15.01 \pm 0.69 | 12.00 \pm 0.94 | 1.19 | 359.18 |
| Deposit-Suspension-feeders | Fine sands | 2 | -13.57 \pm 0.02 | 11.10 \pm 0.44 | 2 | -14.31 \pm 0.21 | 11.44 \pm 0.09 | 0.81 | 294.95 |
| Suspension-feeders | Fine sands | 11 | -14.61 \pm 0.61 | 10.98 \pm 0.37 | 12 | -16.11 \pm 0.53 | 11.32 \pm 0.52 | 1.54 | 283.07 |
| Omnivores | Fine sands | 5 | -16.55 \pm 0.33 | 12.12 \pm 0.79 | 6 | -17.44 \pm 1.17 | 11.92 \pm 0.92 | 0.91 | 257.49 |
| Carnivores | Medium sands | 9 | -16.43 \pm 0.69 | 12.60 \pm 0.60 | 9 | -15.66 \pm 0.61 | 13.04 \pm 0.69 | 0.90 | 60.48 |
| Deposit-feeders | Medium sands | 3 | -16.80 \pm 0.40 | 12.38 \pm 1.26 | 2 | -16.82 \pm 0.25 | 11.75 \pm 0.14 | 0.63 | 181.99 |
| Suspension-feeders | Medium sands | 4 | -15.50 \pm 0.70 | 9.91 \pm 0.85 | 8 | -18.59 \pm 0.93 | 10.29 \pm 0.77 | 3.12 | 277.06 |
| Omnivores | Medium sands | 2 | -17.08 \pm 0.23 | 13.81 \pm 0.30 | 2 | -18.33 \pm 0.69 | 12.79 \pm 1.61 | 1.62 | 230.79 |

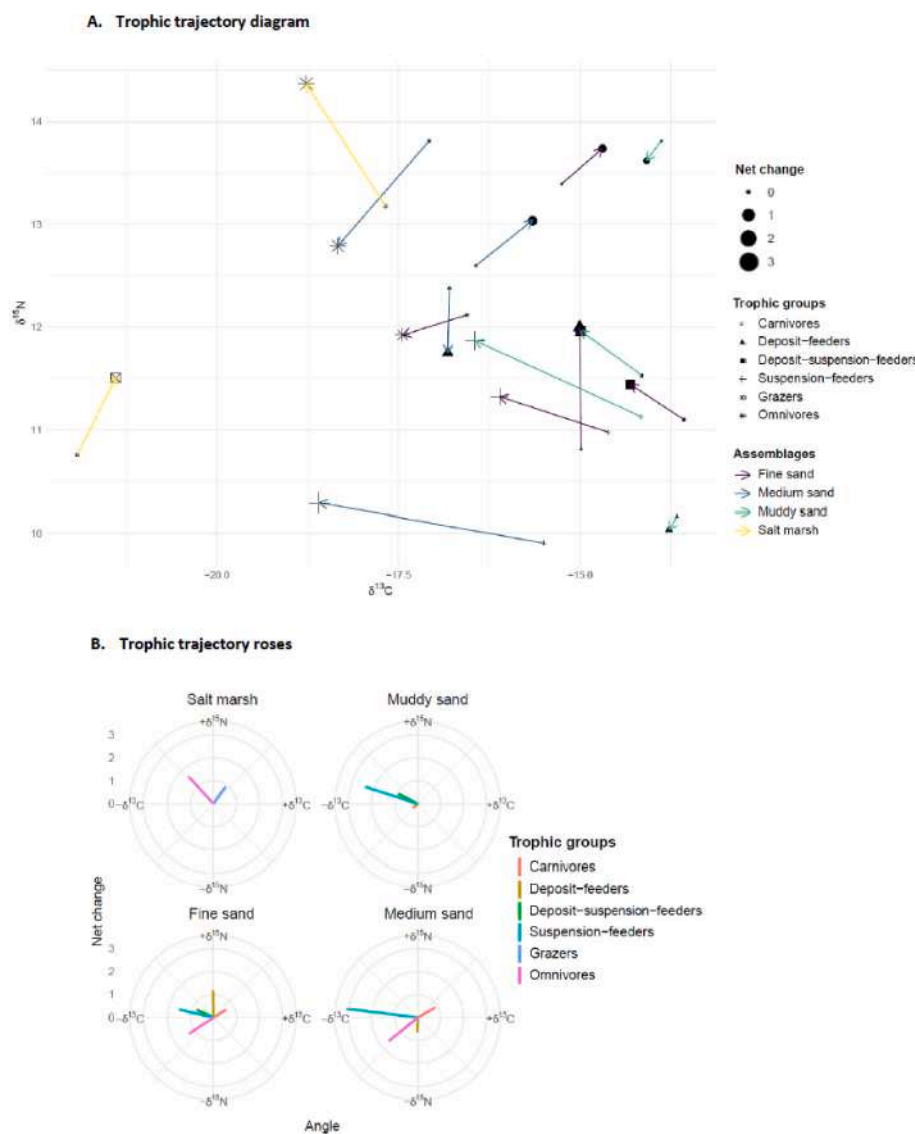


Fig. 6. Temporal trajectories of trophic groups between March and September. Stable Trophic trajectory diagram (A): Arrows represent trophic trajectory in the $\delta^{13}\text{C}/\delta^{15}\text{N}$ space between March and September for each trophic group in each assemblage (color). Length of arrows and size of dots corresponds to the net change (Euclidean distance) and inform about the magnitude of change. Different symbols correspond to trophic groups. Trophic trajectory roses (B): Angles α and net changes are represented in trophic trajectory rose for each trophic group (color) in each habitat (panel). Angle α values ($0-90^\circ$: $+\delta^{13}\text{C}$ and $+\delta^{15}\text{N}$; $90-180^\circ$: $+\delta^{13}\text{C}$ and $-\delta^{15}\text{N}$; $180-270^\circ$: $\delta^{13}\text{C}$ and $-\delta^{15}\text{N}$; $270-360^\circ$: $\delta^{13}\text{C}$ and $+\delta^{15}\text{N}$).

influence of *Ulva* spp. in the diet and stable isotope composition of marine crustaceans has also been demonstrated by experimental (Karez et al., 2000; Salathé and Riera, 2012) and *in situ* (Adin and Riera, 2003) studies. The contrast with the results obtained by Quillien et al. (2016),

Park et al. (2016) and Green and Fong (2016), may be explained by the mega-tidal conditions which characterize the study area. In the bay of Saint-Brieuc, tides are a strong driving factor. Daily resuspension and redistribution of algal mats and limited long-term static accumulation of

algae make potential anoxic episodes restricted to very limited zones (i. e. beaches on the upper shore), where *Ulva* spp. are all the more collected by local authorities as part of precautionary sanitary measures (e.g. 12 682 tons has been collected in 2021). This phenomenon potentially limits the integration of *Ulva* spp. in the food web. Furthermore, the bay of Saint-Brieuc shelters benthic producers on muddy and muddy sand habitats, which contrasts from the sandy beaches located in the bay of Douarnenez.

Marine POM and MPB displayed stable isotope compositions which were the most likely to represent the actual basis of food webs within the different habitats, regarding $\delta^{13}\text{C}$ ranges displayed by the benthic communities. Marine POM was the only source exhibiting a significant ^{13}C -depletion between March and September, which was also observed for suspension-feeders from all habitats, as well as by mixed deposit/suspension-feeders and some omnivores. In contrast, the low shift in $\delta^{13}\text{C}$ values of deposit-feeders between March and September suggests a low temporal variability in the composition of benthic producers. This is also in accordance with the low shift observed for SOM values, especially in fine and medium sands. Deposit-feeders are often quite, or even very, selective with regard to the total SOM (Levinton, 1989), which is a composite source by definition, so they only use a portion of it, and benthic diatoms represent a particularly easy-to-use source with a high food quality within the SOM.

Christianen et al. (2017) reported that energy in the Wadden sea ecosystem is mainly provided by locally produced organic matter and in a lesser extent by pelagic producers. Such contribution of MPB has also been highlighted, at lower geographic scales in salt marsh consumers in the Mont Saint-Michel bay (Créach et al., 1997), and for cockles in Marennes-Oléron Bay (Kang et al., 1999). Other intertidal studies also revealed the fuelling of higher trophic levels by MPB and pelagic primary production (van Oevelen et al., 2006). In the bay of Saint-Brieuc, where muddy habitats are limited (64 ha), our results suggest that the food web is mainly fuelled by pelagic producers and, to a lesser extent, by benthic producers. However, salt marsh muddy creeks could also support a part of the MPB production, in addition with muddy sands. Such assumption will require further investigations to be accurately quantified (Méléder et al., 2020; Morelle et al., 2020).

These overall considerations and assumptions do not exclude contributions from other food sources at finer local scale in this highly dynamic system as already observed in the Roscoff Aber bay (Ouisse et al., 2011), in the Wadden Sea (Christianen et al., 2017), or in this study for the macrofauna inhabiting salt marsh creeks.

4.4. Spatial patterns in benthic-pelagic coupling

Large scale spatial heterogeneity in the carbon stable isotope composition of consumers has been observed by Christianen et al. (2017) in the Wadden Sea for species that forage either on benthic or pelagic sources. In a large part of the Wadden sea, a dominant use of pelagic food sources was observed for the common cockle suspension-feeder *Cerastoderma edule*, while the use of benthic producer was suggested for some spatially limited areas. Conversely, for the Baltic clam *Limecola balthica*, which is a facultative deposit and suspension-feeder, $\delta^{13}\text{C}$ indicated a high benthic contribution to its diet in most of the flat, contrasting with a dominant pelagic contribution in some limited areas.

In our study, spatial patterns have been revealed at the scale of trophic groups, with higher $\delta^{13}\text{C}$ values for suspension-feeders, deposit-suspension-feeders and carnivores in muddy and fine sands compared to medium sands. They were maintained between March and September and confirmed by the correlation between $\delta^{13}\text{C}$ values and emersion time for some trophic groups. In addition, some contrasted temporal trophic trajectories among habitat were evidenced. Trajectory metrics (net changes and angle α) revealed a congruent negative shift in marine POM and suspension-feeders $\delta^{13}\text{C}$ values between March and September. However, while direction in the δ space was similar

suspension-feeders at assemblage scale, differences were observed in net changes values. This contrasting pattern in the magnitude of change suggests a decreasing influence of pelagic sources in the diet of suspension-feeders from muddy and sandy habitats compared to medium sands. Deposit-suspension-feeders showed similar direction but lower net changes than suspension-feeders, confirming both their higher dependence to benthic primary producers and their ability to feed on pelagic producers. The low variability of deposit-feeder $\delta^{13}\text{C}$ values was in accordance with the temporal stability observed for sedimentary organic matter in medium sands and suggested a low temporal variability in the stable isotope composition of MPB.

Lower net changes exhibited by suspension-feeders in muddy and fine sand habitats suggest a major resuspension of MPB in the water column as already shown in different intertidal areas (De Jonge and Van Beuselom, 1992; Liénart et al., 2017; Riera and Richard, 1996; Sauriau and Kang, 2000; Underwood and Chapman, 1998). Suspended particulate organic matter corresponds to a dynamic mixture of pelagic and benthic algae due to the resuspension of MPB. Microphytobenthos growth is favoured in muddy and muddy sands habitats (Morelle et al., 2020), and its spatio-temporal distribution is driven by highly variable physical and biological factors (Méléder et al., 2020). MPB resuspension is known to be favoured by hydrodynamics and bioturbation activities of some macrofauna species such as *C. edule* (Rakotomalala et al., 2015). The bay of Saint-Brieuc is characterized by megatidal conditions and high density of *C. edule*, reaching 2000 ind.m² in muddy sands. MPB can be easily resuspended at relatively low current velocities (~10 cm s⁻¹) on silty sediment (Blanchard et al., 1997; Kang et al., 2015; Ubertini et al., 2015). Resuspension is increased by the coverage and the important dynamics of tidal channels (Sturbois et al., 2021a), which may contribute to organic matter fluxes. Emersion time regulates the trophic availability of MPB for some consumers (suspension and surface deposit feeders). Hydrodynamics and tides favour the trophic connectivity between muddy sand and fine sand habitats located at lower levels through the exportation of microphytobenthos in the water column. However, the exportation of the tidally resuspended MPB seems limited to fine sand habitats and suggests spatial contrast in benthic-pelagic coupling. De Jonge and Van Beuselom (1992) and Riera and Richard (1996) found similar results, demonstrating that the influence of the MPB exported in the water column is limited to close adjacent habitats.

4.5. Small spatial scale variability in food web structure

Despite a slight increase in IEve in relation to the ^{13}C -depletion of suspension and deposit-suspension-feeders, the stability of structural properties and the strong overlap observed at site scale between March and September highlight the temporal stability of the system. Dissimilarity among assemblages was strongly influenced by the $\delta^{13}\text{C}$ decreasing gradient of consumers from muddy to fine and medium sands assemblages, while no such pattern was observed for $\delta^{15}\text{N}$. This gradient illustrates the spatial variability in the benthic pelagic coupling, with a higher influence of MPB in the upper level compared to low shore habitats. The decrease in the similarity between the low levels of the muddy and medium sands observed between March and September (in relation with the trophic trajectory of suspension-feeders in medium sands) highlights the two main energy pathways supported by pelagic and benthic producers.

Quillien et al. (2016) showed an overall simplification of community-wide food web structure and functioning in sandy beach harbouring green tides. They notably highlighted a significant community-wide shift in $\delta^{13}\text{C}$ over time progressively splitting up into two distinct isotopic niches. A linear arrangement of trophic web components indicated a single carbon pathway where *Ulva* spp. mats were present on the shore. No such simplification was observed at site or assemblages scale in the study area. Conversely, the selected indices of trophic structure and functioning were stable or increased during the year. Assemblages still overlapped over time and no overall ^{13}C

enrichment of consumers was observed in accordance with $\delta^{13}\text{C}$ composition of *Ulva*. Overall, the temporal consistency observed in the food web structure in the different habitats confirm that the summer *Ulva* bloom did not play a major role in the trophic functioning off the bay of Saint-Brieuc.

4.6. Implications of food web dynamics for sampling strategy

The trajectories of trophic groups can occur, notably: 1) if shift occurs in stable isotope compositions of the consumed sources; 2) if they change their diets (i.e. use different sources depending on the availability of these sources or the same sources in different proportions); 3) if within groups the dominant species vary and as species within groups have different diets, this inevitably leads to a group average isotopic deviation (in this case some species may have faster growth rates and different tissue turnover and hence an impact on the average of the trophic group); and 4) isotopic variations due to ontogenetic variations within a species.

In the Wadden sea, Christianen et al. (2017) suggested that different factors are potentially involved in the spatial heterogeneity of food web $\delta^{13}\text{C}$ values: spatial variability in benthic production; differential consumption of benthic and pelagic producers; and/or the differential contribution of resuspended benthic primary producers for consumers feeding entirely on pelagic producers. Fine scale variations in the local environment may also influence food web properties (Ouisse et al., 2011). Our study highlights these spatio-temporal variations in the stable isotope compositions of sources and consumers. The different degrees of trophic connectivity with a low influence of salt marshes and variations in benthic-pelagic coupling in relation with the distribution and the resuspension of MPB confirm the importance of sampling food webs at large spatial and temporal scales for a better integration of dynamics.

Similarly, differences in the influence of *Ulva* spp. on benthic food web properties between the Bay of Saint-Brieuc and the sandy beaches of Douarnenez indicate that effects on ecosystems are not spatially consistent at regional scale, and claims for local studies integrating local physical and biological driven factors.

4.7. Food webs studies: a baseline for conservation process

As the first attempt to characterize intertidal benthic food webs of the bay of Saint-Brieuc, this study provides valuable information for managers about the functioning and energy pathways supporting the specific benthic communities. First, the influence of salt-marsh plants on benthic macrofauna is limited. Such result remains fundamental for the consideration of trophic functioning at larger scale in the bay, but does not question the value of salt marsh already shown for juveniles of some fish species (Carpentier et al., 2014; Joyeux et al., 2017; Lafage et al., 2021; Sturbois et al., 2016) or birds (Ponsero et al., 2009b, 2019). Second, the seasonal increase in biomass of *Ulva* spp. does not influence the functioning of the local benthic food webs. This result was unexpected given that two local bird species, *Mareca penelope* and *Branta bernicla*, feed on this algae (Ponsero et al., 2009b). These results pointed that green tides may represent a trophic cul-de-sac for the benthic macrofauna inhabiting the bay of Saint-Brieuc.

Users and stakeholders do not give due consideration to muddy habitats and regularly ask for managements in these habitats (sands deposits, harbour management or dredging). As shown by our results, they now have to consider that MPB partially supports the food web in muddy sands, and that resuspended MPB is exported in fine sands habitat. This process may also be supported by benthic producers of the salt marsh muddy creeks.

Despite all habitats are used by birds, muddy and fine sand assemblages are the most available due to low emersion time of medium sands (Ponsero et al., 2016; Sturbois et al., 2015). Our study highlights that waders trophic resource (i.e. benthic invertebrates) is supported by

pelagic and benthic producers with a decreasing inshore/offshore gradient of MPB influence. The bay of Saint-Brieuc is characterized by *C. edule* fishing grounds exploited by professional and recreational fishers and muddy habitats, where young cockles can feed on MPB (Sauriau and Kang, 2000), are known to be favourable areas for settlement (Ponsero et al., 2009a).

In this context, governance processes of the bay of Saint-Brieuc must integrate the conservation of muddy habitats to inform and sensitize stakeholders, users and managers about the importance of muddy habitats for waders populations and fishing activities, and to avoid cascading effect further up the food webs leading to potential ecological and economical consequences.

5. Conclusion

Results highlighted that the benthic trophic network is, most likely, based on phytoplankton, microphytobenthos and SOM. The trophic connectivity between salt marsh and benthic habitats within the bay was limited to some macrofauna species inhabiting muddy creeks within the salt marsh. Unexpectedly, the influence of *Ulva* spp. in the trophic functioning of the different assemblages appeared quite limited. Spatial patterns illustrates the constancy of the spatial variability in the benthic pelagic coupling, with a higher influence of microphytobenthos in the upper level compared to low shore assemblages. This first attempt to characterize intertidal benthic food web constitutes a relevant baseline for the conservation of the bay of Saint-Brieuc where a National nature reserve has been created in 1998 for the conservation of overwintering birds. The spatio-temporal patterns of the benthic food web also confirms the importance to consider food web variability at spatial and temporal scales from sampling designs to data analysis. The ability of the stable isotope trajectory analysis framework to highlight spatio-temporal patterns was also demonstrated.

CrediT authorship contribution statement

Anthony Sturbois: Conceptualization, Methodology, Validation, Formal analysis, Data curation, Writing - original draft, Visualization, Project administration, Funding acquisition, Investigation. **Pascal Riera:** Conceptualization, Methodology, Validation, Writing -review & editing, Investigation, Supervision. **Nicolas Desroy:** Conceptualization, Methodology, Validation, Writing -review & editing, Investigation, Supervision. **Titouan Bréban:** Investigation, Writing - review & editing. **Alexandre Carpentier:** Methodology, Validation, Writing - review & editing. **A. Ponsero:** Writing -review & editing. **Gauthier Schaal:** Conceptualization, Methodology, Validation, Writing -review & editing, Investigation, 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2022.105572>.

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