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

Sturbois A. ^{1,2,3,4,*}, Riera P. ⁵, Desroy Nicolas ³, Brébant Titouan ³, Carpentier A. ⁶, Ponsero A. ^{2,7}, Schaal G. ⁴

¹ Vivarmor Nature, 18 C rue du Sabot, 22440, Ploufragan, France

² Réserve naturelle nationale de la Baie de Saint-Brieuc, site de l'étoile, 22120, Hillion, France

³ Ifremer, Laboratoire Environnement et Ressources Bretagne nord, 38 rue du Port Blanc, 35800, Dinard, France

⁴ Laboratoire des Sciences de l'Environnement Marin (LEMAR), UMR 6539 CNRS/UBO/IRD/IFREMER, BP 70, 29280, Plouzané, France

⁵ Sorbonne Université, CNRS, Station Biologique de Roscoff, UMR7144, Place Georges Teissier, CS90074, 29688, Roscoff Cedex, France

⁶ Université de Rennes 1, BOREA, Muséum National d'Histoire Naturelle, Sorbonne Université, Université de Caen Normandie, Université des Antilles), Campus de Beaulieu, 35000, Rennes, France

⁷ Saint-Brieuc Agglomération Baie d'Armor, 5 rue du 71ème RI, 22000, Saint-Brieuc, France

* Corresponding author : A. Sturbois, email address : anthony.sturbois@espaces-naturels.fr

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* 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.

Highlights

- ▶ The benthic invertebrates food web structure was studied in a large intertidal area using $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ values.
- ▶ Stable isotope compositions were variable in space and time for some sources and consumers.
- ▶ Phytoplankton, microphytobenthos and SOM were the main sources supporting the benthic food web.
- ▶ Spatial variability in the benthic pelagic coupling was constant between March and September.
- ▶ The influence of salt marsh vegetation and *Ulva* blooms was limited.

Keywords : marine food web, benthic assemblages, $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$, trophic connectivity, benthic pelagic coupling, stable isotope trajectory analysis

68 I. Introduction

69 Coastal areas are among the most productive marine systems in the world,
70 sustaining many ecological processes and ecosystems services (Costanza et al.,
71 1997). The production of bays and estuaries is provided by a wide diversity of
72 primary producers, including phytoplankton, seaweeds, seagrass, mangroves, salt
73 marsh plants, macroalgae, and benthic diatoms (Bouillon et al., 2011). All these
74 primary producers contribute to an important pool of detrital organic matter, which
75 plays a major role in the biogeochemistry and ecology of bays and estuaries
76 ecosystems. Due to this diversity, understanding the fate of primary production within
77 coastal ecosystems, and especially within food webs, is challenging (Mann, 1988).
78 Furthermore, the contribution of these different producers to local food webs has
79 been reported to vary within and among coastal systems (Chanton and Lewis, 2002;
80 Deegan and Garritt, 1997; Domingos and Lana, 2017), leading to a lack of a
81 commonly accepted paradigm for food web functioning across variable spatial and
82 temporal scales.

83 Because coastal food webs depend on primary food sources which can be either
84 sessile or mobile, assessing vertical (i.e. benthic-pelagic coupling) and horizontal (i.e.
85 organic matter fluxes across habitats/ecosystems) trophic connectivity between
86 adjacent habitat is crucial (Kang et al., 2015; Schaal et al., 2008). Trophic
87 connectivity varies among systems from near total isolation to strong mixing. Water
88 motion facilitates the movement of carbon as dissolved or particulate matter in
89 aquatic ecosystems (Guimond and Tamborski, 2021; Polis et al., 1997).
90 Hydrodynamics influences coastal productivity through a variety of mechanisms
91 (Largier, 1993). In tidal environments, the periodic movement of the tide is
92 responsible for organic matter redistribution, enhancing trophic connectivity among
93 different habitats and assemblages (Polis et al., 1997). Redistribution range depends
94 on tidal amplitude across meso, macro and megatidal systems (Domingos and Lana,

95 2017; Ziegler et al., 2019). Resulting hydrodynamics can lead to the accumulation
96 and/or dispersal of water column constituents, including sediment, phytoplankton,
97 and particulate detritus (Young et al., 2021), and potentially influence production
98 pathways and food web structure. Higher water motion increases material processing
99 (e.g. microphytobenthos resuspension) between benthic and pelagic compartments
100 (Ubertini et al., 2012) which can be amplified by biological factors, such as
101 bioturbation (Rakotomalala et al., 2015).

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

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

117 Organic matter inputs (e.g. detrital plants or algae) from vegetated systems may
118 diversify food webs structure and energy pathways (Hyndes and Lavery, 2005;
119 Nordström et al., 2015; Quillien et al., 2016; Schaal et al., 2008). Such additional
120 food resources may originate from close productive habitats such as salt marshes
121 (Nordström et al., 2014). It may also results from seasonal eutrophication with the

122 proliferation of green algae, which may have important consequences on the
123 structure of benthic food webs (Quillien et al. 2016) and fish assemblages (Jones et
124 al., 2020).

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

136

137 In this study, we focused on the structure and the dominant sources that support the
138 food web in an intertidal sandflat influenced by mega-tidal conditions and
139 characterised by a variety of primary producers. We specifically explored $\delta^{13}\text{C}$ and
140 $\delta^{15}\text{N}$ values from sources to benthic invertebrates consumers at the scale of the
141 entire sandflat and for benthic assemblages which constitute the mosaic of habitat
142 within the bay. Classical analyses ($\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ raw values, graphical inference,
143 indices of structure) were coupled with distance- and direction-based metrics of the
144 new Stable Isotope Trajectory Analysis (SITA) framework (Sturbois et al., 2021b).

145 This new method provides an assessment of stable isotope data at different levels of
146 biological organization, from individuals to ecosystems to derive structural and
147 functional trajectories. We hypothesized that: (1) due to the aforementioned
148 characteristics of the bay, spatial gradients and temporal variability would drive the
149 sources supporting the food web, (2) the variability would induces spatial and

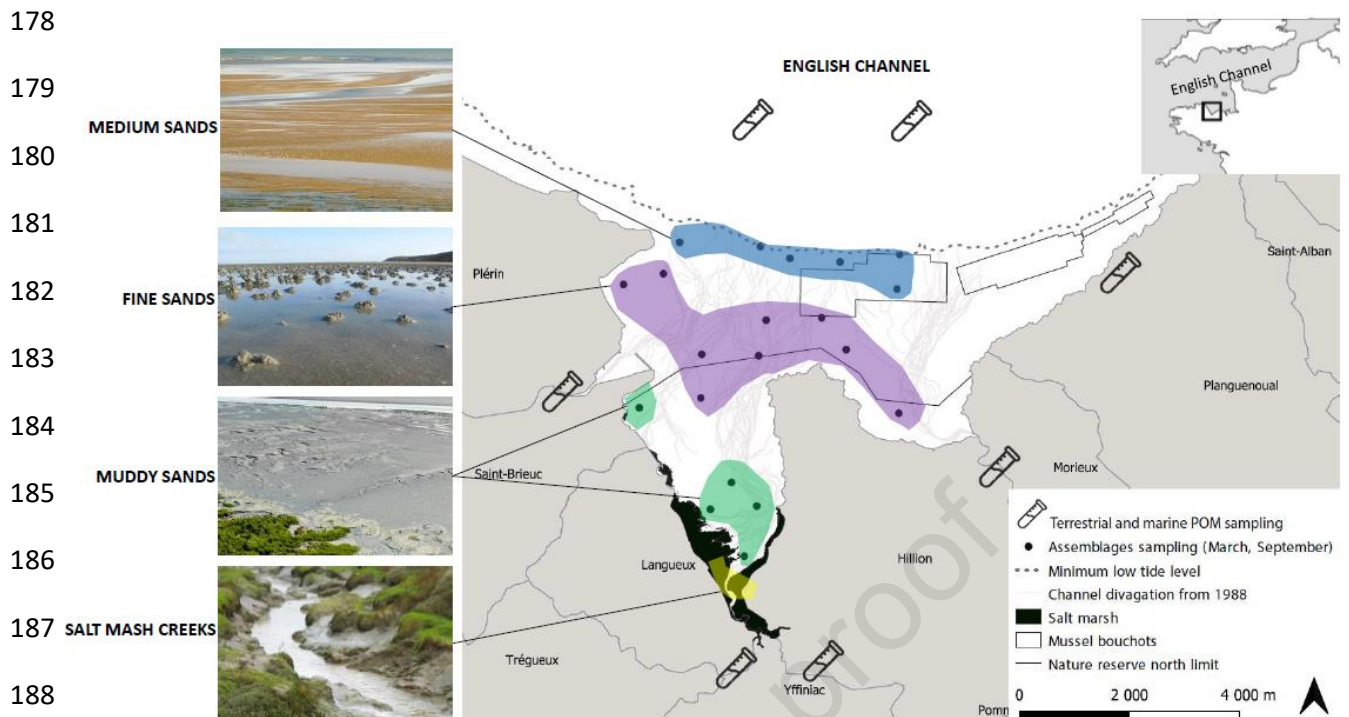
150 temporal difference in the food web structure among habitats. Implications in
151 sampling strategy and conservation processes were finally discussed.

152 **2. Material and methods**

153 **2.1 Study area and sampling design**

154 Fieldwork was conducted in the bay of Saint-Brieuc, France (Figure 1), a 2900 ha
155 tidal flat divided in two coves (Yffiniac and Morieux coves). The area is mainly
156 dominated by fine to medium sands, while the most sheltered parts are characterised
157 by muddy sands. The bay is under the influence of a semi-diurnal megatidal regime.
158 Tidal range varies between 4 m at neap tides and nearly 13 m during spring tides,
159 generating strong tide currents rising between 0.3 and 0.5 m/s in this part of the bay.
160 The upper shore is dominated by salt marshes (125 ha) characterised by a current
161 dynamic of extension and a good conservation status (Sturbois and Bioret, 2019).
162 The bay suffers from eutrophication, resulting in strong ephemeral macroalgae
163 proliferation and cyclic green tides episodes (Charlier et al., 2007; Gravier, 2012)
164 (Supplementary material, appendix A). The national Nature Reserve of Saint-Brieuc
165 was created in 1998 for the protection of shore birds. Because overwintering and
166 migratory waders forage on macrofauna (Ponsero et al., 2016; Ponsero and Le Mao,
167 2011; Sturbois et al., 2015), their protection required the conservation of marine
168 habitats and benthic resources.

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



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

192

193 2.2 Sample collection and laboratory processes

194 *Sources* – Samples were collected in early March and September 2019. Sedimentary
 195 organic matter (SOM) was collected at each station by scraping the upper 1 cm of
 196 the sediment during the low tide. For each station, one subsample was acidified
 197 (10% HCl) and re-dried overnight at 60°C, whereas the other subsample remained
 198 untreated. Values of $\delta^{13}\text{C}$ from acidified subsamples were combined with those of δ
 199 ^{15}N from untreated subsamples to compute the SOM isotope values undisturbed by
 200 calcium carbonate residues ($\delta^{13}\text{C}$) and by acidification ($\delta^{15}\text{N}$) (Androuin et al., 2019).
 201 Benthic diatoms (Microphytobenthos, MPB), abundant in the muddy/sandy sediments
 202 of the area at the end of spring/early summer, were collected in June 2019 and July
 203 2020 by scraping the surface of the sediment and extracted according to a method
 204 of Couch (1989), modified by Riera et al. (1999). The diatoms were collected on
 205 previously combusted glass fiber filters, briefly washed with 10% HCl and rinsed with

206 Milli-Q water and kept frozen (-20°C) until analysis. Stable isotope compositions of
207 2019 and 2020 were averaged.

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

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

218 *Consumers* - Benthic macrofauna was sampled in March and September 2019 from
219 the four assemblages using a 1/32m² hand corer (diameter: 20cm), at a depth of 25
220 cm (Supplementary material, appendix B). Sampling was coupled with spade
221 prospection for overdispersed megafauna, or for species typically difficult to sample
222 using hand corers (e.g. the lugworm *Arenicola marina*). The content of the cores was
223 gently sieved through a 1-mm square mesh sieve. Macrofauna was then sorted on
224 the field and preserved in plastic vials. The beach-hopper *Orchestia gammarellus*
225 was captured by hand in the vegetation bordering salt marsh creeks. In the
226 laboratory, animals were identified to the lowest possible taxonomic level, rinsed and
227 stored at -20°C until further treatment. Samples consisted of individual muscle
228 tissues of large species (bivalves, annelids, echinoderms) or, whenever necessary
229 for small species, pooled individuals (for the small gastropod *Peringia ulvae*) and
230 whole individual (for amphipods species). Species containing calcium carbonates
231 (e.g. the burrowing brittle-star *Acrocnida spatulispina* or the slippershell snail
232 *Crepidula fornicata*) were split into two acidified and non-acidified subsamples.

233 Values of $\delta^{13}\text{C}$ from acidified subsamples and $\delta^{15}\text{N}$ and from untreated subsamples
234 were combined. All samples were rinsed, dried at 60°C for 48 h, and ground into fine
235 powder using a marble mortar.

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

240 **2.3 Stable isotope analysis**

241 Ground samples were packed into 5 x 8 mm ultra-clean tin capsules and analysed
242 using an elemental analyser (EA Flash 2000 from ThermoFisher Scientific) coupled
243 with an isotope ratio mass spectrometer (Delta V Plus from ThermoFisher Scientific)
244 at the stable isotope platform of the Pole Spectrométrie Océan at the University of
245 Bretagne Occidentale (Brest, France). Stable isotope ratios were reported in the
246 standard δ notation as units of parts per thousands (‰) relative to the international
247 reference standard: $\delta X = [(R_{\text{Sample}}/R_{\text{Standard}}) - 1] * 10^3$ where X is ^{13}C and ^{15}N and R is
248 the corresponding ratio of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$. Reference standard used were
249 Vienna-Pee Dee Belemnite for ^{13}C and atmospheric N_2 for ^{15}N (precision: 0.1).

250

251 **2.4 Data analysis**

252 Data sets were investigated to analyse spatial patterns and temporal variability of the
253 intertidal benthic food web between March and September. Analyses were
254 conducted in terms of composition and structure at the bay scale (i.e. entire
255 community), and at the finer scale of the different benthic assemblages. Each
256 species has been assigned to a trophic group: carnivores, deposit-feeders, deposit-
257 suspension-feeders, suspension-feeders, grazers, omnivores. This assignation was
258 performed with respect to primary literature on specific taxa, expert knowledge and
259 three publicly available databases: polytraits (<http://polytraits.lifewatchgreece.eu>), the

260 World Register of Marine Species (WoRMS Editorial Board, 2020), and Biological
261 Trait Information Catalogue (BIOTIC, <http://www.marlin.ac.uk/biotic/>). Trajectory
262 analysis was performed to quantify and characterize the magnitude (distance) and
263 the nature (direction) of temporal shift in the $\delta^{13}\text{C}/\delta^{15}\text{N}$ -space for trophic groups. All
264 analyses were performed within the R environment.

265 Spatial differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were tested with a one-way ANOVA against the
266 factor 'Assemblages'. The food web structure was analysed through community-wide
267 metrics (Layman et al., 2007):

268 - *$\delta^{13}\text{C}$ range (CR)*: Distance between the highest and the lowest $\delta^{13}\text{C}$ values
269 of the community (i.e., maximum $\delta^{13}\text{C}$ - minimum $\delta^{13}\text{C}$). CR is one representation
270 of basal source diversity within a food web;

271 - *$\delta^{15}\text{N}$ Range (NR)*: Distance between highest and the lowest $\delta^{15}\text{N}$ values of
272 the community (i.e., maximum $\delta^{15}\text{N}$ - minimum $\delta^{15}\text{N}$). NR is one representation of
273 the total length (i.e. total number of trophic levels) within a food web;

274 - *Total Area (TA)*: Convex hull area encompassed by all species in the $\delta^{13}\text{C}$ -
275 $\delta^{15}\text{N}$ 2D δ space. This represents a measure of the total amount of niche space
276 occupied, and thus a proxy for the total extent of trophic diversity within a food web;

277 - *Mean distance to centroid (CD)*: Average Euclidean distance of each species
278 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
279 all species in the food web. This metric provides a measure of the average degree of
280 trophic diversity within a food web;

281 - *Mean nearest neighbor distance (NND)*: Mean of the Euclidean distances to
282 each species' nearest neighbor in bi-plot space, and thus a measure of the overall
283 density of species packing.

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

286 - *Isotopic similarity* (ISim): Overlap in the total isotopic niches as the ratio
287 between the isotopic niche of the intersection and of the union of the two groups
288 considered. It ranges from 0 when there is no isotopic overlap to 1 when the group
289 with the lowest isotopic richness fills a subset of the isotopic space filled by the group
290 with the highest isotopic richness;

291 - *Isotopic divergence* (IDiv): distribution of points (close to the centroid or
292 edges) within the convex hull. IDiv is minimal (i.e. tends to 0) when most of the points
293 are close to the centre of gravity of the convex hull, and organisms with the most
294 extreme stable isotope values are rare in a community. IDiv tends to 1 when all the
295 points are located on the edges of the convex hull and organisms with the most
296 extreme stable isotope value(s) dominate the foodweb;

297 - *Isotopic Evenness* (IEve): regularity in the distribution of organisms along the
298 shortest tree that links all the points. IEve tends to 0 when most of organisms are
299 packed within a small region of the stable isotope space while a few others are far
300 from this cluster. IEve tends to 1 when organisms are evenly distributed in the stable
301 isotope space.

302 The new Stable isotope trajectory analysis (SITA) framework was used to measure
303 shifts in stable isotope values for sources and trophic groups (Sturbois et al., 2021b).
304 The quantitative analysis of stable isotope dynamics in response to ecological and
305 environmental changes has been explored in the past through the comparative
306 analysis of temporal trajectories in a two-dimensional (usually $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$)
307 isotopic space (δ space). For instance, Schmidt et al. (2007) and Wantzen et al.
308 (2002) quantified the direction and magnitude of temporal changes in food web
309 structure based on the geometric properties of trajectories in the δ space. Schmidt et
310 al. (2007) used specifically circular statistics and charts to represent and test
311 direction shifts in the δ space. Turner et al. (2010) characterized attributes of path
312 trajectories (size, direction and shape) over data sets containing more than two
313 temporal samples to provide a quantitative description and tested changes in stable

314 isotope compositions change in response to spatial and temporal gradients. Building
315 on these previous works and on the recent Community trajectory analysis framework
316 (De Cáceres et al., 2019; Sturbois et al., 2021c), the SITA framework goes further in
317 the explicit quantitative description, analysis and representation of the magnitude and
318 the nature of changes in stable isotope composition”.

319 Length- and direction-based SITA metrics were calculated. The net change
320 (Euclidian distance between March and September for a given group) and the angle
321 α (0-360° direction in the δ -space considering the Y axis, $\delta^{15}\text{N}$, as the North, i.e. 0°)
322 were calculated to assess the magnitude and the nature of change in the $\delta^{13}\text{C}/\delta^{15}\text{N}$ -
323 space, respectively. Net changes and angle α were represented through trajectory
324 diagrams and trajectory roses (Sturbois et al., 2021b) and temporal differences in
325 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean values for sources and trophic groups were represented through
326 bar plots and tested with permutation Student's t-tests (package '*RVAAMemoire*',
327 '*perm.t.test*' function, 999 permutations).

328

329 **3. Results**

330 **3.1 Primary food sources**

331 **3.1.1 Bay scale**

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

338

339 Table I: Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean \pm sd) of the various food sources collected in March and
 340 September 2019. n: number of samples. Marine and terrestrial particulate organic matter (POM_SEA,
 341 POM_TER). Sedimentary organic matter in the different assemblages from salt marsh to muddy, fine
 342 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 sp.</i>	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 spp.</i>	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
<i>Microphythobenthos</i>	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

343

344 3.1.2 Temporal variability

345 The SOM samples of all assemblages were characterized by the lowest variability in
 346 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Figure 3, Table 1). The stable isotope composition of *Ulva*
 347 *spp.* was characterized by an increase in both isotopes in September (angle α :
 348 50.57° , trajectory length : 6.49), although this variation was not significant for $\delta^{13}\text{C}$
 349 ($p=0.094$, Supplementary material, Appendix C). POMs followed an inverse pattern
 350 (243.49° , 7.41). Significant $\delta^{13}\text{C}$ shifts between March and September were
 351 observed, with a decrease for POM_SEA ($p=0.004$), and an increase for terrestrial
 352 POM ($p=0.032$).

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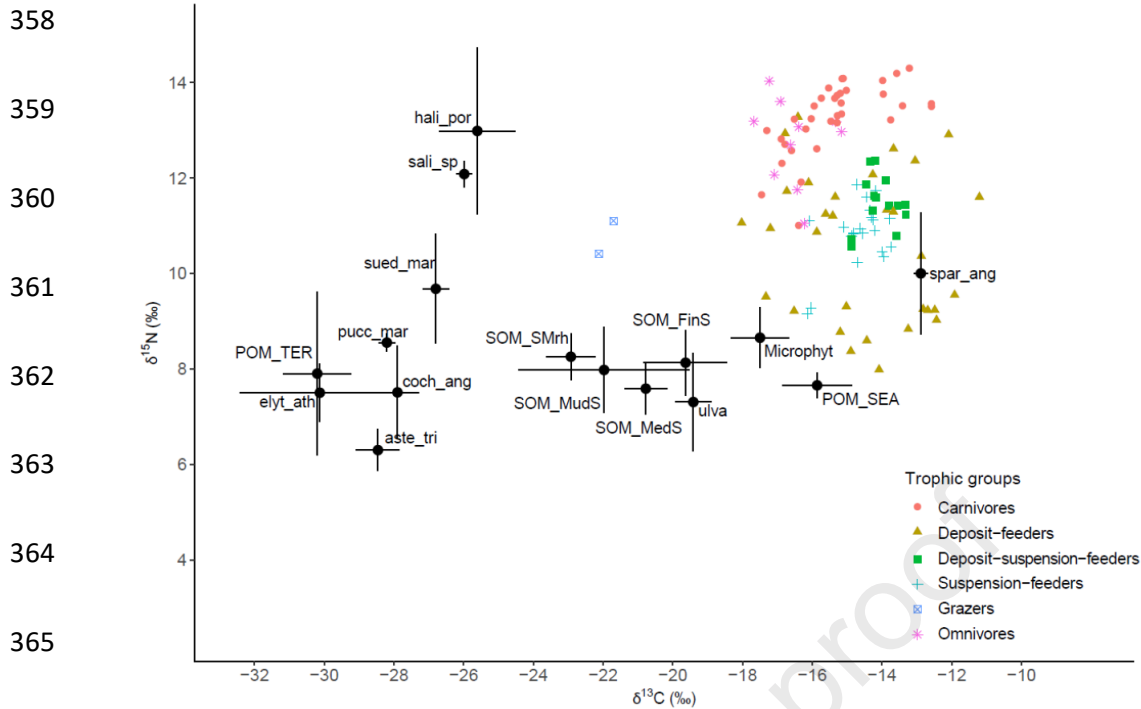
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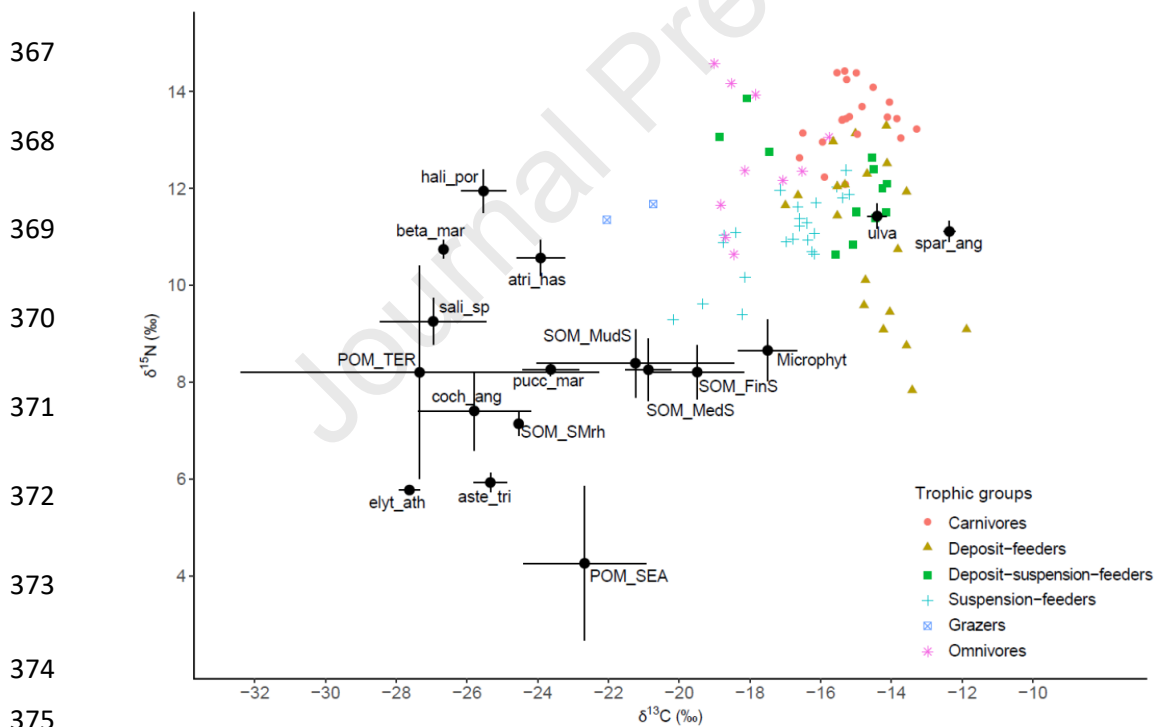
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A. March



B. September



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

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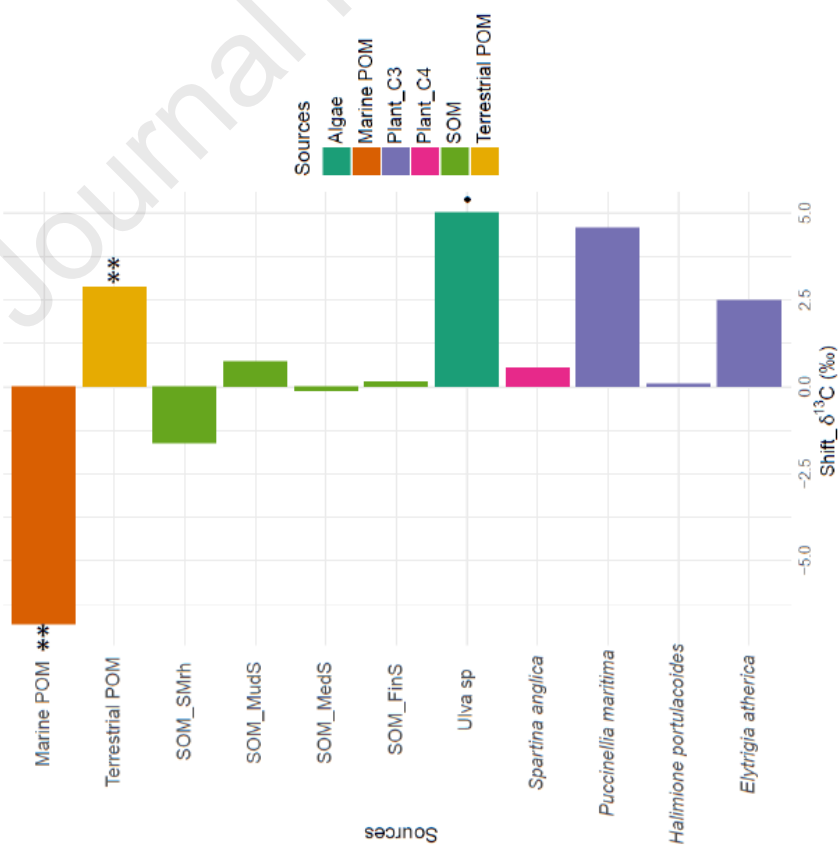
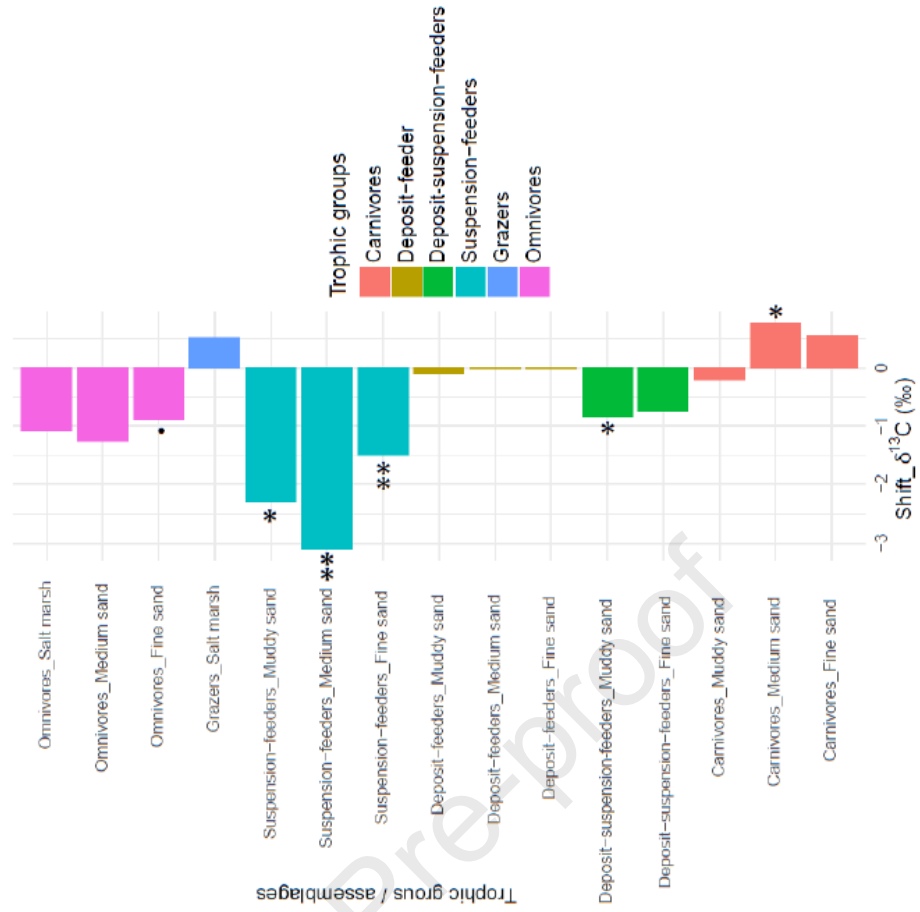
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A. Sources**B. Consumers**

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Figure 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

409 marsh creeks (SOM_SMrh), and muddy (SOM_MudS), fine (SOM_FinS), and medium (SOM_MedS)
 410 sands), *Ulva* sp, and the four main C3 (*Puccinellia maritima*, *Halimione portulacoides*, *Elytrigia atherica*)
 411 and C4 salt marsh plants (*Spartina anglica*). Consumers (B): consumers are represented by colors and
 412 temporal shift in $\delta^{13}\text{C}$ values is provided for each habitat. Mean significant differences tested with
 413 Permutation Student's t-tests are summarized as *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$). Mean
 414 differences near the significant level are also represented (., $P < 0.1$).

415

416 3.2 Consumers

417 3.2.1 Bay scale

418 Benthic consumers displayed a wide range of stable isotope compositions in both
 419 months (Table II). In March, mean $\delta^{13}\text{C}$ values ranged from -21.90 ± 0.30 ‰ in the
 420 grazer *O. gammarellus* to -12.58 ± 0.94 ‰ in the deposit-feeder *P. ulvae* (Figure 2,
 421 A.). Mean $\delta^{15}\text{N}$ values ranged from 8.81 ± 0.50 ‰ in the deposit-feeder *Bathyporeia*
 422 *sarsi* to 13.46 ± 0.73 ‰ in the carnivore *Sigalion mathildae*. In September, $\delta^{13}\text{C}$
 423 mean values ranged from -21.39 ± 0.93 ‰ still for *O. gammarellus*, to -11.88 ± 0.94
 424 ‰ in the deposit-feeder *Bathyporeia pilosa* (Figure 2, B.). $\delta^{15}\text{N}$ mean values ranged
 425 from 9.08 ± 0.50 ‰ in the deposit-feeder *Bathyporeia pilosa*, 14.37 ± 0.29 ‰ in the
 426 omnivore *Hediste diversicolor*. Omnivores and carnivores exhibited among the
 427 highest $\delta^{15}\text{N}$ values, while deposit-feeders and suspension-feeders among the lowest
 428 with an important variability (Figure 2).

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

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

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

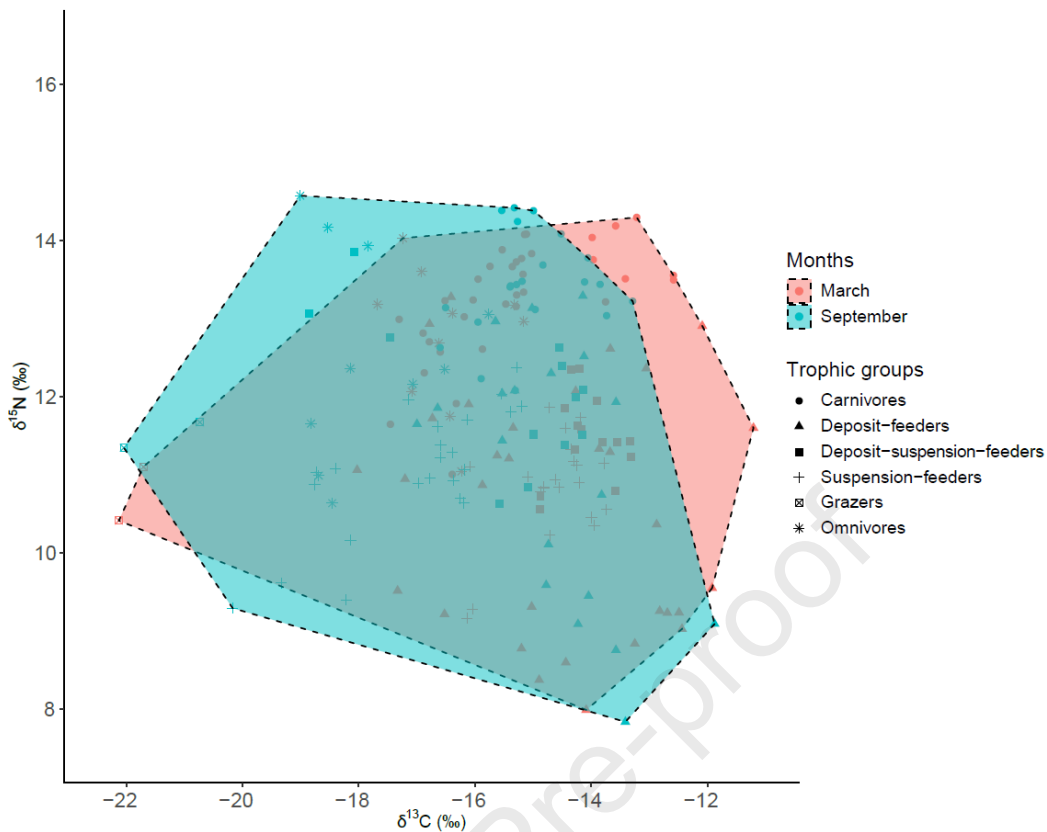
444 Total areas were similar in March (43.46 % 2) and September (46.64 % 2) (Table III,
 445 Figure 4). The food web centroid was characterized by a $\delta^{13}\text{C}$ decrease (-0.95‰) but
 446 the food web still strongly overlapped in March and September (Isotopic Similarity =
 447 0.728). CD remained similar over time (1.99 vs 2.02) revealing a stable trophic
 448 diversity. In September, species were more evenly distributed, decreasing the trophic
 449 redundancy as shown by the increase in NND (0.28 vs 0.36), SDNND (0.24 vs 0.31),
 450 and IEve (0.61 vs 0.80).

451

452 Table III: Food web structure properties at site (whole bay) and assemblage scale in March and
 453 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
 454 $\delta^{15}\text{N}$ centroids values (‰). CD: Mean distance to centroid. NND: Mean of the Euclidean distances to
 455 each species to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ centroids. SDNND: Standard deviation of nearest neighbor distance.
 456 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	
457	March	Whole bay	10.92	6.31	-15.30	11.41	1.99	0.284	0.24	43.46	0.73	0.61
458		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
459		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	2.57	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
460		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	15.079	0.74	0.90
461		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

462



463

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

468

469 3.2.2 Assemblage scale

470 3.2.2.1 Stable isotope composition

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

479 assemblages (Table III). $\delta^{15}\text{N}$ were significantly different between assemblages (F:
480 5.16, p -value < 0.01).

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

487

488 3.2.2.2 Structure

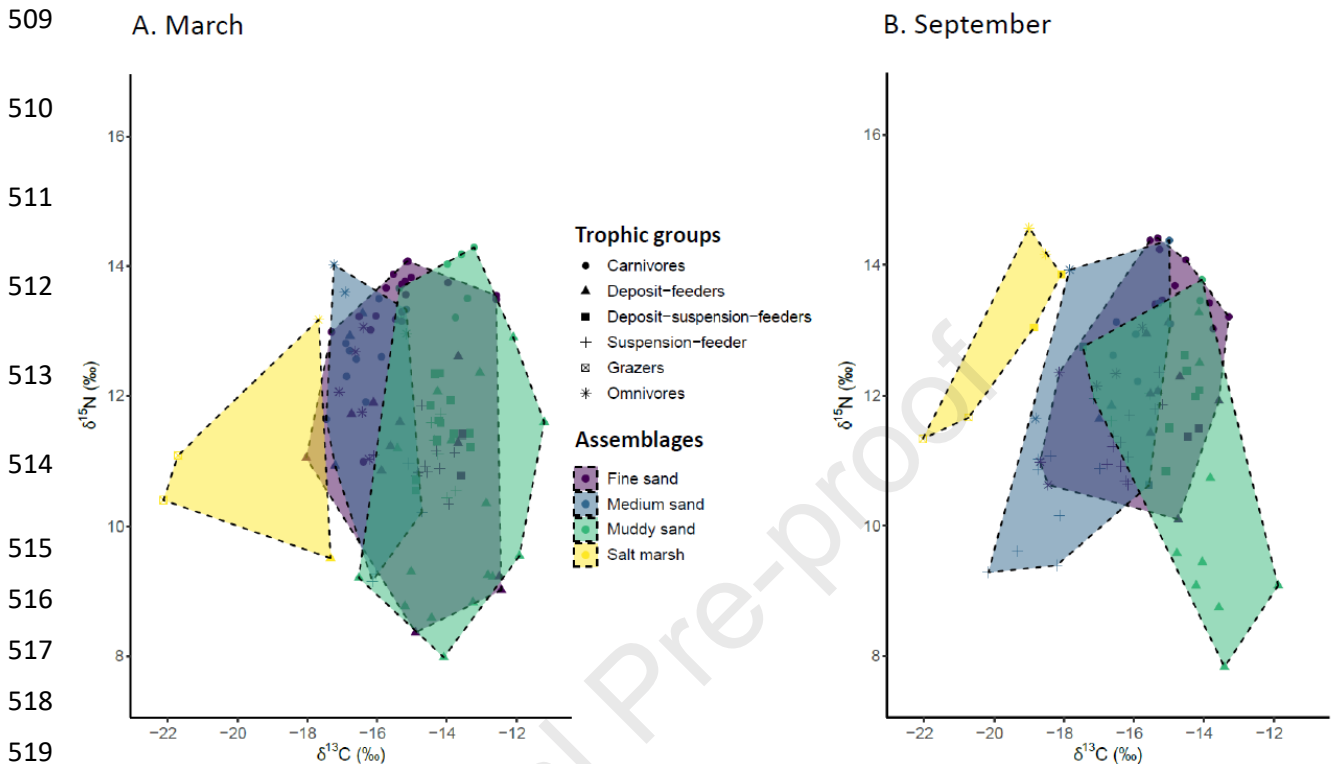
489 TA was higher in March for muddy (21.92 ‰²) and fine sands (23.16 ‰²) compared
490 to medium sands (9.12 ‰²) and salt marsh (9.59 ‰²) (Table III, Figure 5). In

491 September, the TA of the different sand assemblages were equivalent, following a
492 decrease in muddy and fine sands and an increase in medium sands.

493 Little convex hull overlap was observed between the salt marsh and other
494 assemblages. An overall decreasing $\delta^{13}\text{C}$ gradient from muddy ($\delta^{13}\text{C}$ centroids in
495 March: -13.93 ‰, September: -14.46 ‰), to fine (-15.01 ‰, -15.08 ‰) and medium (-
496 16.41 ‰, -17.34 ‰) sands assemblages led to a partial convex hull overlap. The
497 lowest isotopic similarity among sand assemblages were observed between muddy
498 and medium sands in both months (March: 0.139, September: 0.149). In March, fine
499 sands were more similar to muddy sands (0.607) than medium sands (0.351). In
500 September, overlap became more balanced (0.401 vs 0.441, respectively), revealing
501 more similarity in isotopic niche between assemblages. More specifically, dissimilarity
502 at the lower levels of the food web increased in September between muddy and
503 medium sands indicating some differences in stable isotopes values mainly implying
504 suspension-feeders (Figure 5B).

505 In sand assemblages, CD ranged from 1.40 to 1.76 in March, and from 1.50 to 1.91
506 in September. Species sampled in muddy and medium sands were more evenly

507 distributed in the δ -space in September as shown by the increase in NND, SDNND,
 508 IDiv and IEve values (Table III).



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

524

525

526 3.2.2.3 Trajectories of trophic groups

527 Significant decreases in $\delta^{13}\text{C}$ value between March and September were observed in
 528 muddy sands in suspension-feeders ($p=0.012$, Supplementary material, Appendix C)
 529 and deposit-suspension-feeders ($p=0.020$), and for suspension-feeders from fine
 530 ($p=0.002$) and medium sands ($p=0.002$) (Figure 3 and 7, A & B). A moderate
 531 increase in $\delta^{13}\text{C}$ value was observed in carnivores from medium sands ($p=0.022$).
 532 Contrasts among assemblages were observed in trophic groups stable isotope
 533 compositions between March and September. Medium sands suspension-feeders
 534 exhibited the longest trajectory (Euclidean distance= 3.12), while muddy sand

535 deposit-feeders were characterized by the lower shift (0.16) (Table IV, Figure 7, A &
 536 B). Trophic groups stable isotope compositions of consumers remained contrasted
 537 between assemblages but the temporal shifts of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, were similar for
 538 some trophic groups among assemblages. Suspension-feeders exhibited very similar
 539 directions ($283.90 \pm 3.70^\circ$) and among the highest changes (2.27 ± 0.68 , Euclidean
 540 distance), characterized by a ^{13}C -depletion and a moderate increase in $\delta^{15}\text{N}$. Similar
 541 temporal patterns across assemblages were also observed in deposit/suspension-
 542 feeders from muddy (0.95 , 297.24°) and fine (0.81 , 294.95°) sands, and in omnivores
 543 and carnivores from fine and medium sands respectively. Inversely, deposit-feeders
 544 exhibited contrasting trajectories in muddy (0.16 , 221.10°), fine (1.19 , 359.20°) and
 545 medium sands (0.63 , 182.00°) mainly influenced by shifts in $\delta^{15}\text{N}$. In salt marsh
 546 creeks, omnivores and grazers both exhibited singular trajectories.

547

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

Trophic groups	Assemblages	n	March		September		Trajectory metrics		
			$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	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	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

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A. Trophic trajectory diagram

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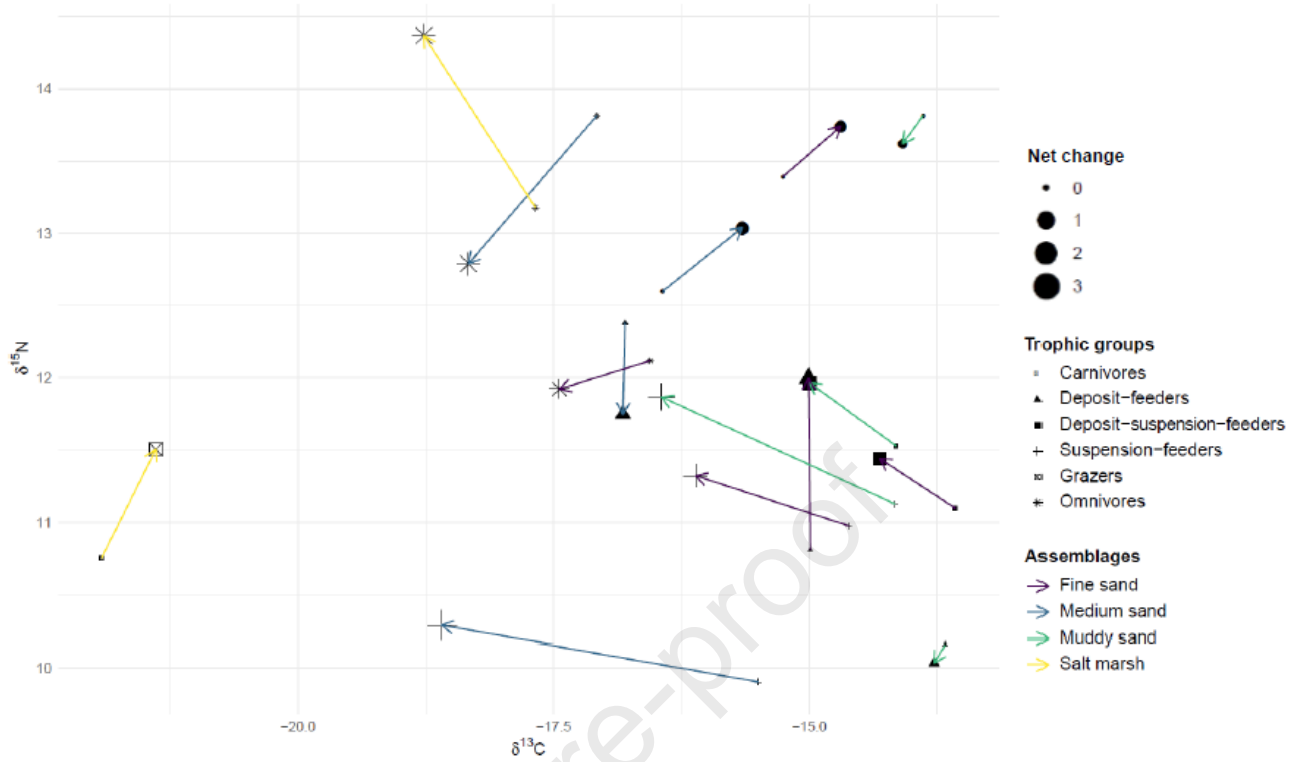
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B. Trophic trajectory roses

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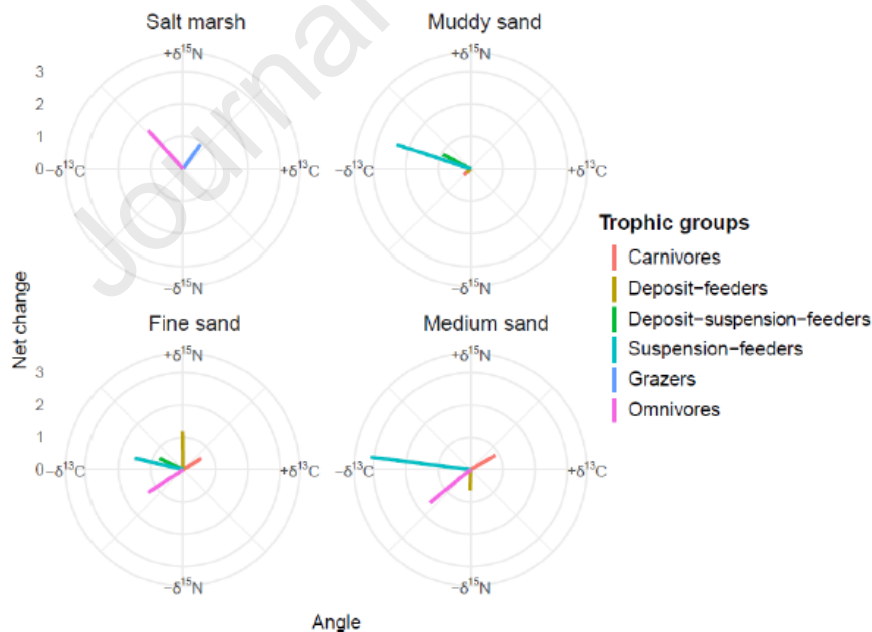
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572 Figure 6: Temporal trajectories of trophic groups between March and September. Stable Trophic
 573 trajectory diagram (A): Arrows represent trophic trajectory in the $\delta^{13}\text{C}/\delta^{15}\text{N}$ space between March and
 574 September for each trophic group in each assemblage (color). Length of arrows and size of dots
 575 corresponds to the net change (Euclidean distance) and inform about the magnitude of change.
 576 Different symbols correspond to trophic groups. Trophic trajectory roses (B): Angles α and net changes
 577 are represented in trophic trajectory rose for each trophic group (color) in each habitat (panel). Angle α
 578 values (0-360°) represent the nature of change in the δ -space (0-90°: $+\delta^{13}\text{C}$ and $+\delta^{15}\text{N}$; 90-180°: $+$
 579 $\delta^{13}\text{C}$ and $-\delta^{15}\text{N}$; 180-270°: $-\delta^{13}\text{C}$ and $-\delta^{15}\text{N}$; 270°-360°: $-\delta^{13}\text{C}$ and $+\delta^{15}\text{N}$).

580 **4. Discussion:**

581

582 **4.1 Spatio-temporal patterns as a potential alternative to track trophic links**

583 Consumers and their food sources stable isotope compositions are commonly used
584 to determine the composition diet. The use of isotopic mixing models is a way to
585 convert isotopic data into estimates of food source contributions from the various
586 components of a consumer's diet (Phillips et al., 2014). The use of source pools
587 characterized by distinct isotope values allows for the full exploitation of the mixing
588 model analysis. Inversely, a multiplicity of sources or strong similarity in their stable
589 isotope composition may decrease the relevance of mixing models in answering
590 questions about trophic relationships (Fry, 2013; Layman et al., 2012). When mixing
591 models are not correctly applied or when the data sets do not allow their proper
592 application (Fry, 2013; Phillips et al., 2014), conclusions may lead to an incomplete
593 picture. It may mislead the description of functioning and dynamics with potential
594 overstating conservation progress or misdirecting conservation actions.

595 The source pools described in this study were highly diversified and characterised by
596 strong overlap and high dynamics, potentially limiting the relevance of mixing models
597 and claiming for an alternative approach. The present study therefore focused on
598 stable isotope trajectories of sources and consumers to infer trophic relationships.

599 Spatial and temporal covariation of stable isotope composition between sources and
600 consumers has previously proven to be very useful in identifying the sources at the
601 base of food webs (Leclerc et al., 2013; Melville and Connolly, 2003; Vanderklift and
602 Wernberg, 2010).

603

604 **4.2 Saltmarsh influence on the sandflat food web**

605 The productivity of salt marshes during summer is high, reaching 30 tonnes of dry
606 matter per ha per year (Lefeuvre et al., 2000). The outwelling hypothesis states that
607 salt marshes export organic matter, dissolved carbon and nutrients to tidal adjacent

608 habitats from tidal channels to estuaries and coastal ocean (Odum, 1968; Teal,
609 1962). The influence of salt marsh vegetation on food webs is highly variable,
610 ranging from almost insignificant (Christianen et al., 2017), to very important, and
611 reflected in the stable isotope composition of marshes inhabiting consumers
612 (Nordström et al., 2014; Riera et al., 1999), or adjacent habitats assemblages
613 (Conway-Cranos et al., 2015).

614 In the study area, salt marshes are characterised by good conservation status but
615 only cover a limited area [125 ha, Sturbois and Bioret (2019)], compared to other
616 comparable coastal bays of the French Atlantic coast, such as the bay of Mont-Saint-
617 Michel [4000 ha, Lafage et al., (2021)], the bay of Seine [1200 ha, Lafage et al.,
618 2021)], or the bay of Aiguillon [1100 ha, Joyeux et al., (2017)]. Trophic connectivity
619 relies on the relative proportion of allochthonous and autochthonous resources rather
620 than only on asymmetric production among habitats, especially when the nutritional
621 value of allochthonous sources (i.e. salt marsh detritus) is lower than local, fresh
622 sources (Mann, 1982). Differences in the proportion of resources result from
623 interaction among productivity, permeability, and transport vectors that lead to many
624 states of trophic connectivity (Domingos and Lana, 2017).

625 The influence of C3 plants was limited to the grazer *O. gammarellus*, the omnivore *H.*
626 *diversicolor* and the deposit-suspension-feeder *Scrobicularia plana* inhabiting the
627 muddy salt marsh creeks. *O. gammarellus* is a known consumer of salt marsh
628 detritus [*H. portulacoides* in particular (Joyeux et al., 2017; Laffaille et al., 2001)]. *H.*
629 *diversicolor* is a very generalistic omnivore able to: feed on sediment,
630 microphytobenthos, macroalgae, detritus and plant material; predate small
631 invertebrates; suspension feed by secreting and using a mucobag as a filter when
632 drawing down particles in its burrow; and garden by sprouting seeds (Durou et al.,
633 2007; Scaps, 2002; Zhu et al., 2016).

634 Only a few evidences have been reported in the use of salt marsh vegetation in the
635 study area: juveniles of *Dicentrarchus labrax* were proven to feed on ^{13}C -depleted
636 preys inhabiting salt marshes (Sturbois et al., 2016), or *Branta bernicla*, on
637 *Puccinellia maritima* (Ponsero et al., 2009b). As no benthic species displayed such a
638 ^{13}C depletion, which would be consistent with the significant assimilation of such
639 sources further on the shore, no evidence was found that salt marsh plants support
640 the benthic food webs in unvegetated sandy habitats. The influence of the C4 plant
641 *S. anglica* was also discarded according to its ^{13}C enriched values. The capacity of
642 salt marsh plants to fuel intertidal benthic habitat seems limited, especially for
643 macrofauna species which exhibit limited mobility in a large flat characterised by
644 megatidal and dispersive conditions.

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

651 Salt marsh muddy creeks are characterized by a large production of benthic diatoms.
652 Mulletts (*Chelon spp.*) feeding on biofilm and associated meiofauna contribute to the
653 exportation pathway of the biofilm (Carpentier et al., 2014). Regularly reach by the
654 tide at high tide, salt marshes are submerged when water height exceeds 10.70 m,
655 which represents 45% of the tide cycles (76% for associated creeks) (Sturbois et al.,
656 2016). Megatidal conditions associated with strong currents may also contribute to
657 the effective resuspension of sediments and microphytobenthos (personal
658 observation), exporting benthic diatoms in the water column and further away in the
659 bay. The importance of resuspended microphytobenthos as a major food source for

660 macrobenthos in mudflat environments is a long known mechanism (De Jonge and
661 Van Beuselom, 1992; Riera and Richard, 1996).

662

663 **4.3 Sources supporting the food web: limited influence of seasonal *Ulva* spp.** 664 **blooms**

665 The year 2019 was characterised by important *Ulva* spp. biomass which
666 progressively accumulated during summer (Supplementary materials, Appendix A).
667 In the close bay of Douarnenez, Quillien et al. (2016) found evidence of a direct
668 consumption of *Ulva* spp. fragments by a few species (*Owenia fusiformis*, *Acrocnida*
669 *spatulispina*), and an indirect influence on the whole food web through the isotopic
670 modification of SOM and POM due to *Ulva* spp. presence. On the western coast of
671 Korea, Park et al. (2016) showed that blooming green macroalgae support an
672 intertidal macrobenthic food web with a certain variability depending on both feeding
673 strategies of consumers and resource availability. From field experiments with
674 varying macroalgal mat thickness (0.5, 1.5 and 4 cm) over eight weeks, Green and
675 Fong (2016) quantified the effects on macrofauna on a Californian lagoon mudflat.
676 They found that the predominant mechanism triggering negative effects on
677 macrofauna for the highest macroalgal biomasses was the development of anoxic
678 conditions. Sulfide accumulation for the 4 cm treatment reduced ecosystem
679 functioning, favouring subsurface deposit feeding such as capitellids.
680 *Ulva* spp. was ^{13}C - and ^{15}N -enriched in September compared to March, which
681 provided an opportunity to investigate the potential role of *Ulva* spp. in the food web.
682 Our results reveal that the influence of *Ulva* spp. on the entire food web can be
683 considered as low, regarding the limited area concerned by stranded *Ulva* spp. in
684 February (12 ha), and the absence of such isotopic enrichment at the community
685 scale in September. For example, *A. spatulispina* sampled in September were ^{13}C -
686 depleted, suggesting no *Ulva* spp. influence and contrasting with the results of
687 Quillien et al. (2016). The moderate ^{13}C - and ^{15}N -enrichment observed for carnivores

688 may reveal accidental ingestion of *Ulva* fragments when hunting and feeding on
689 preys, but the low magnitude of the trophic trajectory suggest a very limited influence.
690 Such a low influence of *Ulva* spp. in the diet and stable isotope composition of
691 marine crustaceans has also been demonstrated by experimental (Karez et al., 2000;
692 Salathé and Riera, 2012) and *in situ* (Adin and Riera, 2003) studies. The contrast
693 with the results obtained by Quillien et al. (2016), Park et al. (2016) and Green and
694 Fong (2016), may be explained by the mega-tidal conditions which characterize the
695 study area. In the bay of Saint-Brieuc, tides are a strong driving factor. Daily
696 resuspension and redistribution of algal mats and limited long-term static
697 accumulation of algae make potential anoxic episodes restricted to very limited zones
698 (i.e. beaches on the upper shore), where *Ulva* are all the more collected by local
699 authorities as part of precautionary sanitary measures (e.g. 12 682 tons has been
700 collected in 2021). This phenomenon potentially limits the integration of *Ulva* spp. in
701 the food web. Furthermore, the bay of Saint-Brieuc shelters benthic producers on
702 muddy and muddy sand habitats, which contrasts from the sandy beaches located in
703 the bay of Douarnenez.

704 Marine POM and MPB displayed stable isotope compositions which were the most
705 likely to represent the actual basis of food webs within the different habitats,
706 regarding $\delta^{13}\text{C}$ ranges displayed by the benthic communities . Marine POM was the
707 only source exhibiting a significant ^{13}C -depletion between March and September,
708 which was also observed for suspension-feeders from all habitats, as well as by
709 mixed deposit/suspension-feeders and some omnivores. In contrast, the low shift in
710 $\delta^{13}\text{C}$ values of deposit-feeders between March and September suggests a low
711 temporal variability in the composition of benthic producers. This is also in
712 accordance with the low shift observed for SOM values, especially in fine and
713 medium sands. Deposit-feeders are often quite, or even very, selective with regard to
714 the total SOM (Levinton, 1989), which is a composite source by definition, so they

715 only use a portion of it, and benthic diatoms represent a particularly easy-to-use
716 source with a high food quality within the SOM.
717 Christianen et al. (2017) reported that energy in the Wadden sea ecosystem is
718 mainly provided by locally produced organic matter and in a lesser extent by pelagic
719 producers. Such contribution of MPB has also been highlighted, at lower geographic
720 scales in salt marsh consumers in the Mont Saint-Michel bay (Créach et al., 1997),
721 1997), and for cockles in Marennes-Oléron Bay (Kang et al., 1999). Other intertidal
722 studies also revealed the fuelling of higher trophic levels by MPB and pelagic primary
723 production (van Oevelen et al., 2006). In the bay of Saint-Brieuc, where muddy
724 habitats are limited (64 ha), our results suggest that the food web is mainly fuelled by
725 pelagic producers and, to a lesser extent, by benthic producers. However, salt marsh
726 muddy creeks could also support a part of the MPB production, in addition with
727 muddy sands. Such assumption will require further investigations to be accurately
728 quantified (Méléder et al., 2020; Morelle et al., 2020).

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

734

735 **4.4 Spatial patterns in benthic-pelagic coupling**

736 Large scale spatial heterogeneity in the carbon stable isotope composition of
737 consumers has been observed by Christianen et al. (2017) in the Wadden Sea for
738 species that forage either on benthic or pelagic sources. In a large part of the
739 Wadden sea, a dominant use of pelagic food sources was observed for the common
740 cockle suspension-feeder *Cerastoderma edule*, while the use of benthic producer
741 was suggested for some spatially limited areas. Conversely, for the Baltic clam

742 *Limecola balthica*, which is a facultative deposit and suspension-feeder, $\delta^{13}\text{C}$
743 indicated a high benthic contribution to its diet in most of the flat, contrasting with a
744 dominant pelagic contribution in some limited areas.

745 In our study, spatial patterns have been revealed at the scale of trophic groups, with
746 higher $\delta^{13}\text{C}$ values for suspension-feeders, deposit-suspension-feeders and
747 carnivores in muddy and fine sands compared to medium sands. They were
748 maintained between March and September and confirmed by the correlation between
749 $\delta^{13}\text{C}$ values and emersion time for some trophic groups. In addition, some contrasted
750 temporal trophic trajectories among habitat were evidenced. Trajectory metrics (net
751 changes and angle α) revealed a congruent negative shift in marine POM and
752 suspension-feeders $\delta^{13}\text{C}$ values between March and September. However, while
753 direction in the δ space was similar suspension-feeders at assemblage scale,
754 differences were observed in net changes values. This contrasting pattern in the
755 magnitude of change suggests a decreasing influence of pelagic sources in the diet
756 of suspension-feeders from muddy and sandy habitats compared to medium sands.
757 Deposit-suspension-feeders showed similar direction but lower net changes than
758 suspension-feeders, confirming both their higher dependence to benthic primary
759 producers and their ability to feed on pelagic producers. The low variability of
760 deposit-feeder $\delta^{13}\text{C}$ values was in accordance with the temporal stability observed for
761 sedimentary organic matter in medium sands and suggested a low temporal
762 variability in the stable isotope composition of MPB.

763 Lower net changes exhibited by suspension-feeders in muddy and fine sand habitats
764 suggest a major resuspension of MPB in the water column as already shown in
765 different intertidal areas (De Jonge and Van Beuselom, 1992; Liénart et al., 2017;
766 Riera and Richard, 1996; Sauriau and Kang, 2000; Underwood and Chapman,
767 1998). Suspended particulate organic matter corresponds to a dynamic mixture of
768 pelagic and benthic algae due to the resuspension of MPB. Microphytobenthos

769 growth is favoured in muddy and muddy sands habitats (Morelle et al., 2020), and its
770 spatio-temporal distribution is driven by highly variable physical and biological factors
771 (Mélédér et al., 2020). MPB resuspension is known to be favoured by hydrodynamics
772 and bioturbation activities of some macrofauna species such as *C. edule*
773 (Rakotomalala et al., 2015). The bay of Saint-Brieuc is characterized by megatidal
774 conditions and high density of *C. edule*, reaching 2000 ind.m² in muddy sands. MPB
775 can be easily resuspended at relatively low current velocities (~10 cm s⁻¹) on silty
776 sediment (Blanchard et al., 1997; Kang et al., 2015; Ubertini et al., 2015).
777 Resuspension is increased by the coverage and the important dynamics of tidal
778 channels (Sturbois et al., 2021a), which may contribute to organic matter fluxes.
779 Emersion time regulates the trophic availability of MPB for some consumers
780 (suspension and surface deposit feeders). Hydrodynamics and tides favour the
781 trophic connectivity between muddy sand and fine sand habitats located at lower
782 levels through the exportation of microphytobenthos in the water column. However,
783 the exportation of the tidally resuspended MPB seems limited to fine sand habitats
784 and suggests spatial contrast in benthic-pelagic coupling. De Jonge and Van
785 Beuselom (1992) and Riera and Richard (1996) found similar results, demonstrating
786 that the influence of the MPB exported in the water column is limited to close
787 adjacent habitats.

788

789 **4.5 Small spatial scale variability in food web structure.**

790 Despite a slight increase in IEve in relation to the ¹³C-depletion of suspension and
791 deposit-suspension-feeders, the stability of structural properties and the strong
792 overlap observed at site scale between March and September highlight the temporal
793 stability of the system. Dissimilarity among assemblages was strongly influenced by
794 the $\delta^{13}\text{C}$ decreasing gradient of consumers from muddy to fine and medium sands
795 assemblages, while no such pattern was observed for $\delta^{15}\text{N}$. This gradient illustrates
796 the spatial variability in the benthic pelagic coupling, with a higher influence of MPB

797 in the upper level compared to low shore habitats. The decrease in the similarity
798 between the low levels of the muddy and medium sands observed between March
799 and September (in relation with the trophic trajectory of suspension-feeders in
800 medium sands) highlights the two main energy pathways supported by pelagic and
801 benthic producers.

802 Quillien et al. (2016) showed an overall simplification of community-wide food web
803 structure and functioning in sandy beach harbouring green tides. They notably
804 highlighted a significant community-wide shift in $\delta^{13}\text{C}$ over time progressively splitting
805 up into two distinct isotopic niches. A linear arrangement of trophic web components
806 indicated a single carbon pathway where *Ulva* spp. mats were present on the shore.
807 No such simplification was observed at site or assemblages scale in the study area.
808 Conversely, the selected indices of trophic structure and functioning were stable or
809 increased during the year. Assemblages still overlapped over time and no overall ^{13}C
810 enrichment of consumers was observed in accordance with $\delta^{13}\text{C}$ composition of
811 *Ulva*. Overall, the temporal consistency observed in the food web structure in the
812 different habitats confirm that the summer *Ulva* bloom did not play a major role in the
813 trophic functioning off the bay of Saint-Brieuc.

814

815 **4.6 Implications of food web dynamics for sampling strategy**

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

824 In the Wadden sea, Christianen et al. (2017) suggested that different factors are
825 potentially involved in the spatial heterogeneity of food web $\delta^{13}\text{C}$ values: spatial
826 variability in benthic production; differential consumption of benthic and pelagic
827 producers; and/or the differential contribution of resuspended benthic primary
828 producers for consumers feeding entirely on pelagic producers. Fine scale variations
829 in the local environment may also influence food web properties (Ouisse et al., 2011).
830 Our study highlights these spatio-temporal variations in the stable isotope
831 compositions of sources and consumers. The different degrees of trophic
832 connectivity with a low influence of salt marshes and variations in benthic-pelagic
833 coupling in relation with the distribution and the resuspension of MPB confirm the
834 importance of sampling food webs at large spatial and temporal scales for a better
835 integration of dynamics.
836 Similarly, differences in the influence of *Ulva* spp. on benthic food web properties
837 between the Bay of Saint-Brieuc and the sandy beaches of Douarnenez indicate that
838 effects on ecosystems are not spatially consistent at regional scale, and claims for
839 local studies integrating local physical and biological driven factors.

840

841 **4.7 Food webs studies: a baseline for conservation process**

842

843 As the first attempt to characterize intertidal benthic food webs of the bay of Saint-
844 Brieuc, this study provides valuable information for managers about the functioning
845 and energy pathways supporting the specific benthic communities. First, the
846 influence of salt-marsh plants on benthic macrofauna is limited. Such result remains
847 fundamental for the consideration of trophic functioning at larger scale in the bay, but
848 does not question the value of salt marsh already shown for juveniles of some fish
849 species (Carpentier et al., 2014; Joyeux et al., 2017; Lafage et al., 2021; Sturbois et
850 al., 2016) or birds (Ponsero et al., 2009b, 2019). Second, the seasonal increase in
851 biomass of *Ulva* spp. does not influence the functioning of the local benthic food

852 webs. This result was unexpected given that two local bird species, *Mareca penelope*
853 and *Branta bernicla*, feed on this algae (Ponsero et al., 2009b). These results pointed
854 that green tides may represent a trophic cul-de-sac for the benthic macrofauna
855 inhabiting the bay of Saint-Brieuc.

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

862 Despite all habitats are used by birds, muddy and fine sand assemblages are the
863 most available due to low emersion time of medium sands (Ponsero et al., 2016;
864 Sturbois et al., 2015). Our study highlights that waders trophic resource (i.e. benthic
865 invertebrates) is supported by pelagic and benthic producers with a decreasing
866 inshore/offshore gradient of MPB influence. The bay of Saint-Brieuc is characterized
867 by *C. edule* fishing grounds exploited by professional and recreational fishers and
868 muddy habitats, where young cockles can feed on MPB (Sauriau and Kang, 2000),
869 are known to be favourable areas for settlement (Ponsero et al., 2009a).

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

875 **5. Conclusion**

876 Results highlighted that the benthic trophic network is, most likely, based on
877 phytoplankton, microphytobenthos and SOM. The trophic connectivity between salt
878 marsh and benthic habitats within the bay was limited to some macrofauna species

879 inhabiting muddy creeks within the salt marsh. Unexpectedly, the influence of *Ulva*
880 spp. in the trophic functioning of the different assemblages appeared quite limited.
881 Spatial patterns illustrates the constancy of the spatial variability in the benthic
882 pelagic coupling, with a higher influence of microphytobenthos in the upper level
883 compared to low shore assemblages. This first attempt to characterize intertidal
884 benthic food web constitutes a relevant baseline for the conservation of the bay of
885 Saint-Brieuc where a National nature reserve has been created in 1998 for the
886 conservation of overwintering birds. The spatio-temporal patterns of the benthic food
887 web also confirms the importance to consider food web variability at spatial and
888 temporal scales from sampling designs to data analysis. The ability of the stable
889 isotope trajectory analysis framework to highlight spatio-temporal patterns was also
890 demonstrated.

891

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903

904 **Supplementary material:**

905 **Appendix A:** *Ulva* cover between February and October

- 906 **Appendix B:** List of species sampled in the different assemblages
- 907 **Appendix C:** Permutation Student's t-test for stable isotope compositions between
908 March and September
- 909
- 910 **Appendix D:** Frequency distribution of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of all organisms sampled in
911 March and September in the four assemblages
- 912

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

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

	$\delta^{13}\text{C}_{\text{rg}}$	$\delta^{15}\text{N}_{\text{rg}}$	$\delta^{13}\text{C}_{\text{ctr}}$	$\delta^{15}\text{N}_{\text{ctr}}$	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	2.57	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

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	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

The image contains two tables. The first table is a large grid with 20 rows and 4 columns. The second table is a narrow vertical table with 20 rows and 1 column. Both tables are empty.

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The diagram consists of two parts. The left part is a grid with 8 rows and 4 columns, formed by 9 horizontal lines and 5 vertical lines. The right part is a single column with 8 rows, formed by 9 horizontal lines and 2 vertical lines.

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MEDIUM SANDS



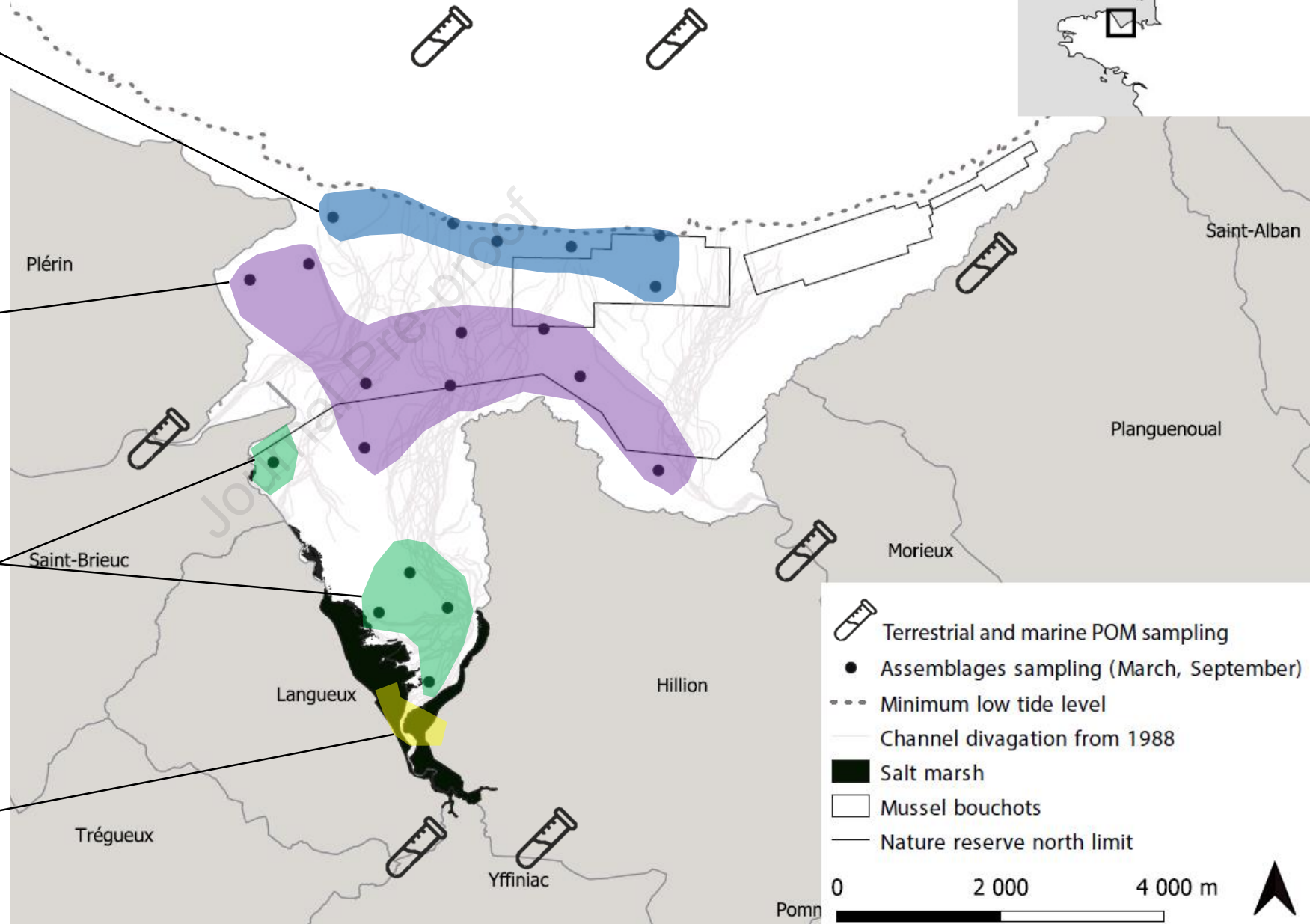
FINE SANDS



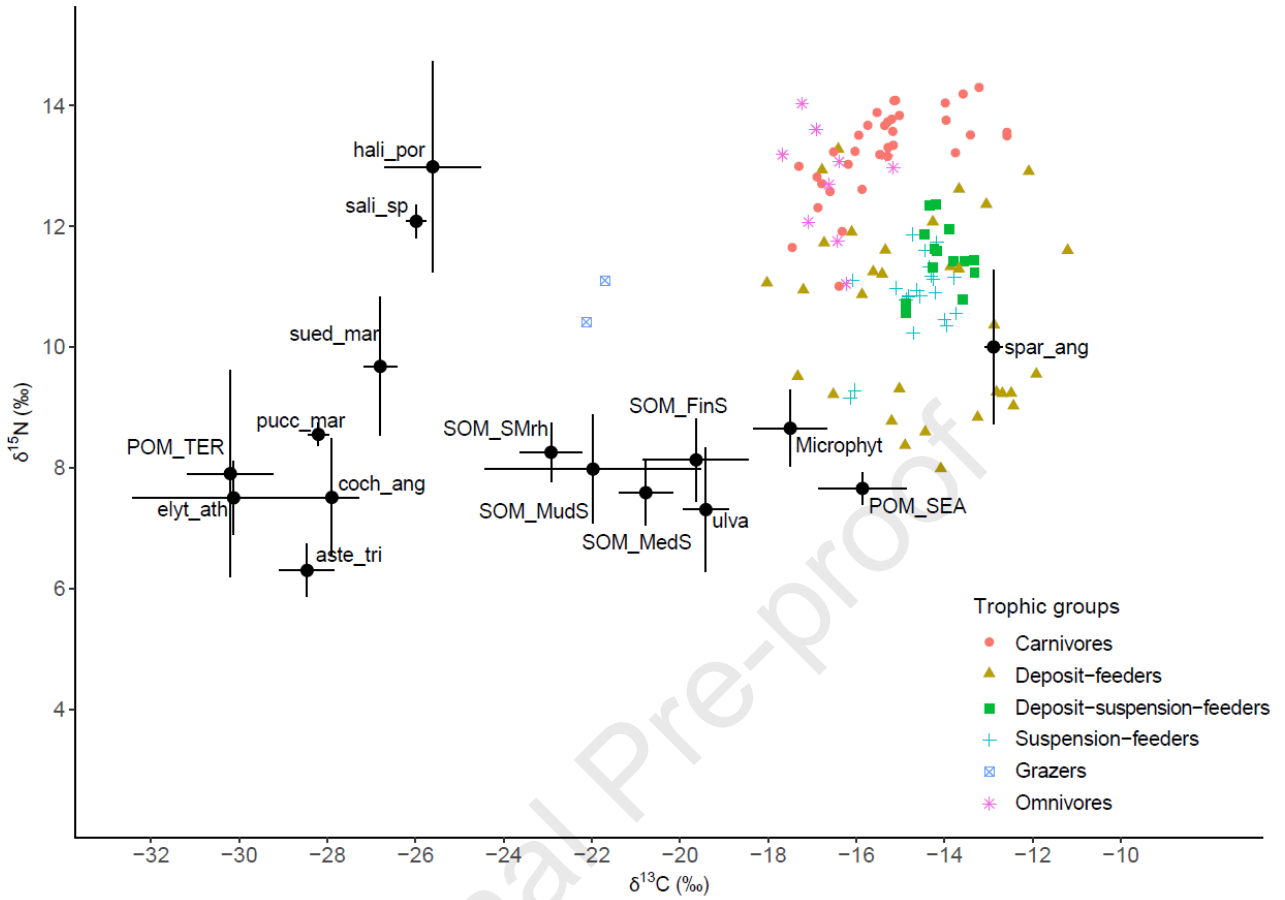
MUDDY SANDS



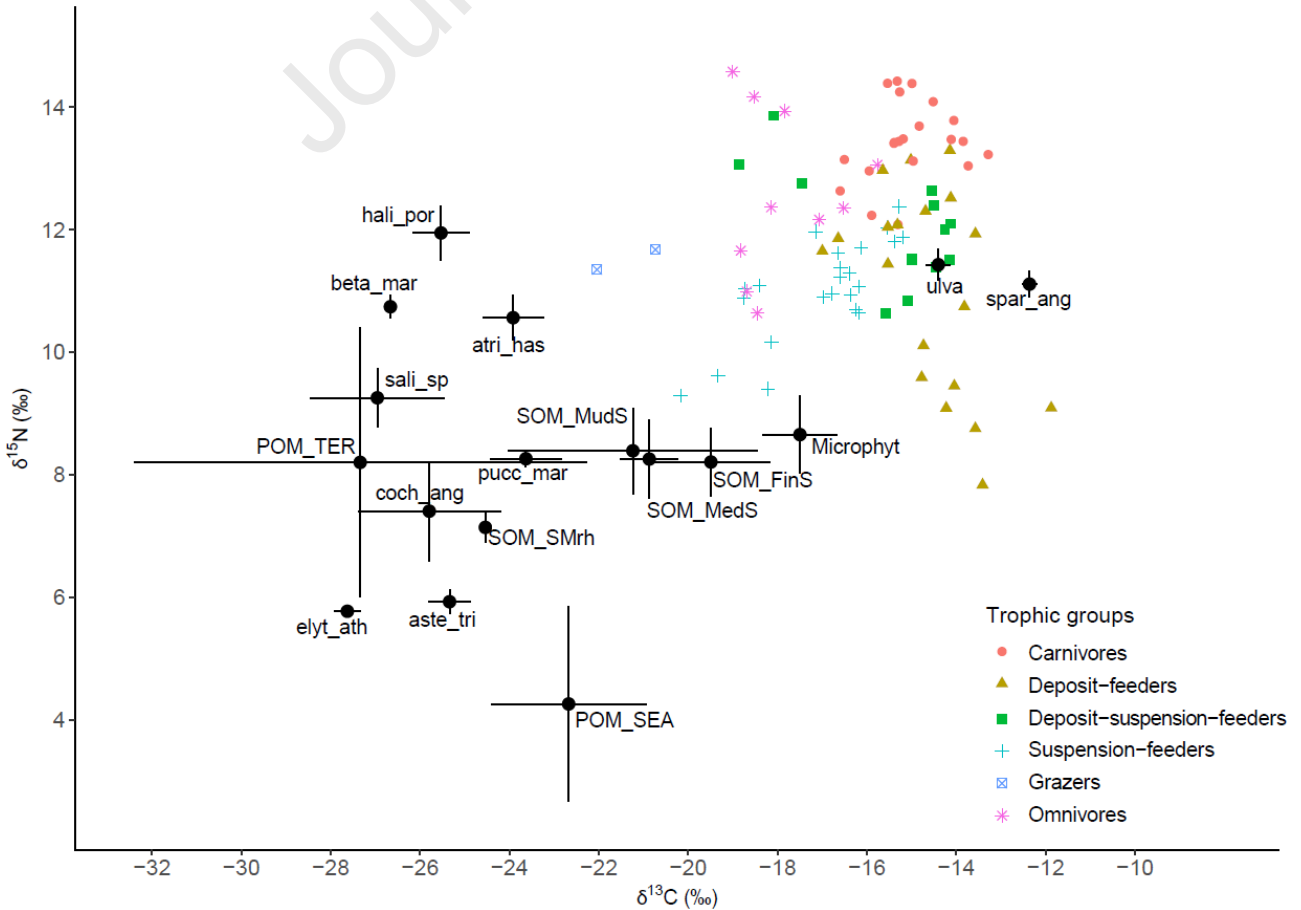
SALT MASH CREEKS



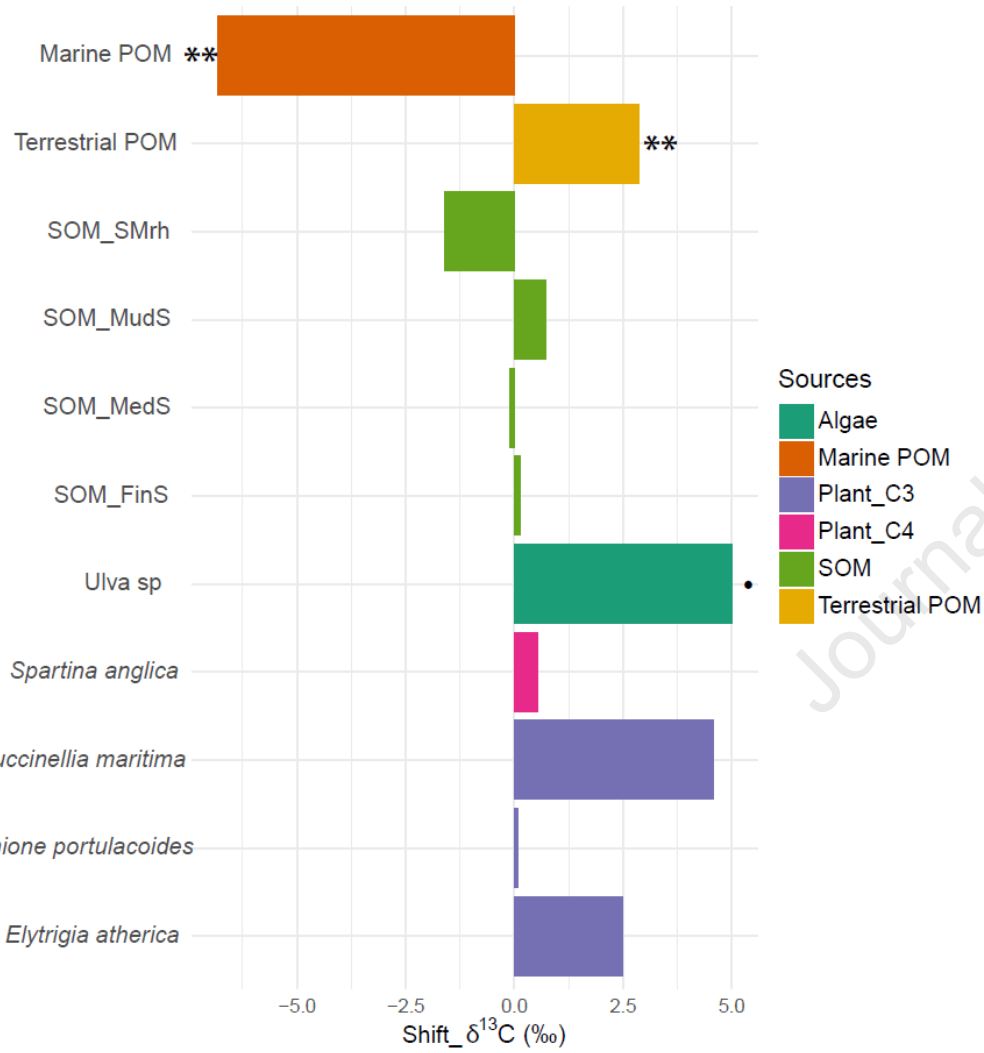
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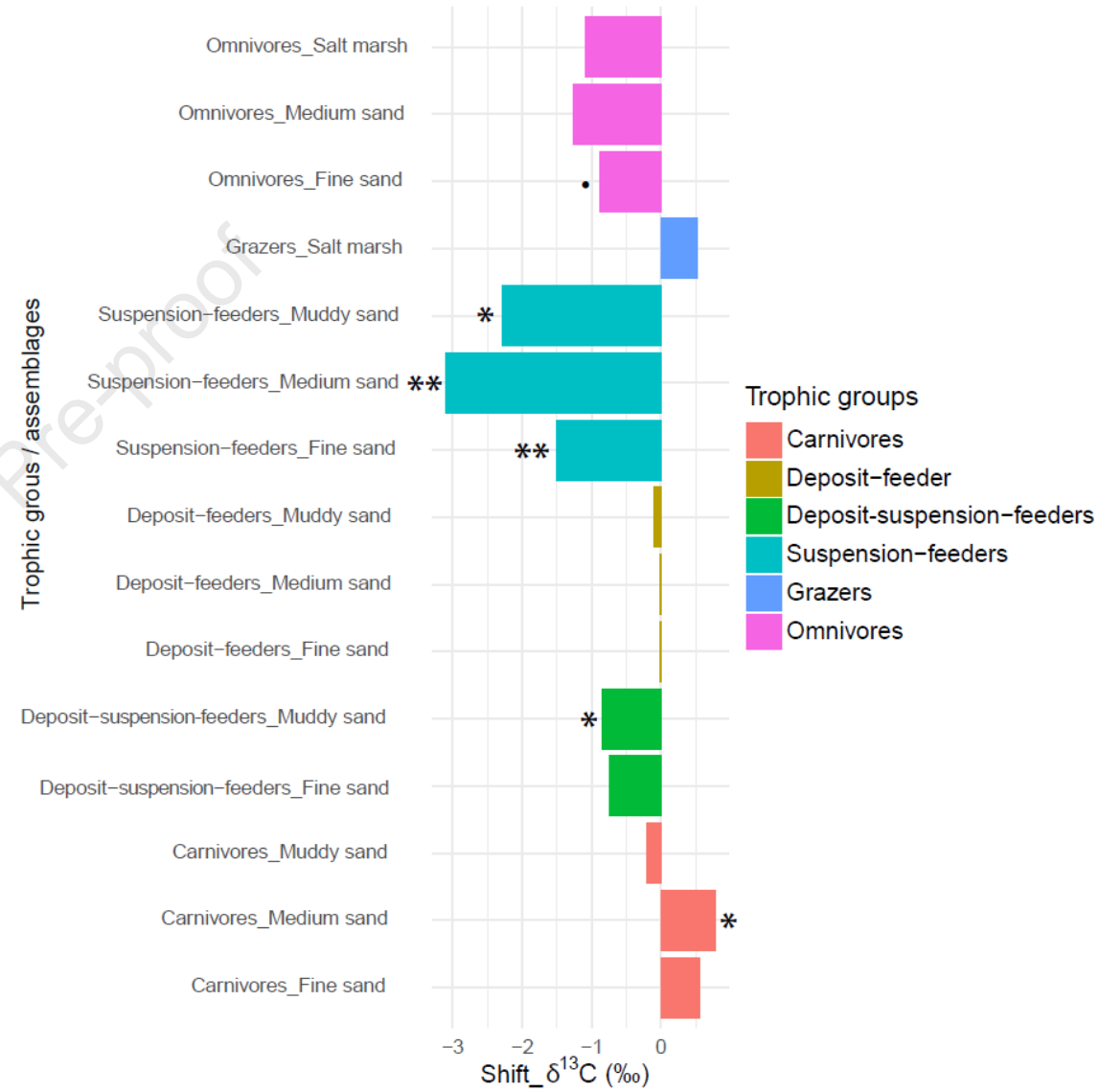
B. September

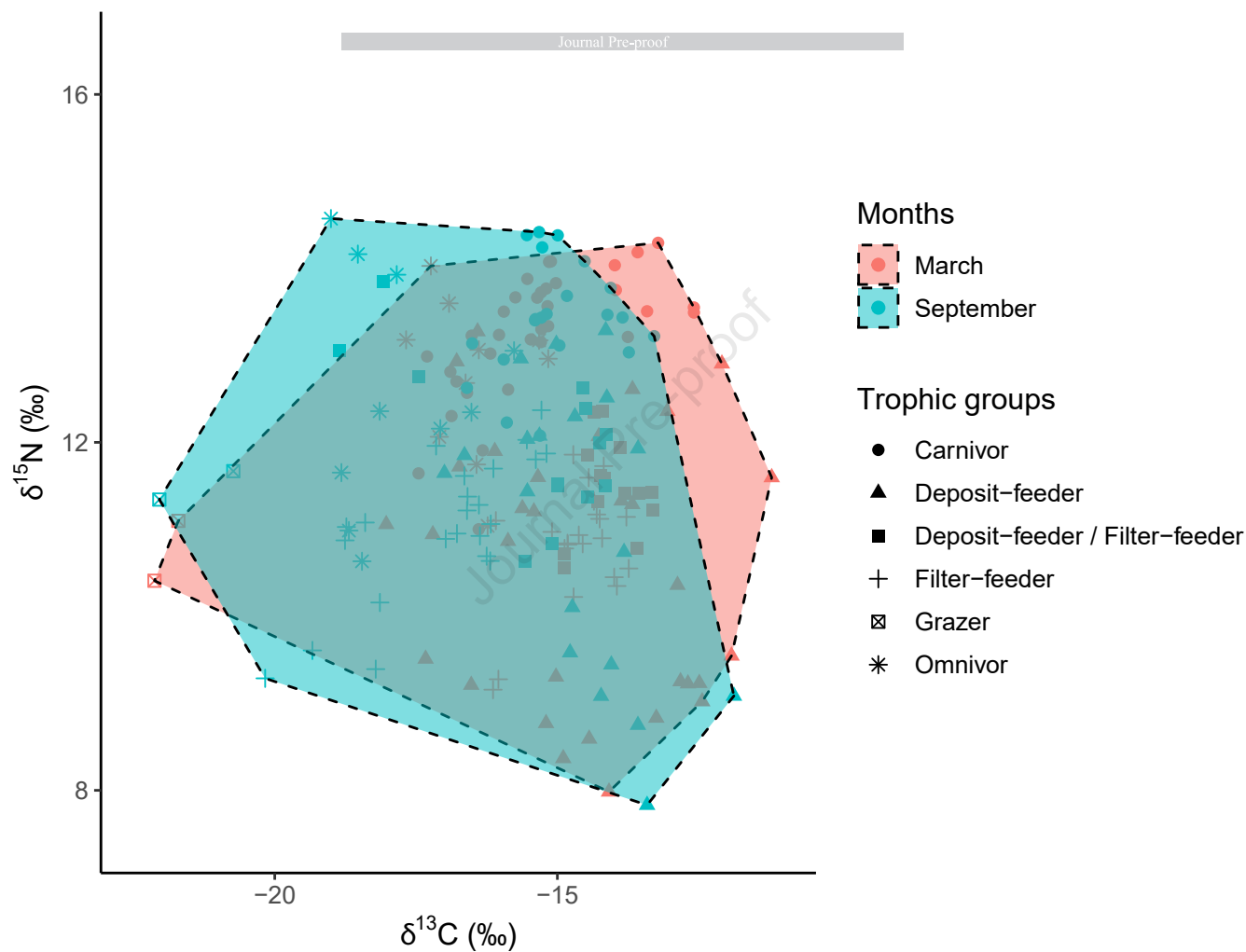


A. Sources

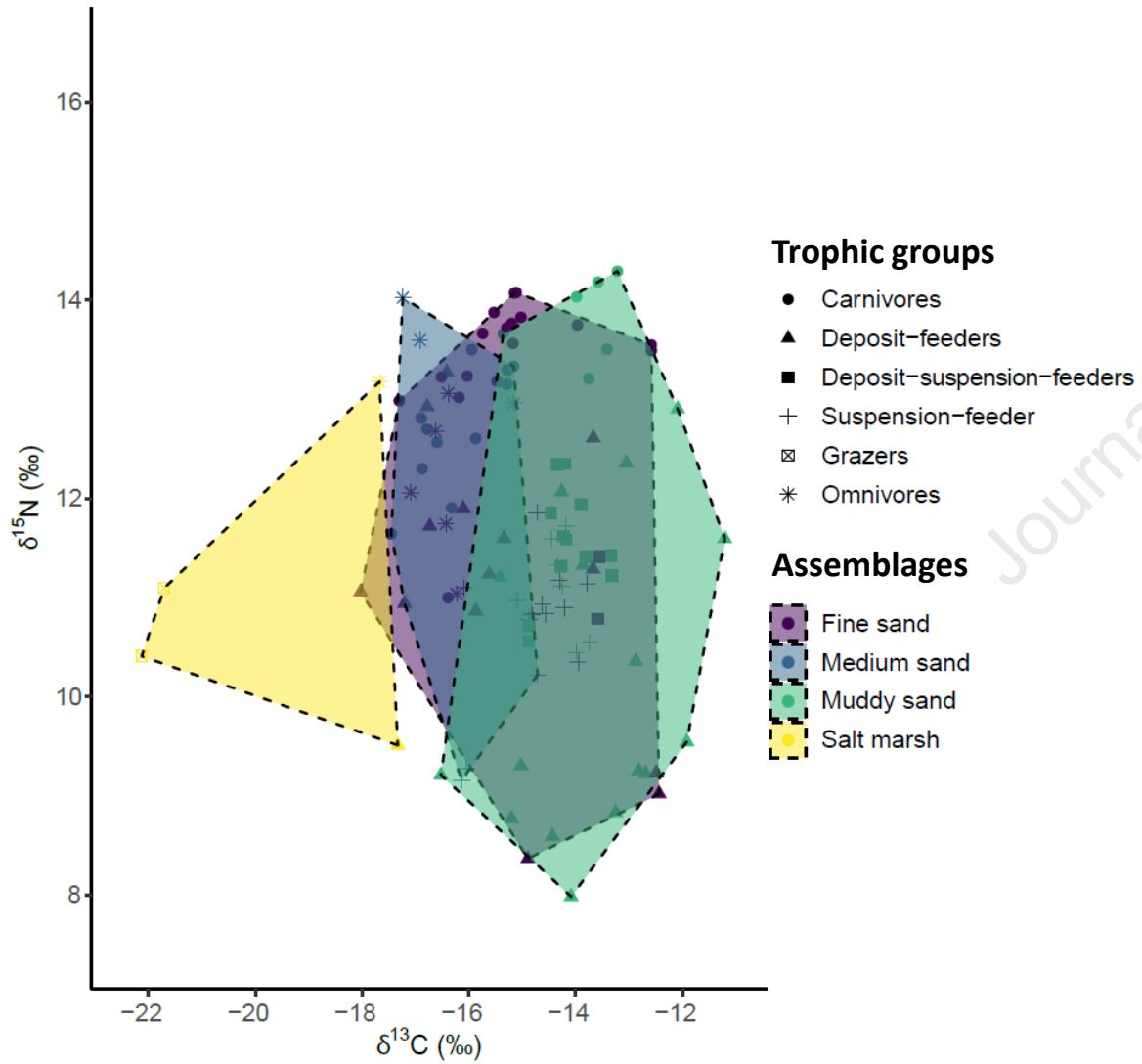


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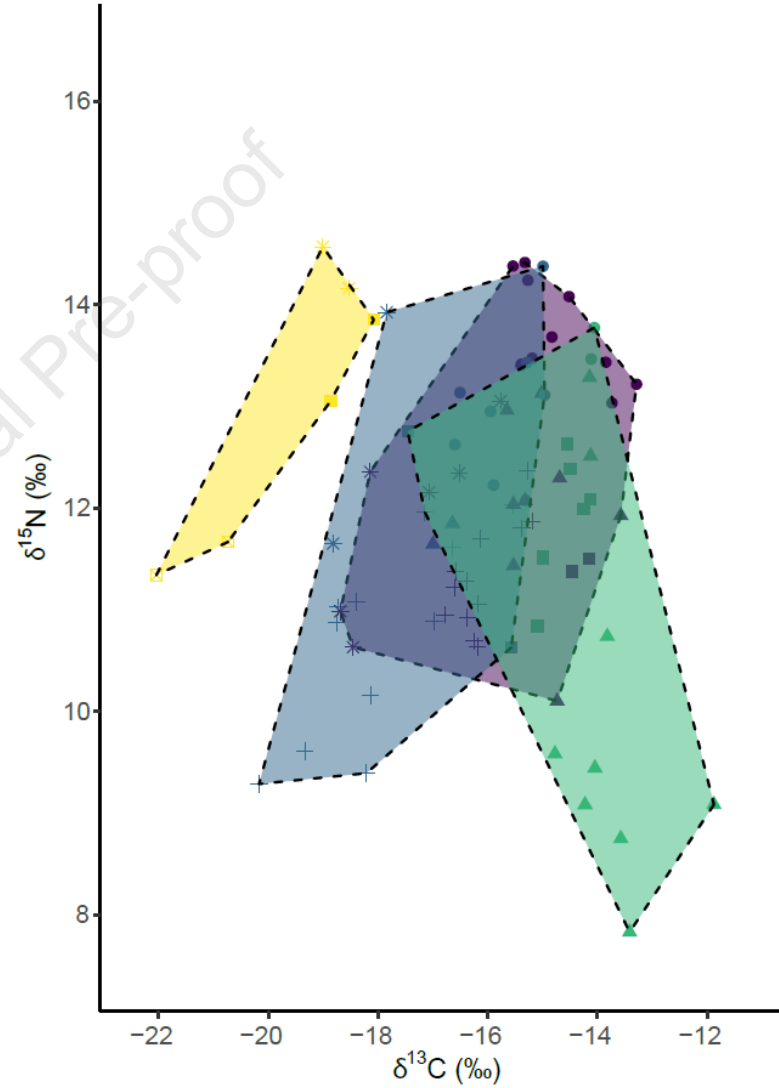




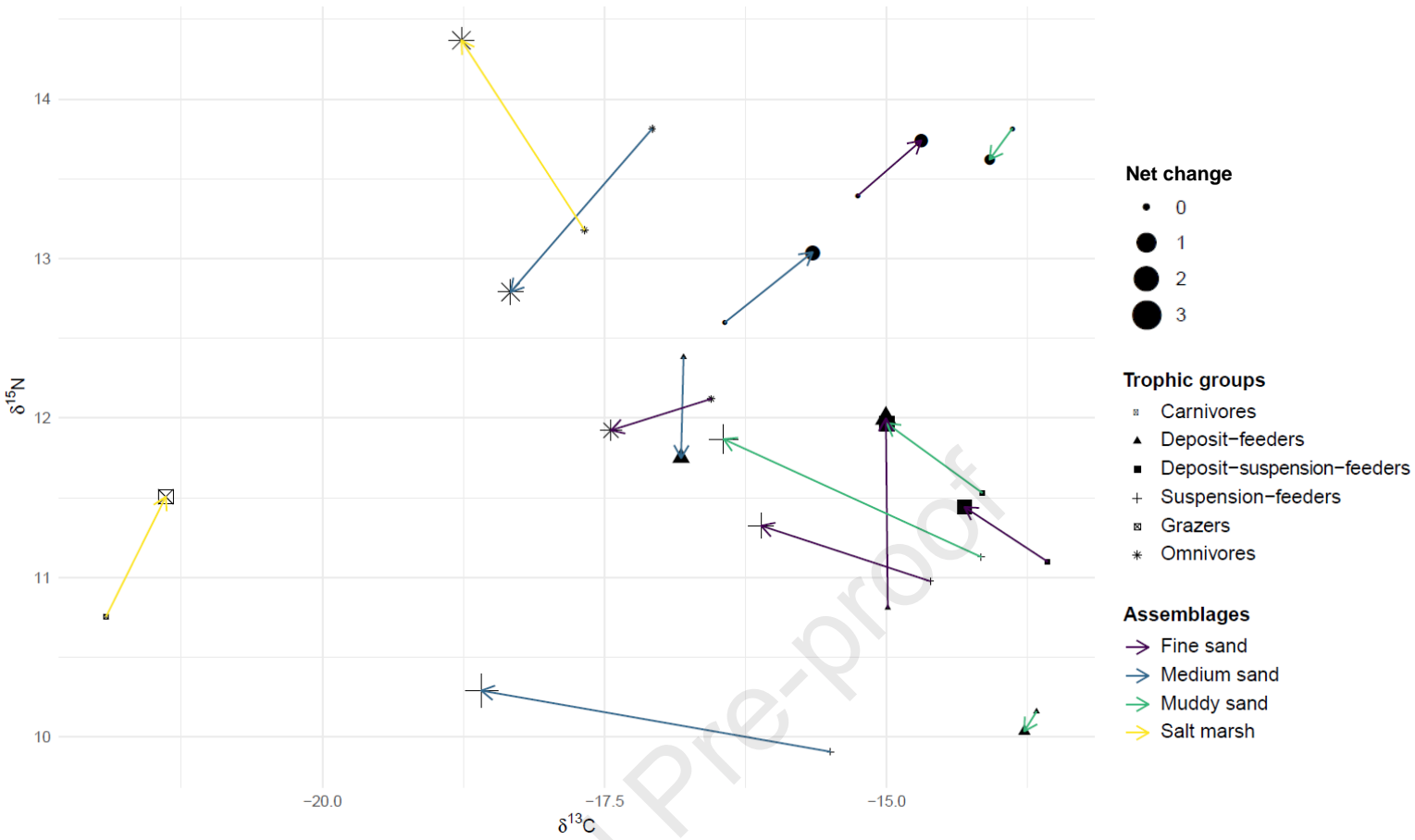
A. March



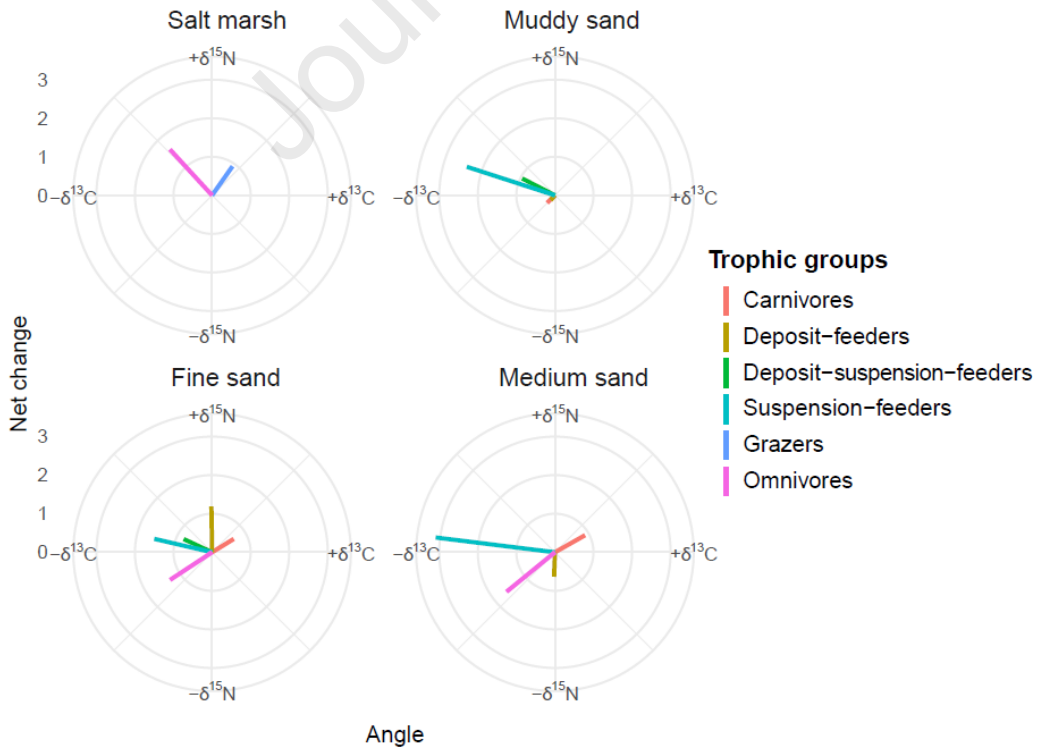
B. September



A. Trophic trajectory diagram



B. Trophic trajectory roses



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 Brébant:** Investigation, Writing - review & editing. **Alexandre Carpentier:** Methodology, Validation, Writing - review & editing. **Alain Ponsoero:** Writing -review & editing. **Gauthier Schaal:** Conceptualization, Methodology, Validation, Writing -review & editing, Investigation, Supervision.

Declaration of interests

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

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

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