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1 **Title**

2 Seasonal stratification leads to changes within the benthic food web of the Gulf of Lions (northwestern
3 Mediterranean)

4

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18

19 Seasonal change within benthic food web

20

21

22 Abstract

23 Like most continental shelves, the Gulf of Lions in the northwestern Mediterranean Sea provides
24 multiple ecological services and is subject to multiple natural and anthropogenic pressures. In this
25 context, this marine habitat must be described to monitor its evolution and ensure its protection. We
26 used carbon and nitrogen stable isotope analysis to describe the structure of the benthic food web.
27 Two sampling campaigns, corresponding to two contrasting situations in terms of water stratification,
28 were carried out in 2018. One in April when the water column was still well mixed and the annual peak
29 of phytoplankton production had already occurred, the other in September after several months of
30 thermal stratification and low primary productivity. Results revealed that the structure of the food
31 web changed in terms of range, extent and degree of trophic diversity. Between the two sampling
32 dates, isotopic niches of the taxa remained evenly distributed but the niche space shrunk. Temporal
33 changes in stable isotope compositions were greater for active suspension feeders, surface deposit
34 feeders and their direct predators than for other functional groups feeding deep in the sediment or
35 hunting a wider range of prey. The increase in nitrogen isotope ratios of primary consumers is either
36 the result of a fasting effect due to reduced food availability or a change in feeding behavior due to
37 reduced digestibility of primary food sources.

38

39 Keywords

40 benthos, benthic-pelagic coupling, oligotrophy, thermocline, stable isotope analysis

41

42 1. Introduction

43

44 The edge of the continents under the sea represents only 5.5% of the world ocean (Reineck and Singh,
45 1973). This transitional zone, called the continental shelf, receives solid and dissolved discharges from
46 river run-off, is characterized by high primary production and is the feeding ground for many marine
47 species. Continental shelves are thus under great anthropic pressure to exploit the living resources
48 and also mineral and fossil fuel deposits they contain (Amoroso et al., 2018; Grassle, 2013; Rajput and
49 Thakur, 2016). Their shallowness and proximity to the mainland also make these marine areas suitable
50 for the deployment of offshore wind farms. These multiple uses are a major concern for marine
51 biodiversity conservation in these environments.

52 In the Mediterranean Sea, continental shelves are generally narrow and particularly uneven (Harris et
53 al., 2014). In the northwestern basin, the Gulf of Lions defines a continental shelf that extends over
54 15,000 km². In this area, benthic communities depend on organic matter from the water column for
55 their food. Sinking particles mainly derive from epipelagic marine primary production, even though
56 inputs of continental origin from rivers can be significant locally (Bourgeois et al., 2011; Charles et al.,
57 2014; Darnaude et al., 2004). Whatever their origin, primary food sources at the basis of the benthic
58 food web mainly consist of dying or decaying matter.

59 The Mediterranean Sea has the oceanographic characteristics of oligotrophic seas, with alternating
60 periods of mixing and stratification (Miquel et al., 1994; Moutin et al., 2012). From autumn to late
61 spring, the water mass is well mixed and phytoplankton biomass, ranging from 0.2 to 1.4 mg Chl-a m⁻³
62 (Hunt et al., 2017), is relatively high. In summer, due to heat input from solar radiation, thermal
63 stratification separates a warm surface water layer from the deep cold water mass. The upper water
64 layer is depleted in nutrients and the deep water is light limited (Mignot et al., 2014). Phytoplankton
65 biomass drastically decreases by one to two orders of magnitude (0.027 mg Chl-a m⁻³ in Mena et al.,
66 2019). This period usually follows a spring phytoplankton bloom, and is sometimes followed by small
67 blooms in autumn. Therefore, most of the carbon export to the bottom occurs outside the summer
68 period (Miquel et al., 1994).

69 The biogeochemical and ecological functions in these oligotrophic systems are determined by the size
70 structure and taxonomic diversity of phytoplankton communities. Different size fractions are
71 associated with different elemental composition (Ward et al., 2012) and the substantial increase in
72 carbon and nitrogen stable isotope ratios between pico-, nano- and micro-particle size fractions is a
73 general feature of suspended particulate organic matter (Hunt et al., 2017). In the northwestern
74 Mediterranean, analyses of chlorophyll in the different size fractions have shown that the contribution
75 of picophytoplankton is maximal when the total chlorophyll-a biomass is low, with the contribution of

76 picophytoplankton reaching more than 60% of the total biomass in late summer (Charles et al., 2005,
77 Lantoiné, 1995).

78 Within the food web, the stable isotope composition of consumers reflects the stable isotope
79 composition of their food source (Michener and Lajtha, 2007; Rau et al., 1981). The carbon isotope
80 composition of consumers provides information on the basal food source, while the nitrogen isotope
81 composition indicates their trophic position in the food web. Because terrestrial organic matter is
82 isotopically distinct from marine organic matter and there is isotopic heterogeneity in the size classes
83 of marine organic particles (Rau et al., 1990), if changes occur at the base of the food web, changes in
84 the stable isotope composition of consumers can be expected.

85 The benthic food webs of the habitats surrounding the Gulf of Lions such as nearshore, deep or pro-
86 deltaic environments are documented (Carlier et al., 2007; Charles et al., 2017; Darnaude et al., 2004;
87 Fanelli et al., 2013, 2011; Nahon et al., 2012). This description should be extended to the continental
88 shelf which is heavily trawled (Jac et al., 2021) but also eligible to host the first French floating
89 offshore wind farm in the Mediterranean Sea. It is therefore necessary to document the functioning of
90 the benthic ecosystem in this area to properly assess the environmental effects of future changes and
91 pressures. This study aims to describe the trophic structure of the coastal terrigenous mud community
92 (UNEP/MAP, 2019) in two contrasting seasons by carrying out stable carbon and nitrogen isotope
93 analysis on suspended particulate organic matter, sediment and benthic fauna.

94

95

96 **2. Material and methods**

97 **2.1. Study area**

98 The study was carried out in the Gulf of Lions, Mediterranean Sea, France (Figure 1). In this region, the
99 continental shelf extends over 15,000 km², is interrupted at a depth of 110-120 m, varies in width
100 from 5 to 70 km and is incised on its outer edge by several submarine canyons. The biogeochemical
101 functioning of the Gulf of Lions is strongly influenced by the Rhone River, which is the main source of
102 freshwater and nutrients to the Mediterranean Sea (Sempéré et al., 2000). The sampling took place
103 within the Parc Naturel Marin du Golfe du Lion, 14 km off Port-La-Nouvelle, at a depth of 72 m
104 (42°55'20" N; 3°16'09" E), within an area eligible to host one of the future French floating offshore
105 wind farms.

106

107 **2.1. Water column**

108 Salinity and temperature were measured at the study site at both sampling periods (i.e., April and
109 September 2018) using the Sea-Bird Scientific (USA) SeaCAT CTD SBE 19plus V2 profiler. We collected
110 monthly temperature data recorded at the closest long-term observation site on the Gulf of Lions

111 shelf (Plateau Observatory Laboratoire Arago, POLA station (42°28'18" N; 03°15'30" E),
112 <https://www.obs-banyuls.fr/en/observe/observation-sites.html>).

113

114 **2.2 Sampling of food sources and consumers**

115 Sampling was conducted on 20th April and 19th September 2018. To determine the stable isotope
116 composition of suspended particulate organic matter (SPOM) available to benthic primary consumers,
117 water samples were collected above the sediment, 70 m depth, using a 10L-Niskin® and filtered
118 through 200 µm mesh to remove zooplanktonic organisms and large detritus. SPOM was recovered by
119 filtration through pre-combusted Whatman GF/F filters (25 mm in diameter, 0.7 µm pore size). The
120 filters were then placed in individual Petri dishes and dried in an oven at 50°C overnight. The dried
121 filters were kept in the dark in a desiccator until analysis.

122 Sediment organic matter (SOM) was collected with a Van Veen grab. A sample of the upper
123 undisturbed sediment layer (i.e. <1 cm thick) was collected in three grabs. Samples were frozen and
124 freeze-dried using a Christ Alpha 1-4LD freeze-dryer. They were then ground using a mortar and
125 pestle.

126 Demersal fish and epibenthic invertebrate megafauna were collected using a 2-metre beam trawl. The
127 trawl was equipped with a chain and a 20 mm mesh net. The benthic infauna was sampled with a
128 Charcot dredge. The dredge opening was 59 x 23 cm (width x height) and the mesh size of the bag was
129 0.5 mm. Three 10-minute hauls were made with each gear. Back in the laboratory, organisms were
130 identified to the lowest possible taxonomic level using available dichotomous identification keys and
131 faunal identification guides. Part of the dorsal muscle of fish specimens was extracted while other
132 animals were kept overnight in filtered seawater (GF/F) to empty the digestive tracts. Bivalves and
133 gastropods were then de-shelled. All samples were stored individually, frozen at -20°C and then
134 freeze-dried. The dried samples were ground to homogeneous powders using TissueLyser II (Qiagen).

135 Taxa were classified into five functional feeding groups (FFG) based on information available in
136 databases such as the Biological Traits Information Catalogue developed by the Marine Life
137 Information Network (Marlin, 2006); reviews on feeding behaviors (e.g. Jumars et al., 2015; Riisgård
138 and Larsen, 2000); primary literature on species feeding behavior; morphology of feeding structures
139 and expert knowledge. On this basis, we considered that active suspension feeders (AS) feed
140 suspended micro-organisms and detritus by active pumping of the surrounding water. They create the
141 water current that direct food particles to their feeding appendages (Riisgård and Larsen, 2000;
142 MarLIN, 2006; Jumars et al., 2015). Passive suspension feeders (PS) passively capture suspended
143 particles relying on the natural water flow or particle motion to bring particles in contact with their
144 feeding structures (Riisgard and Larsen, 2000; MarLIN, 2006; Jumars et al., 2015). Surface deposit
145 feeders (SD) feed on fragmented particulate organic matter from the surface of the substratum

146 (MarLIN, 2006). Sub-surface deposit feeders (SSD) feed on fragmented particulate organic matter
 147 within the substratum (MarLIN, 2006). Carnivores (C) are mobile predator and scavenging species that
 148 feed on prey and/or dead organisms (MarLIN, 2006).

149

150 2.3 Stable isotope analysis

151 Stable isotope analyses were performed with a continuous flow mass spectrometer (Delta V+ with a
 152 conflo IV interface, Thermo Scientific, Bremen, Germany) coupled to an elemental analyzer (Flash EA
 153 2000, Thermo Scientific, Milan, Italy) at the Pôle Spectrométrie Océan (Plouzané, France). Results
 154 were expressed in standard δ notation based on international standards, Vienna Pee Dee Belemnite
 155 (VPDB) for $\delta^{13}\text{C}$ and atmospheric nitrogen (Atmos. N_2) for $\delta^{15}\text{N}$ following the formula:

156

$$157 \quad \delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3 \quad (\text{in } \text{‰})$$

158

159 where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Reference gas calibration was done using reference materials: USGS-61,
 160 USGS-62 and USGS-63. Analytical error was estimated by replicate measurements (every six samples)
 161 of an internal standard Thermo –Acetanilide. Measurement uncertainty was estimated $\pm 0.08 \text{ ‰}$ and \pm
 162 0.11 ‰ for Nitrogen and Carbon respectively.

163 Some samples contained carbonates that primarily reflected the $\delta^{13}\text{C}$ values of CO_2 dissolved in the
 164 water rather than the $\delta^{13}\text{C}$ values of the diet (DeNiro and Epstein, 1978). Accordingly, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
 165 were analyzed separately. For measurements of $\delta^{13}\text{C}$ values in SPOM, SOM, crustaceans and
 166 echinoderms, a subsample was acidified to remove the inorganic carbon prior analysis, while the
 167 remaining material was used for $\delta^{15}\text{N}$ analyses (Pinnegar and Polunin, 1999).

168

169 2.4 Data treatment

170 For each date of sampling, taxa were presented as a collection of points in the δ plane, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
 171 values determining their position on the horizontal and the vertical axis, respectively. “Community-
 172 wide” metrics proposed by Layman et al. (2007) were calculated to quantitatively compare the
 173 distribution of points within the δ plane between the sampling dates. The ranges of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$
 174 values (CR and NR, respectively), were computed as the difference between the highest and lowest
 175 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values; the total area (TA), was the area of the minimum convex envelope containing
 176 the whole set of points; the mean distance to the centroid (CD) was the mean Euclidean distance of
 177 each point to the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value for all points; the mean nearest neighbor distance
 178 (MNND), was the mean of the Euclidean distances to each point’s nearest neighbor and, SDNND was
 179 the standard deviation to this mean. As the calculation of these metrics depends on species richness,
 180 and the number and identity of collected species vary from one sampling to another, metrics were

181 calculated only from taxa present on both dates (i.e. April and September). For each of these taxa, the
182 trophic seasonal trajectory (length and direction) was calculated as the Euclidean vector defined by
183 the displacement of the taxon's position in the δ plane between the two sampling dates (Sturbois et
184 al., 2022).

185 Two-factor analyses of variance were performed to simultaneously assess the effect of sampling date
186 and taxa or feeding group factors on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean
187 values between dates was then tested for each taxon and each feeding group, by running permutation
188 Student's t-tests. All data were analyzed using the R software environment 3.4.3 (R Core Team, 2020),
189 with the glm: fitting generalized linear models and the 'perm.t.test' function, 1000 permutations, from
190 the Student's t-test in the R package 'RVAideMemoire' ([https://cran.r-](https://cran.r-project.org/package=RVAideMemoire)
191 [project.org/package=RVAideMemoire](https://cran.r-project.org/package=RVAideMemoire)). A p-value of less than 0.05 meant that the null hypothesis 'no
192 difference between means' or 'no interaction between factors' was rejected.

193

194 3. Results

195 3.1 Seasonal thermal stratification

196 Regardless of the date, April or September, salinity remained close to 38.2 over the entire height of
197 the water column (Figure 2a). We observed the formation of the 10-20 m thick summer thermocline
198 (Figure 2b, 2c). From May to October, the stratification divided the water column into a deep layer
199 with a temperature close to 13°C and a superficial layer with an average temperature between 20 and
200 24°C. Otherwise, from late autumn to April, the water column was well mixed and the average
201 temperature was close to 13°C. The sampling dates framed the stratification period of the water
202 column of the Gulf of Lion continental shelf.

203

204 3.2 Sample collection

205 All fish, most crustaceans, echinoderms, cnidarians and mollusks were collected by beam trawl. The
206 Charcot dredge sampled small crustaceans, sub-surface deposit feeders and nearly all annelids. A total
207 of 54 taxa was sampled, 43 in April, 38 in September and 28 were common to both sampling
208 campaigns (Table 1 and Table 2). We collected more species in April than in September, but many taxa
209 were represented by only one individual (Table 2). Therefore, statistical tests, Layman metrics and
210 trophic trajectories were conducted on taxa collected during the two sampling campaigns and
211 represented by several individuals (Table 1).

212

213 3.3 Stable isotope analysis

214 3.3.1 Basal food sources

215 The only significant temporal change in the isotopic composition of food sources between the two
 216 sampling dates was detected in the $^{13}\text{C}/^{12}\text{C}$ ratio of suspended particulate organic matter (SPOM). The
 217 SPOM was significantly depleted in ^{13}C in April ($-24.6 \pm 0.5 \text{‰}$) in comparison with September ($-23.7 \pm$
 218 0.2‰) (Permutation Student's t-tests, $p = 0.002$). The $\delta^{15}\text{N}$ values were scattered on both dates (4.4
 219 to 6.9 ‰ in April, 4.5 to 8.1 ‰ in September) and no significant difference was detected. Regarding
 220 sediment organic matter (SOM), stable isotope compositions of SOM were similar (Table 1, Figure 3)
 221 between the two dates of sampling (mean $\delta^{13}\text{C} = -21.8 \text{‰}$, mean $\delta^{15}\text{N} = 4.4 \text{‰}$).

222

223 3.3.2 Consumers

224 Figure 3 shows the consumer positions in the $\delta^{13}\text{C} - \delta^{15}\text{N}$ plane for all species collected on both
 225 sampling dates. The relative position of the trophic groups to each other remained unchanged
 226 between April and September. The lowest trophic levels were active suspension feeders (blue dots,
 227 e.g. *Acanthocardia echinata*, *Ampelisca sp.*, *Maera grossimana*) and surface deposit feeders (yellow
 228 dots, e.g. *Alpheus glaber*, *Goneplax rhomboides*, *Tuberapseudes echinatus*). Compared to these
 229 groups, passive suspension feeders (pink dots), mainly cnidarians (*Alcyonium palmatum*, *Pennatula*
 230 *phosphorea*, *Veretillum cynomorium*) and echinoderms (*Ocnus planci*, *Antedon bifida*), occupied a
 231 higher trophic position. The overall high $\delta^{15}\text{N}$ values of sub-surface suspension feeders (green dots,
 232 e.g. *Oestergrenia digitata*, *Sternaspis scutata*, *Notomastus sp.*, *Glandiceps sp.*) were close to the
 233 median value recorded for carnivores (red dots). Across all dates and taxa, the carnivorous annelid
 234 *Scoletoma sp.* had the highest $\delta^{15}\text{N}$ value (i.e. 12.1 ‰). Otherwise, the highest trophic levels were
 235 occupied by fish. The distribution of consumer positions in the $\delta^{13}\text{C} - \delta^{15}\text{N}$ niche space appeared to
 236 contract between April and September.

237 Statistical analyses were performed on taxa and feeding groups represented by several individuals and
 238 present at both sampling dates (Table 1). Two-factor controlled analyses of variance indicated that
 239 differences in $\delta^{13}\text{C}$ values were significant between taxa and between feeding groups (taxa, $df = 16$, $F =$
 240 20.04 , $p < 0.001$; feeding groups, $df = 4$, $F = 7.39$, $p > 0.001$) but not between sampling dates. In contrast,
 241 the effect of the sampling date on $\delta^{15}\text{N}$ (Figure 4) was different depending on the identity of the taxa
 242 (time x taxa, $df = 16$, $F = 8.88$, $p < 0.001$) and feeding groups (time x feeding groups, $df = 4$, $F = 3.03$,
 243 $p = 0.020$). Regarding active suspension feeders and surface deposit feeders, mean $\delta^{15}\text{N}$ values
 244 significantly increased between April and September (permutation Student's t-tests, $p = 0.0019$, for
 245 both feeding groups). No temporal change was detected for the passive suspension feeder *O. placi*
 246 (permutation Student's t-tests, $p = 0.198$) and the sub-surface deposit feeders, *O. digitata* and *S.*
 247 *scutata* (permutation Student's t-tests, $p = 0.587$ and $p = 0.231$, respectively). Among carnivores, $\delta^{15}\text{N}$
 248 increase was mainly in *Liocarcinus depurator* and *Astropecten aranciacus* (permutation Student's t-
 249 tests, $p = 0.011$ and $p = 0.007$, respectively) and to a lesser extent the fish, *Trigla lyra* (permutation

250 Student's t-tests, $p=0.045$). Changes for other carnivores (i.e., *Galeodea rugosa*, *Lumbrineris* sp,
251 *Labioleanira ylheni* and *Nephtys fallax*) were not statistically significant between the two sampling
252 dates.

253

254 3.3.3 Layman's community-wide metrics

255 Layman's metrics (Table 3) were calculated based on the benthic community reduced to taxa
256 represented by several individuals and collected on both sampling dates. The diversity of trophic levels
257 (NR), i.e. the difference between the maximum and minimum values of $\delta^{15}\text{N}$, decreased from 6.9 ‰ in
258 April to 5.0 ‰ in September. The diversity of basal food sources, $\delta^{13}\text{C}$ range (CR), also decreased from
259 4.5 ‰ in April to 3.1 ‰ in September but remained narrow. From April to September, the extent of
260 trophic diversity, total area (TA), occupied by consumers in the $\delta^{13}\text{C} - \delta^{15}\text{N}$ plane decreased from 20.2
261 to 13.8 (Table 3, Figure 5); the average distance from each point to the centroid of all samples (CD)
262 suggests that the degree of diversity was reduced from 2.5 to 1.9 ‰; species spacing (MNND) and
263 evenness of species packing (SDNND) decreased from 0.32 to 0.23 ‰ and from 0.27 to 0.19 ‰,
264 respectively. The most striking difference between the two sampling campaigns was the contraction in
265 the dispersion of consumer positions in the $\delta^{13}\text{C} - \delta^{15}\text{N}$ niche space.

266

267 3.3.4 Trophic trajectories

268 The trajectories of food sources and taxa in the $\delta^{13}\text{C} - \delta^{15}\text{N}$ plane are shown in Figure 5. The length of
269 move was different for different taxa. The longest trajectories were for active suspension feeders,
270 most surface deposit feeders and low trophic level carnivores. The direction of the trajectories
271 showed an enrichment in ^{15}N and ^{13}C between the two dates of sampling. The positions of high trophic
272 level taxa and taxa that feed on sub-surface deposits remained the same or changed slightly.

273

274

275 4. Discussion

276 Vertical temperature profiles confirmed that sampling campaigns were achieved at two periods
277 characterized by very contrasting conditions. As hypothesized, stable isotope analysis indicates that
278 the structure of the benthic food web of the continental shelf of the Gulf of Lions changed according
279 to the conditions of stratification of the water column. The niche space contracted in summer when
280 the thermal stratification leads to a reduction in the vertical flow of matter. The main changes
281 concerned primary consumers.

282

283 *Changes in the benthic food web*

284 The failure to collect multiple individuals of the same species on both sampling dates suggests
285 substantial changes in the composition of the benthic community. The area of sampling is subject to a
286 heavy trawling pressure (Jac et al., 2021). The probability that the area was not trawled between April
287 and September was low. The effect of trawling on benthic fauna explain that some species were not
288 found, or became scarce, from one period to the next. The mobility of some species, such as fish, also
289 explains why over-dispersed individuals escaped the sampling gear or were temporarily absent from
290 the sampling area. This led us to consider only species represented by several individuals on both
291 sampling dates in order to highlight any significant effect of the season on the stable isotope
292 composition of the benthic fauna. Layman's metrics applied to this set of taxa suggest that the niche
293 space of the community has contracted between the beginning and end of the stratification period.
294 Diversity of the trophic levels, total extent and degree of species spacing decreased between April and
295 September. Statistical analyses indicated that the changes were in nitrogen isotope composition and
296 that the effect of sampling date was different for different taxa or food groups. $\delta^{15}\text{N}$ values of active
297 suspension feeders and surface deposit feeders increased, whereas those of passive suspension
298 feeders and sub-surface deposit feeders remained the same. The $\delta^{15}\text{N}$ of carnivores increased as the
299 $\delta^{15}\text{N}$ of their prey increased. For example, the $\delta^{15}\text{N}$ of the sea star *Astropecten aranciacus* or the
300 swimming crab *Liocarcinus depurator*, which feed on active suspension feeder bivalves and surface
301 deposit feeders (Chartosia et al., 2010), increased. While the $\delta^{15}\text{N}$ value of the gastropod *Galeodea*
302 *rugosa*, which feeds on subsurface deposit feeders (Hughes, 2008), remained the same. High trophic
303 level carnivores showed no or only slight changes (Figure 4). The isotopic half-life of ectotherms
304 increases with body size (Vander Zanden et al., 2015), as predators are generally larger than their
305 prey, the effect observed in low trophic level carnivores was probably attenuated in higher trophic
306 level carnivores.

307

308 *Sources of food web changes*

309 Just as the stable isotope composition of sedimentary organic matter (SOM) remained the same,
310 those of sub-surface deposit feeders did not change between the two sampling dates. $\delta^{13}\text{C}$ value, -
311 21.8 ‰, was much higher than those of SOM, between -27.2 and -24.2‰, reported for the area under
312 direct influence of the Rhone (Bourgeois et al., 2011). This indicates that SOM at the study site was
313 mainly of marine origin. $\delta^{13}\text{C}$ values of suspended particulate organic matter (SPOM), -24.6‰ in April
314 and -23.7‰ in September, were close to values reported, -23 to -19 ‰, for fresh marine
315 phytoplankton (Darnaude et al., 2004; Druffel et al., 1992; Fry and Sherr, 1989; Harmelin-Vivien et al.,
316 2008). The ^{13}C -depletion in April suggests that continental material may have contributed to SPOM at
317 that time (Harmelin-Vivien et al., 2008). This is consistent with the observation that during spring,
318 rivers, especially the Rhone River, spread fine organic particles strongly depleted in ^{13}C over a large

319 part of the Gulf of Lions (Auger et al., 2011; Cauwet et al., 1990), whereas during summer the
320 contribution of continental sources is extremely low because river flows are at their lowest (Durrieu de
321 Madron et al., 2008). Regarding nitrogen stable isotope ratios, values, 5.7‰ in April and 6.0‰ in
322 September, did not explain the differences in $\delta^{15}\text{N}$ values of primary consumers.
323 Therefore, the increase of $\delta^{15}\text{N}$ values in active suspension feeders and surface deposit feeders
324 between April and September resulted from either a change in the trophic status (Romero-Romero et
325 al., 2021) or a fasting effect (Doi et al., 2017). Fasting in marine invertebrates induces a significant
326 increase in $\delta^{15}\text{N}$ values with no or moderate increase in $\delta^{13}\text{C}$ values (Doi et al., 2017; Kaufman et al.,
327 2008). During summer thermal stratification period, flow of matter to the benthos are lower than in
328 winter or spring (Miquel et al., 1994). Stratification of the water column leads to a general decrease in
329 phytoplankton productivity (Mignot et al., 2014). Most of the phytoplankton biomass, mainly
330 picoplankton cells (Lantoiné, 1995), is concentrated in a deep chlorophyll maximum located below the
331 thermocline. Picoplankton are grazed by zooplankton and the entire pelagic food chain adopts the
332 distribution of peak prey abundance on a spatial scale of few meters (Röpke et al., 1993). The vertical
333 downward flow of material available to benthic primary consumers drastically decreases (Coma et al.,
334 2009). Moreover, sinking organic particles consist of fecal pellets. As a result, organic material
335 available to primary consumers is not only more diluted but also becomes less digestible. A set of
336 trophic conditions similar to those faced by sub-surface deposit feeders that feed on poorly digestible
337 and highly diluted sedimentary organic matter. Within benthic food webs, sub-surface deposit feeders
338 are at the trophic level of secondary consumers. It is therefore likely, as shown by Romero-Romero et
339 al. (2021) for abyssal deposit feeders, that microbial communities transformed primary food sources
340 (SPOM and SOM) into compounds more easily digested by primary consumers. Microbivory, which is
341 ubiquitous among detritus feeders, can significantly elevate the trophic position of the fauna (Steffan
342 et al., 2017). This pathway of transformation and transfer of poorly digestible material may also
343 explain why active suspension feeders and surface detritus feeders moved from being primary to
344 secondary consumers during the stratification period.

345

346 5. Conclusion

347 Further studies are needed to fully describe and understand how the functioning and structure of the
348 benthic food web changes with the seasons on the Gulf of Lions continental shelf. For instance, it
349 would be worthwhile to document passive suspension feeders that have been difficult to sample.
350 Nevertheless, this study provides a baseline for a site that will host the first pilot Mediterranean
351 floating offshore wind farm. Our results highlight the need to take into account natural seasonal
352 changes and the existence of pre-existing disturbances related to human activity on the continental
353 shelf. The installation of a wind farm in a heavily trawled area could increase species diversity by

354 acting as fish aggregation device (Girard et al., 2004) and as artificial reef allowing colonization by
355 sessile organisms (Bergström et al., 2014). The organisms that foul the submerged structures of wind
356 turbines could alter the downward flow of organic matter (Ivanov et al., 2021) and allow the
357 development of a more complex benthic food web (Wilson and Elliott, 2009). The expected impact is
358 likely to be most noticeable during periods of thermal stratification, when material fluxes to the
359 benthos are naturally low and infauna is limited by food.

360

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371 **Reference list**

372

373 Amoroso, R.O., Pitcher, C.R., Rijnsdorp, A.D., McConnaughey, R.A., Parma, A.M., Suuronen, P., Eigaard,
 374 O.R., Bastardie, F., Hintzen, N.T., Althaus, F., Baird, S.J., Black, J., Buhl-Mortensen, L., Campbell, A.B.,
 375 Catarino, R., Collie, J., Cowan, J.H., Durholtz, D., Engstrom, N., Fairweather, T.P., Fock, H.O., Ford, R.,
 376 Gálvez, P.A., Gerritsen, H., Góngora, M.E., González, J.A., Hiddink, J.G., Hughes, K.M., Intelmann, S.S.,
 377 Jenkins, C., Jonsson, P., Kainge, P., Kangas, M., Kathena, J.N., Kavadas, S., Leslie, R.W., Lewis, S.G.,
 378 Lundy, M., Makin, D., Martin, J., Mazor, T., Gonzalez-Mirelis, G., Newman, S.J., Papadopoulou, N.,
 379 Posen, P.E., Rochester, W., Russo, T., Sala, A., Semmens, J.M., Silva, C., Tsolos, A., Vanelslander, B.,
 380 Wakefield, C.B., Wood, B.A., Hilborn, R., Kaiser, M.J., Jennings, S., 2018. Bottom trawl fishing footprints
 381 on the world's continental shelves. *Proc. Natl. Acad. Sci. U.S.A.* 115.
 382 <https://doi.org/10.1073/pnas.1802379115>

383 Auger, P.A., Diaz, F., Ulses, C., Estournel, C., Neveux, J., Joux, F., Pujo-Pay, M., Naudin, J.J., 2011.
 384 Functioning of the planktonic ecosystem on the Gulf of Lions shelf (NW Mediterranean) during spring
 385 and its impact on the carbon deposition: a field data and 3-D modelling combined approach.
 386 *Biogeosciences* 8, 3231–3261. <https://doi.org/10.5194/bg-8-3231-2011>

387 Bergström, L., Kautsky, L., Malm, T., Rosenberg, R., Wahlberg, M., Åstrand Capetillo, N., Wilhelmsson,
 388 D., 2014. Effects of offshore wind farms on marine wildlife—a generalized impact assessment. *Environ.*
 389 *Res. Lett.* 9, 034012. <https://doi.org/10.1088/1748-9326/9/3/034012>

390 Bourgeois, S., Pruski, A.M., Sun, M.-Y., Buscail, R., Lantoiné, F., Kerhervé, P., Vétion, G., Rivière, B.,
 391 Charles, F., 2011. Distribution and lability of land-derived organic matter in the surface sediments of
 392 the Rhône prodelta and the adjacent shelf (Mediterranean Sea, France): a multi proxy study.
 393 *Biogeosciences* 8, 3107–3125. <https://doi.org/10.5194/bg-8-3107-2011>

394 Carlier, A., Riera, P., Amouroux, J.-M., Bodiou, J.-Y., Grémare, A., 2007. Benthic trophic network in the
 395 Bay of Banyuls-sur-Mer (northwest Mediterranean, France): An assessment based on stable carbon
 396 and nitrogen isotopes analysis. *Estuar Coast Shelf S* 72, 1–15.
 397 <https://doi.org/10.1016/j.ecss.2006.10.001>

398 Cauwet, G., Gadel, F., de Souza Sierra, M.M., Ewald, M., 1990. Contribution of the Rhône River to
 399 organic carbon inputs to the northwestern Mediterranean Sea. *Cont. Shelf Res.* 10, 1025–1037.

400 Charles, F., Coston-Guarini, J., Lantoiné, F., Guarini, J.-M., Yücel, M., 2014. Ecogeochemical fate of
 401 coarse organic particles in sediments of the Rhône River prodelta. *Estuarine, Coastal and Shelf Science*
 402 141, 97–103. <https://doi.org/10.1016/j.ecss.2014.03.005>

403 Charles, F., Lantoiné, F., Brugel, S., Chrétiennot-Dinet, M.-J., Quiroga, I., Rivière, B., 2005. Seasonal
 404 survey of the phytoplankton biomass, composition and production in a littoral NW Mediterranean site,
 405 with special emphasis on the picoplanktonic contribution. *Estuar Coast. Shelf S.* 65, 199–212.
 406 <https://doi.org/10.1016/j.ecss.2005.06.006>

407 Charles, F., Nozais, C., Lantoiné, F., Rzeznik-Orignac, J., Labrune, C., Coston-Guarini, J., 2017. Trophic
 408 ecology of coastal soft bottoms: A dive into the stew of marine sediment. *Vie Milieu - Life and*
 409 *Environment* 297–304. <https://hal.archives-ouvertes.fr/hal-02572315>

410 Chartosia, N., Kitsos, M.-S., Tzomos, T., Mavromati, E., Koukouras, A., 2010. Diet composition of five
 411 species of crabs (Decapoda, Brachyura) that show a gradual transition from marine to terrestrial life.
 412 *Crustaceana* 83, 1181–1197. <https://doi.org/10.1163/001121610X533502>

- 413 Coma, R., Ribes, M., Serrano, E., Jimenez, E., Salat, J., Pascual, J., 2009. Global warming-enhanced
414 stratification and mass mortality events in the Mediterranean. *P. Natl Acad. Sci. USA* 106, 6176–6181.
415 <https://doi.org/10.1073/pnas.0805801106>
- 416 Darnaude, A., Salen-Picard, C., Harmelin-Vivien, M., 2004. Depth variation in terrestrial particulate
417 organic matter exploitation by marine coastal benthic communities off the Rhone River delta (NW
418 Mediterranean). *Mar. Ecol. Prog. Ser.* 275, 47–57. <https://doi.org/10.3354/meps275047>
- 419 DeNiro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals.
420 *Geochim. Cosmochim. Acta* 42, 495–506. [https://doi.org/doi: DOI: 10.1016/0016-7037\(78\)90199-0](https://doi.org/doi: DOI: 10.1016/0016-7037(78)90199-0)
- 421 Doi, H., Akamatsu, F., González, A.L., 2017. Starvation effects on nitrogen and carbon stable isotopes
422 of animals: an insight from meta-analysis of fasting experiments. *Roy. Soc. Open Sci.* 4, 170633.
423 <https://doi.org/10.1098/rsos.170633>
- 424 Druffel, E.R.M., Williams, P.M., Bauer, J.E., Ertel, J.R., 1992. Cycling of dissolved and particulate organic
425 matter in the open ocean. *J. Geophys. Res.* 97, 15639. <https://doi.org/10.1029/92JC01511>
- 426 Durrieu de Madron, X., Wiberg, P.L., Puig, P., 2008. Sediment dynamics in the Gulf of Lions: The impact
427 of extreme events. *Cont. Shelf Res.* 28, 1867–1876. <https://doi.org/10.1016/j.csr.2008.08.001>
- 428 Fanelli, E., Papiol, V., Cartes, J., Rumolo, P., López-Pérez, C., 2013. Trophic webs of deep-sea
429 megafauna on mainland and insular slopes of the NW Mediterranean: a comparison by stable isotope
430 analysis. *Mar. Ecol. Prog. Ser.* 490, 199–221. <https://doi.org/10.3354/meps10430>
- 431 Fanelli, E., Papiol, V., Cartes, J.E., Rumolo, P., Brunet, C., Sprovieri, M., 2011. Food web structure of the
432 epibenthic and infaunal invertebrates on the Catalan slope (NW Mediterranean): Evidence from $\delta^{13}\text{C}$
433 and $\delta^{15}\text{N}$ analysis. *Deep-Sea Res. Pt I* 58, 98–109. <https://doi.org/10.1016/j.dsr.2010.12.005>
- 434 Fry, B., Sherr, E.B., 1989. $\delta^{13}\text{C}$ Measurements as Indicators of Carbon Flow in Marine and Freshwater
435 Ecosystems, in: Rundel, P.W., Ehleringer, J.R., Nagy, K.A. (Eds.), *Stable Isotopes in Ecological Research*,
436 *Ecological Studies*. Springer New York, New York, NY, pp. 196–229. https://doi.org/10.1007/978-1-4612-3498-2_12
- 438 Girard, C., Benhamou, S., Dagorn, L., 2004. FAD: Fish Aggregating Device or Fish Attracting Device? A
439 new analysis of yellowfin tuna movements around floating objects. *An. Behav.* 67, 319–326.
440 <https://doi.org/10.1016/j.anbehav.2003.07.007>
- 441 Grassle, F.J., 2013. Marine Ecosystems, in: *Encyclopedia of Biodiversity*. Elsevier, pp. 45–55.
442 <https://doi.org/10.1016/B978-0-12-384719-5.00290-2>
- 443 Harmelin-Vivien, M., Loizeau, V., Mellon, C., Beker, B., Arlhac, D., Bodiguel, X., Ferraton, F., Hermand,
444 R., Philippon, X., Salen-Picard, C., 2008. Comparison of C and N stable isotope ratios between surface
445 particulate organic matter and microphytoplankton in the Gulf of Lions (NW Mediterranean). *Cont.*
446 *Shelf Res.* 28, 1911–1919. <https://doi.org/10.1016/j.csr.2008.03.002>
- 447 Harris, P.T., Macmillan-Lawler, M., Rupp, J., Baker, E.K., 2014. Geomorphology of the oceans. *Mar.*
448 *Geol.* 352, 4–24. <https://doi.org/10.1016/j.margeo.2014.01.011>
- 449 Hughes, R., 2008. Laboratory observations on the feeding behaviour, reproduction and morphology of
450 *Galeodea echinophora* (Gastropoda: Cassidae). *Zool. J. Linn. Soc.* 86, 355–365.
451 <https://doi.org/10.1111/j.1096-3642.1986.tb01815.x>

- 452 Hunt, B.P.V., Carlotti, F., Donoso, K., Pagano, M., D’Ortenzio, F., Taillandier, V., Conan, P., 2017.
 453 Trophic pathways of phytoplankton size classes through the zooplankton food web over the spring
 454 transition period in the north-west Mediterranean Sea: Mediterranean zooplankton food web. J.
 455 Geophys. Res. Oceans 122, 6309–6324. <https://doi.org/10.1002/2016JC012658>
- 456 Ivanov, E., Capet, A., De Borger, E., Degraer, S., Delhez, E.J.M., Soetaert, K., Vanaverbeke, J., Grégoire,
 457 M., 2021. Offshore Wind Farm Footprint on Organic and Mineral Particle Flux to the Bottom. Front.
 458 Mar. Sci. 8, 631799. <https://doi.org/10.3389/fmars.2021.631799>
- 459 Jac, C., Desroy, N., Duchêne, J.-C., Foveau, A., Labrune, C., Lescure, L., Vaz, S., 2021. Assessing the
 460 impact of trawling on benthic megafauna: comparative study of video surveys vs. scientific trawling.
 461 ICES J. Mar. Sci. 78, 1636–1649. <https://doi.org/10.1093/icesjms/fsab033>
- 462 Jumars, P.A., Dorgan, K.M., Lindsay, S.M., 2015. Diet of Worms Emended: An Update of Polychaete
 463 Feeding Guilds. Ann. Rev. Mar. Sci. 7, 497–520. <https://doi.org/10.1146/annurev-marine-010814-020007>
- 465 Kaufman, M.R., Gradinger, R.R., Bluhm, B.A., O’Brien, D.M., 2008. Using stable isotopes to assess
 466 carbon and nitrogen turnover in the Arctic sympagic amphipod *Onisimus litoralis*. Oecologia 158, 11–
 467 22. <https://doi.org/10.1007/s00442-008-1122-y>
- 468 Lantoine, F., 1995. Caractérisation des différentes populations du picoplancton (picoeucaryotes,
 469 *Synechococcus* spp., *Prochlorococcus* spp.) dans diverses situations trophiques (Atlantique tropical,
 470 Golfe du Lion).
- 471 Layman, C.A., Arrington, D.A., Montaña, C.G., Post, D.M., 2007. Can stable isotope ratios provide for
 472 community-wide measures of trophic structure? Ecology 88, 42–48. [https://doi.org/10.1890/0012-9658\(2007\)88\[42:CSIRPF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2)
- 474 Marlin, 2006. MarLIN, 2006. BIOTIC - Biological Traits Information Catalogue. Marine Life Information
 475 Network. Plymouth: Marine Biological Association of the United Kingdom. Available from
 476 <www.marlin.ac.uk/biotic>.
- 477 Mena, C., Reglero, P., Hidalgo, M., Sintés, E., Santiago, R., Martín, M., Moyà, G., Balbín, R., 2019.
 478 Phytoplankton Community Structure Is Driven by Stratification in the Oligotrophic Mediterranean Sea.
 479 Front. Microbiol. 10, 1698. <https://doi.org/10.3389/fmicb.2019.01698>
- 480 Michener, R.H., Lajtha, K. (Eds.), 2007. Stable isotopes in ecology and environmental science, 2nd ed.
 481 ed, Ecological methods and concepts series. Blackwell Pub, Malden, MA.
- 482 Mignot, A., Claustre, H., Uitz, J., Poteau, A., D’Ortenzio, F., Xing, X., 2014. Understanding the seasonal
 483 dynamics of phytoplankton biomass and the deep chlorophyll maximum in oligotrophic environments:
 484 A Bio-Argo float investigation. Glob. Biogeochem. Cy. 28, 856–876.
 485 <https://doi.org/10.1002/2013GB004781>
- 486 Miquel, J.C., Fowler, S.W., La Rosa, J., Buat-Menard, P., 1994. Dynamics of the downward flux of
 487 particles and carbon in the open northwestern Mediterranean Sea. Deep Sea Research Part I:
 488 Oceanographic Research Papers 41, 243–261. [https://doi.org/10.1016/0967-0637\(94\)90002-7](https://doi.org/10.1016/0967-0637(94)90002-7)
- 489 Moutin, T., Van Wambeke, F., Prieur, L., 2012. Introduction to the Biogeochemistry from the
 490 Oligotrophic to the Ultraoligotrophic Mediterranean (BOUM) experiment. Biogeosciences 9, 3817–
 491 3825. <https://doi.org/10.5194/bg-9-3817-2012>

- 492 Nahon, S., Nozais, C., Delamare-Deboutteville, J., Escoubeyrou, K., Desmalades, M., Pruski, A.M.,
 493 Karsten, U., Charles, F., 2012. Trophic relationships and UV-absorbing compounds in a Mediterranean
 494 medio-littoral rocky shore community. *J. Exp. Mar. Ecol.* 424–425, 59–65.
 495 <https://doi.org/10.1016/j.jembe.2012.05.009>
- 496 Pinnegar, J.K., Polunin, N.V.C., 1999. Differential Fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among Fish Tissues:
 497 Implications for the Study of Trophic Interactions. *Funct. Ecol.* 13, 225–231.
- 498 Rajput, S., Thakur, N.K., 2016. Continental Margins, in: *Geological Controls for Gas Hydrate Formations*
 499 *and Unconventionals*. Elsevier, pp. 1–34. <https://doi.org/10.1016/B978-0-12-802020-3.00001-1>
- 500 Rau, G.H., Sweeney, R.E., Kaplan, I.R., Mearns, A.J., Young, D.R., 1981. Differences in animal ^{13}C , ^{15}N
 501 and D abundance between a polluted and an unpolluted coastal site: Likely indicators of sewage
 502 uptake by a marine food web. *Estuar. Coast. Shelf S.* 13, 701–707. [https://doi.org/10.1016/S0302-](https://doi.org/10.1016/S0302-3524(81)80051-5)
 503 [3524\(81\)80051-5](https://doi.org/10.1016/S0302-3524(81)80051-5)
- 504 Rau, G.H., Teyssie, J.L., Rassoulzadegan, F., Fowler, S.W., 1990. $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ variations among
 505 sizefractionated marine particles: implications for their origin and trophic relationships. *Mar. Ecol.*
 506 *Prog. Ser.* 59, 33–38.
- 507 Reineck, H.E., Singh, I.B., 1973. Continental Margin, Slope and Ocean Basin. In: *Depositional*
 508 *Sedimentary Environments*. Springer Study Edition. Springer, Berlin, Heidelberg.
 509 https://doi.org/10.1007/978-3-642-96291-2_26.
- 510 Riisgård, H.U., Larsen, P.S., 2000. Comparative ecophysiology of active zoobenthic filter feeding,
 511 essence of current knowledge. *J. Sea Res.* 44, 169–193. [https://doi.org/10.1016/S1385-](https://doi.org/10.1016/S1385-1101(00)00054-X)
 512 [1101\(00\)00054-X](https://doi.org/10.1016/S1385-1101(00)00054-X)
- 513 Romero-Romero, S., Miller, E.C., Black, J.A., Popp, B.N., Drazen, J.C., 2021. Abyssal deposit feeders are
 514 secondary consumers of detritus and rely on nutrition derived from microbial communities in their
 515 guts. *Sci Rep* 11, 12594. <https://doi.org/10.1038/s41598-021-91927-4>
- 516 Röpke, A., Nellen, W., Piatkowski, U., 1993. A comparative study on the influence of the pycnocline on
 517 the vertical distribution of fish larvae and cephalopod paralarvae in three ecologically different areas
 518 of the Arabian Sea. *Deep-Sea Res. Pt II* 40, 801–819.
- 519 Sempéré, R., Charrière, B., Van Wambeke, F., Cauwet, G., 2000. Carbon inputs of the Rhône River to
 520 the Mediterranean Sea: Biogeochemical implications. *Glob. Biogeochem. Cy.* 14, 669–681.
- 521 Steffan, S.A., Chikaraishi, Y., Dharampal, P.S., Pauli, J.N., Guédot, C., Ohkouchi, N., 2017. Unpacking
 522 brown food-webs: Animal trophic identity reflects rampant microbivory. *Ecol Evol* 7, 3532–3541.
 523 <https://doi.org/10.1002/ece3.2951>
- 524 Sturbois, A., Riera, P., Desroy, N., Brébant, T., Carpentier, A., Ponsero, A., Schaal, G., 2022. Spatio-
 525 temporal patterns in stable isotope composition of a benthic intertidal food web reveal limited
 526 influence from salt marsh vegetation and green tide. *Mar. Environ. Res.* 175, 105572.
 527 <https://doi.org/10.1016/j.marenvres.2022.105572>
- 528 UNEP/MAP, M., 2019. List of marine habitat types for the selection of sites to be included in the
 529 national inventories of natural sites of conservation interest in the Mediterranean. United Nations
 530 Environment Programme Mediterranean Action Plan UNEP/MED WG.467/14.
 531 [https://wedocs.unep.org/bitstream/handle/20.500.11822/29736/19wg467_14_eng.pdf?sequence=1](https://wedocs.unep.org/bitstream/handle/20.500.11822/29736/19wg467_14_eng.pdf?sequence=1&isAllowed=y)
 532 [&isAllowed=y](https://wedocs.unep.org/bitstream/handle/20.500.11822/29736/19wg467_14_eng.pdf?sequence=1&isAllowed=y)

- 533 Vander Zanden, M.J., Clayton, M.K., Moody, E.K., Solomon, C.T., Weidel, B.C., 2015. Stable Isotope
534 Turnover and Half-Life in Animal Tissues: A Literature Synthesis. PLoS ONE 10, e0116182.
535 <https://doi.org/10.1371/journal.pone.0116182>
- 536 Ward, B.A., Dutkiewicz, S., Jahn, O., Follows, M.J., 2012. A size-structured food-web model for the
537 global ocean. *Limnol. Oceanogr.* 57, 1877–1891. <https://doi.org/10.4319/lo.2012.57.6.1877>
- 538 Wilson, J.C., Elliott, M., 2009. The habitat-creation potential of offshore wind farms. *Wind Energ.* 12,
539 203–212. <https://doi.org/10.1002/we.324>
- 540

541 Captions of the tables and figures

542

543 Table 1. Information on food sources and consumers collected on both sampling dates. Identity, short
 544 identity name (Name code), feeding groups (FG): active suspension feeders (AS), carnivores (C),
 545 passive suspension feeders (PS), surface deposit feeders (SD), sub-surface deposit feeders (SSD); mean
 546 $\delta^{13}\text{C}$ value (‰); mean $\delta^{15}\text{N}$ value (‰), standard deviation (sd); number of individuals (n). Taxa are
 547 classified by feeding groups. Values in italics report a single measure for a group of several individuals.

548

549 Table 2. Additional information on consumers collected either on April or on September, or
 550 represented only by one individual. Identities, feeding groups (FG): carnivores (C), passive suspension
 551 feeders (PS), surface deposit feeders (SD), sub-surface deposit feeders (SSD); $\delta^{13}\text{C}$ value (‰); $\delta^{15}\text{N}$
 552 value (‰), standard deviation (sd); number of individuals (n).

553

554 Table 3. Layman's community metrics calculated from taxa represented by several individuals at both
 555 sampling dates (April and September).

556

557 Figure 1: Map of the Gulf of Lions. Outline of the "Parc Naturel Marin du Golfe du Lion" (PNMGL).
 558 Locations of the sampling area (study site) and the long-term observation site (POLA).

559

560 Figure 2: Water column salinity (a) and temperature (b) in April and September 2018 at the sampling
 561 site and temperature profile (c) from September 2017 to September 2018 at POLA station, the nearest
 562 continental shelf monitoring site.

563

564 Figure 3: Distribution of taxa in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ plane before and after the thermal stratification period.
 565 The food sources SPOM and SOM correspond to suspended and sediment particulate organic matter,
 566 respectively. Taxa are classified by feeding groups: AS, active suspension feeders; PS, passive
 567 suspension feeders; SD, surface suspension feeders; SSD, sub-surface deposit feeders; and C,
 568 carnivores. Each point corresponds to a taxa or a food source.

569

570 Figure 4: Comparison of $\delta^{15}\text{N}$ values measured in the 19 benthic species sampled at the beginning and
 571 end of the summer stratification period. Taxa are classified by feeding groups: AS, active suspension
 572 feeders; PS, passive suspension feeders; SD, surface deposit feeders; SSD, sub-surface deposit feeders;
 573 and C, carnivores. Horizontal and vertical bars correspond to standard deviations. Correspondence
 574 between the codes and the complete names of species is presented Table 1.

575

576 Figure 5: Trophic trajectories of the taxa sampled both on April and September. The arrows show the
 577 displacement of the species within the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ plane. Solid and empty symbols account for average
 578 position of taxa in April and September, respectively. Polygons account for the area of the isotopic
 579 niche in April (blue) and in September (red). Taxa are classified by trophic groups: AS, active
 580 suspension feeders; PS, passive suspension feeders; SD, surface deposit feeders; SSD, sub-surface
 581 deposit feeders; and C, carnivores.

582 Table 1

583

Sources/phylum	Taxa	Name code	FG	April			September		
				$\delta^{13}\text{C}$ (sd)	$\delta^{15}\text{N}$ (sd)	n	$\delta^{13}\text{C}$ (sd)	$\delta^{15}\text{N}$ (sd)	n
Source	Suspended particulate organic matter	SPOM		-24.6 (0.5)	5.7 (0.9)	6	-23.7 (0.2)	6.0 (1.1)	6
Source	Sediment organic matter	SOM		-21.8 (0.1)	4.4 (0.4)	3	-21.8 (0.2)	4.4 (0.5)	3
Mollusca	<i>Acanthocardia echinata</i>	<i>Aca</i>	AS	-20.6 (0.1)	2.4 (0.1)	5	-20.0 (0.4)	4.2 (0.2)	5
Arthropoda	<i>Ampelisca</i> sp.	<i>Amp</i>	AS	-21.9 -	2.6 -	11	-21.4 -	4.0 -	6
Arthropoda	<i>Maera grossimana</i>	<i>Mae</i>	AS	-21.5 (0.3)	3.1 (0.8)	18	-21.4 -	4.5 -	16
Echinodermata	<i>Astropecten aranciacus</i>	<i>Ast</i>	C	-19.7 (0.5)	4.2 (0.1)	5	-19.0 (0.8)	6.0 (0.6)	5
Mollusca	<i>Galeodea rugosa</i>	<i>Gal</i>	C	-19.5 (0.4)	6.5 (0.0)	4	19.2 (0.9)	6.6 (0.2)	3
Annelida	<i>Glycera fallax</i>	<i>Gly</i>	C	-19.4 -	9.3 -	6	-18.6 (0.4)	9.6 (0.6)	5
Annelida	<i>Labioleanira ylheni</i>	<i>Lab</i>	C	-18.3 (0.3)	7.1 (0.2)	3	-18.3 (0.7)	7.2 (0.4)	3
Arthropoda	<i>Liocarcinus depurator</i>	<i>Lio</i>	C	-21.2 (0.4)	4.8 (0.3)	5	-20.9 (0.8)	7.2 (0.3)	5
Annelida	<i>Lumbrineris</i> sp	<i>Lum</i>	C	-19.8 (0.3)	8.4 (0.3)	12	-19.8 (0.3)	7.8 (0.4)	25
Annelida	<i>Nephtys kersivalensis</i>	<i>Neph</i>	C	-18.0 (0.5)	7.6 (0.6)	5	-18.0 (0.4)	7.7 (0.4)	5
Actinopterygii	<i>Trigla lyra</i>	<i>Tri</i>	C	-19.0 (0.1)	8.5 (0.5)	5	-18.9 (0.4)	9.2 (0.4)	4
Echinodermata	<i>Ocnus planci</i>	<i>Ocn</i>	PS	-17.6 (1.2)	6.4 (0.4)	3	-19.2 (0.6)	5.7 (0.7)	4
Arthropoda	<i>Alpheus glaber</i>	<i>Alp</i>	SD	-21.6 (0.3)	4.2 (0.6)	4	-20.9 (0.1)	5.7 (0.5)	5
Annelida	<i>Cirratulidae</i>	<i>Cir</i>	SD	-21.1 -	4.7 -	5	-21.1 (0.3)	5.5 (0.0)	6
Arthropoda	<i>Goneplax rhomboides</i>	<i>Gon</i>	SD	-22.3 (1.1)	4.3 (1.0)	5	-21.6 (0.1)	5.4 (0.5)	5
Echinodermata	<i>Leptopentacta elongata</i>	<i>Lep</i>	SD	-17.9 (1.3)	4.5 (0.9)	5	-17.5 (0.7)	5.6 (1.1)	5
Arthropoda	<i>Tuberapseudes echinatus</i>	<i>Tub</i>	SD	-21.1 (0.4)	2.6 (0.1)	3	-21.2 -	4.3 -	10
Echinodermata	<i>Oestergrenia digitata</i>	<i>Oes</i>	SSD	-18.6 (0.2)	7.1 (0.3)	5	-18.3 (0.5)	7.3 (0.4)	5
Annelida	<i>Sternaspis scutata</i>	<i>Ste</i>	SSD	-18.5 (0.7)	6.2 (0.2)	6	-18.7 (1.2)	5.8 (0.5)	8

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585 Table 2

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Phylum	Taxa	FG	April					September				
			$\delta^{13}\text{C}$	(sd)	$\delta^{15}\text{N}$	(sd)	n	$\delta^{13}\text{C}$	(sd)	$\delta^{15}\text{N}$	(sd)	n
Actinopterygii	<i>Arnoglossus laterna</i>	C	-18.6	-	10.3	-	1	-	-	-	-	-
Actinopterygii	<i>Callionymus lyra</i>	C	-	-	-	-	18.9	(0.1)	8.0	(0.1)	2	
Actinopterygii	<i>Gobius paganellus</i>	C	-17.6	-	10.7	-	1	18.7	(0.1)	9.9	(0.1)	3
Annelida	<i>Goniadidae</i>	C	-19.2	-	9.8	-	1	19.7	-	9.1	-	1
Annelida	<i>Harmothoe</i> sp.	C	-20.2	-	4.3	-	1	-	-	-	-	
Annelida	<i>Marphysa bellii</i>	C	-17.4	-	8.6	-	1	18.5	(0.3)	7.2	(0.3)	5
Actinopterygii	<i>Merluccius merluccius</i>	C	-	-	-	-	19.3	-	8.8	-	1	
Actinopterygii	<i>Microchirus variegatus</i>	C	-18.1	-	9.6	-	1	19.4	(0.4)	7.4	(0.6)	2
Nemertini	<i>Nemertea</i>	C	-19.3	-	6.4	-	1	-	-	-	-	
Arthropoda	<i>Processa</i> sp.	C	-20.9	-	4.1	-	1	19.9	(1.0)	6.9	(0.5)	6
Annelida	<i>Scoletoma</i> sp.	C	-17.6	-	12.1	-	1	-	-	-	-	
Actinopterygii	<i>Serranus hepatus</i>	C	-18.4	-	9.7	-	1	18.6	-	9.8	-	1
Arthropoda	<i>Solenocera membranacea</i>	C	-	-	-	-	19.5	(0.3)	7.9	(0.4)	5	
Actinopterygii	<i>Trachinus draco</i>	C	-18.3	-	10.3	-	1	-	-	-	-	
Actinopterygii	<i>Trisopterus minutus</i>	C	-	-	-	-	18.9	(0.2)	9.4	(0.5)	2	
Cnidaria	<i>Alcyonium palmatum</i>	PS	-17.2	-	4.8	-	1	16.1	(0.7)	6.3	(0.4)	5
Cnidaria	<i>Andresia</i> sp.	PS	-22.2	(0.2)	4.9	(0.3)	4	-	-	-	-	
Echinodermata	<i>Antedon bifida</i>	PS	-	-	-	-	21.2	(0.5)	5.5	(0.3)	5	
Cnidaria	<i>Pennatula phosphorea</i>	PS	-18.5	-	6.0	-	1	19.0	(0.3)	6.4	(0.2)	4
Annelida	<i>Sabellida</i>	PS	-20.3	-	5.4	-	1	-	-	-	-	
Cnidaria	<i>Veretillum cynomorium</i>	PS	-	-	-	-	21.2	(1.1)	7.2	(0.2)	3	
Annelida	<i>Ampharetidae</i>	SD	-20.8	-	3.9	-	11	-	-	-	-	
Echinodermata	<i>Amphiura filiformis</i>	SD	-20.5	(1.3)	4.9	(2.6)	2	-	-	-	-	
Arthropoda	<i>Inachus dorsettensis</i>	SD	-21.6	-	3.0	-	1	-	-	-	-	
Arthropoda	<i>Macropodia longipes</i>	SD	-21.5	(0.6)	3.6	(0.1)	2	-	-	-	-	
Annelida	<i>Magelona</i> sp.	SD	-21.3	-	3.9	-	1	-	-	-	-	
Annelida	<i>Pista</i> sp.	SD	-	-	-	-	21.0	-	6.0	-	1	
Annelida	<i>Spionidae</i>	SD	-20.1	-	5.5	-	1	20.3	(0.6)	4.0	(0.2)	4
Annelida	<i>Terebellides</i> sp.	SD	-20.0	-	4.5	-	4	-	-	-	-	
Annelida	<i>Capitella</i> sp.	SSD	-16.3	-	9.4	-	1	-	-	-	-	
Prochordata	<i>Glandiceps</i> sp.	SSD	-	-	-	-	18.6	-	8.7	-	1	
Annelida	<i>Maldanidae</i>	SSD	-	-	-	-	19.1	(0.2)	7.9	(0.3)	4	
Annelida	<i>Notomastus</i> sp.	SSD	-17.8	-	7.0	-	1	-	-	-	-	
Mollusca	<i>Nucula</i> sp.	SSD	-	-	-	-	19.0	(0.6)	5.5	(0.4)	2	

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588 Table 3

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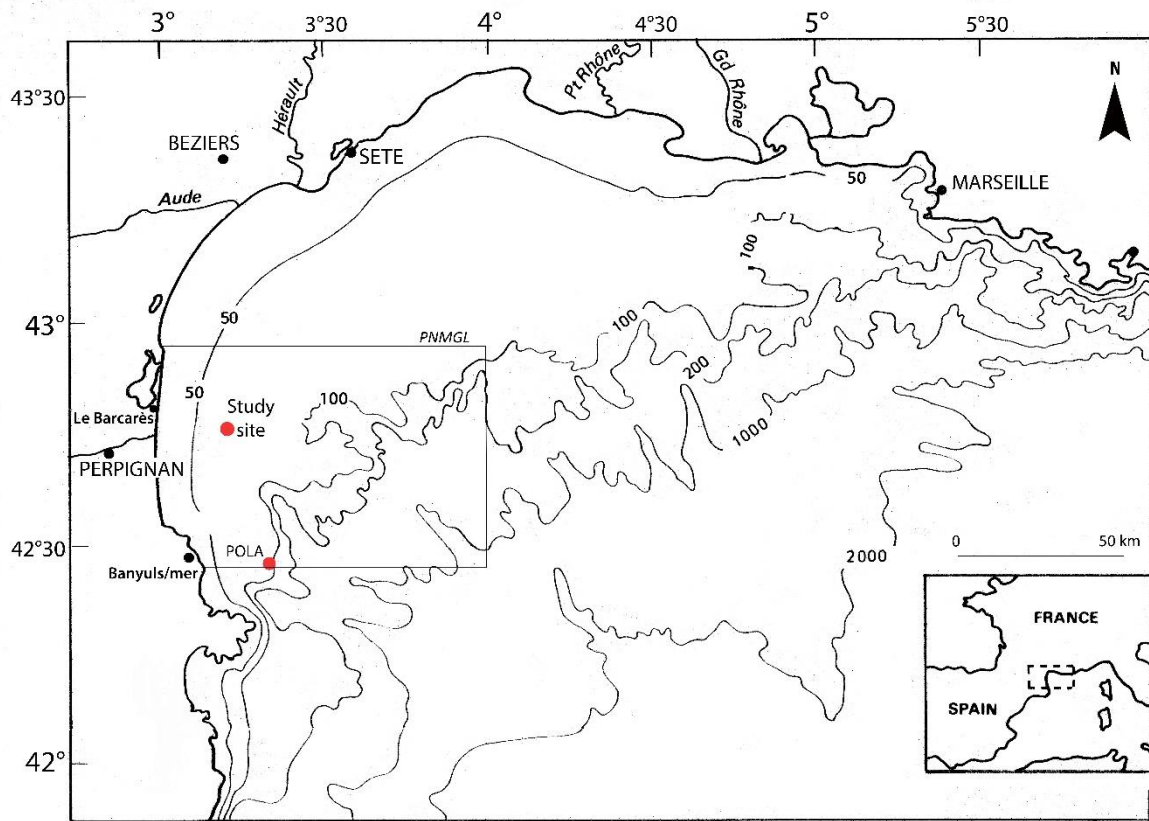
Metric, <i>information</i>	April	September
$\delta^{15}\text{N}$ range (NR), <i>diversity of trophic levels</i>	6.9	5.0
$\delta^{13}\text{C}$ range (CR), <i>diversity of basal resources</i>	4.5	3.1
Total area (TA), <i>extent of trophic diversity</i>	20.2	13.8
Mean distance to centroid (CD), <i>degree of trophic diversity</i>	2.5	1.9
Mean nearest neighbor distance (MNND), <i>density of species packing</i>	0.32	0.23
Standard deviation of MNND (SDMNND), <i>evenness of species packing</i>	0.27	0.19

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592 Figure 1

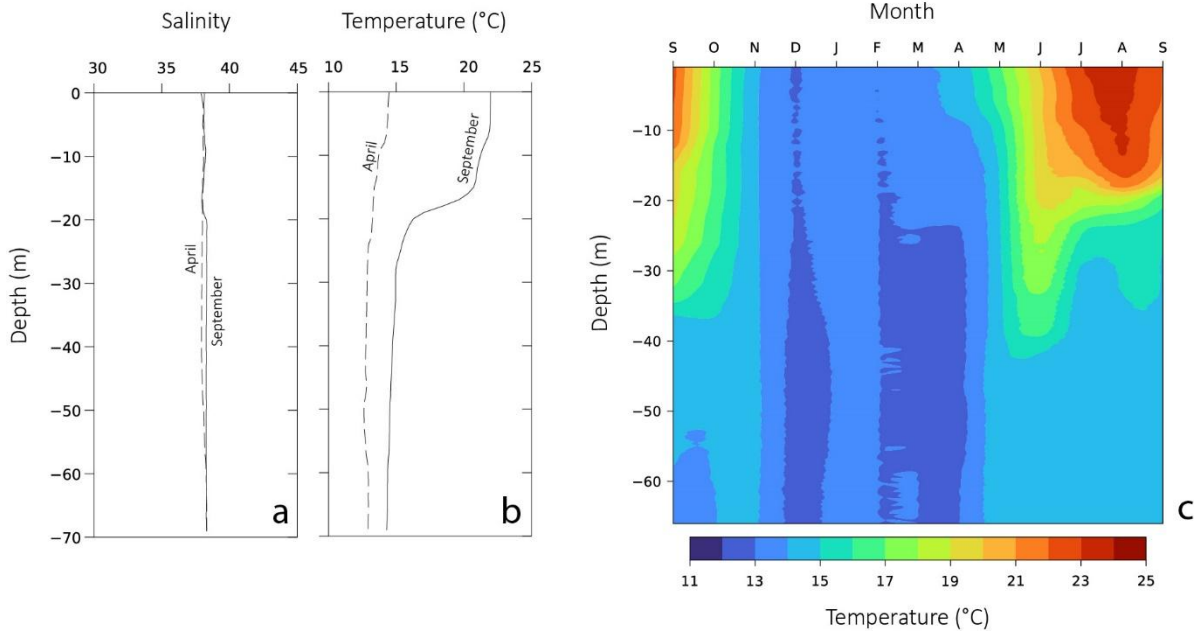
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596 Figure 2

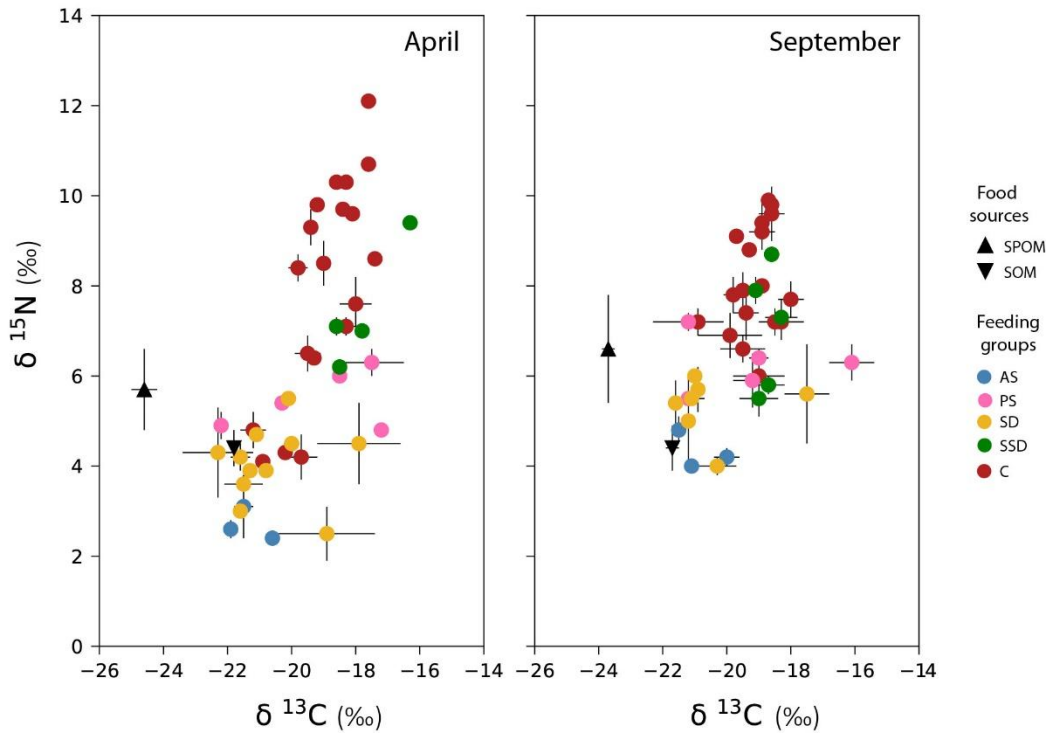


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598 Figure 3

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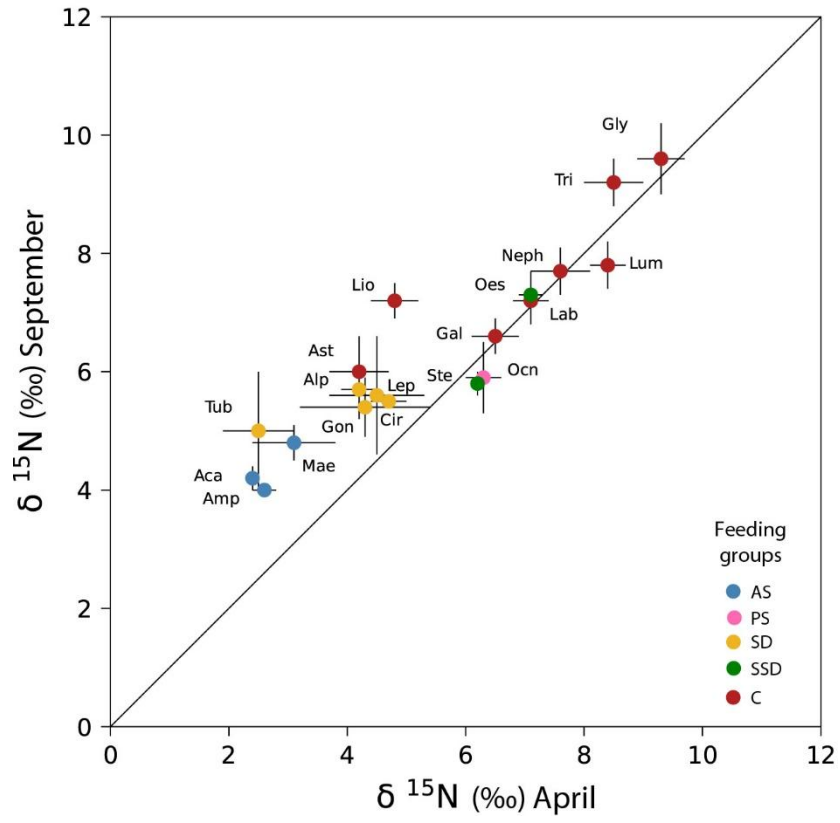


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603 Figure 4

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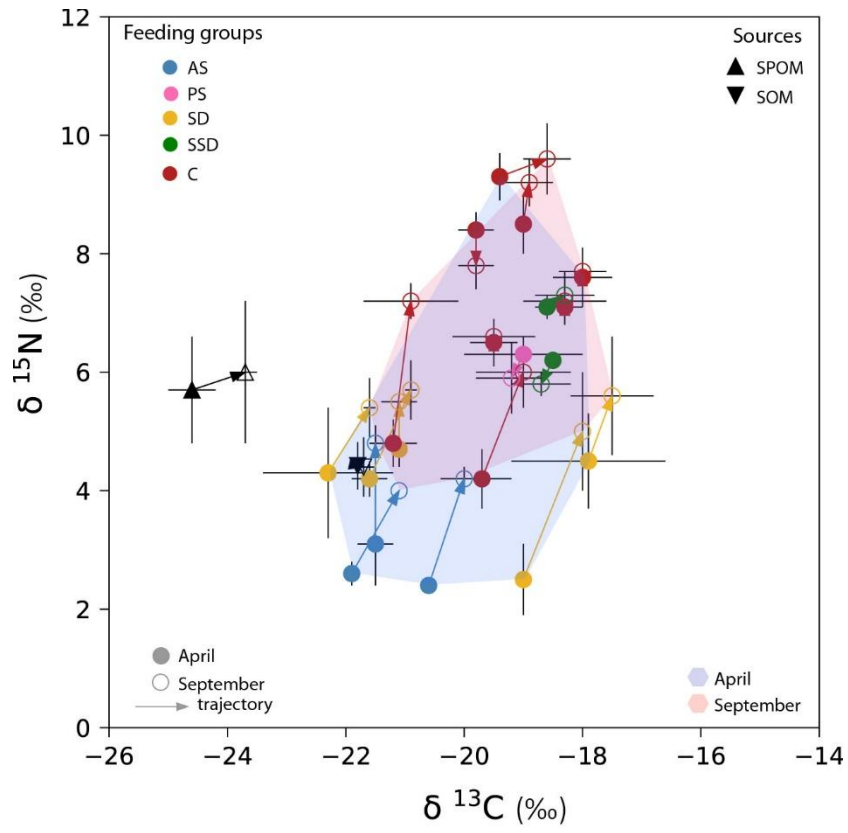


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606 Figure 5

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