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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 Due to its extensive continental shelf, the Gulf of Lion, situated in the northwestern Mediterranean Sea,
24 plays a crucial role in providing ecological services amidst various natural and anthropogenic pressures.
25 Exposed to the impacts of climate change and suitable for marine energy development projects, the
26 conservation of marine biodiversity in this environment raises significant concerns. To detect any
27 potential disturbances in the functioning of the terrigenous mud community on the continental shelf,
28 we conducted stable carbon and nitrogen isotope analyses on suspended particulate organic matter,
29 sediments, and benthic fauna. Since seasonality is a structuring factor for the functioning of such an
30 oligotrophic ecosystem, we conducted two sampling campaigns in 2018 to capture contrasting
31 scenarios of water column stratification — one in April during well-mixed conditions and high
32 phytoplankton production, and another in September at the end of the summer thermal stratification
33 period characterized by low primary productivity. Stable isotope analysis revealed changes in the
34 structure of the benthic food web in response to seasonal stratification of the water column. While
35 isotopic niches of taxa remained evenly distributed, the total niche space contracted between sampling
36 dates, primarily affecting low trophic level consumers. The observed contraction aligns with that
37 reported at the base of the pelagic food web. These results enhance our understanding of the
38 functioning of the continental shelf of the Gulf of Lion. The intense trawling pressure on the study site
39 affected sampling. In this context, this research contributes not only to the knowledge of seasonal
40 trophic variations but also provides a reference state to understand the future of this Mediterranean
41 continental shelf.

42

43

44 Keywords

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

46

47 1. Introduction

48

49 The submerged continental shelves representing only 5.5% of the global oceanic area (Reineck and
50 Singh, 1973) play a crucial role in marine ecosystems. These transitional zones receive inputs of both
51 solid and dissolved materials from river runoff. They are characterized by high primary production and
52 serve as feeding grounds for numerous marine species (Hall, 2002). Additionally, their shallowness and
53 proximity to coastlines make them suitable for various human activities, including the exploitation of
54 living resources, mineral resources, fossil fuel deposits (Amoroso et al., 2018; Grassle, 2013; Rajput and
55 Thakur, 2016), and the deployment of offshore wind farms (Loughney et al., 2021). This multifaceted
56 use raises significant concerns regarding the conservation of marine biodiversity in these environments.

57 In the Mediterranean Sea, continental shelves are often narrow and notably heterogeneous (Harris et
58 al., 2014). The Gulf of Lions, located in the northern part of western basin, defines a substantial
59 continental shelf extending over 15,000 km². Benthic communities, in this region, rely on organic matter
60 from the water column as their primary food source (Cresson et al., 2020). The sinking particles primarily
61 originate from epipelagic marine primary production, although locally significant inputs of continental
62 origin from rivers are observed (Bourgeois et al., 2011; Charles et al., 2014; Darnaude et al., 2004).
63 Regardless of their origin, the food sources at the base of the benthic food web consist mainly of
64 decaying or dying matter (Turner, 2015).

65 The Mediterranean Sea exhibits typical oceanographic characteristics of an oligotrophic system,
66 characterized by alternating periods of mixing and stratification (Miquel et al., 1994; Moutin et al.,
67 2012). During autumn through late spring, the water mass is well mixed, and phytoplankton biomass,
68 ranging from 0.2 to 1.4 mg Chl-a m⁻³ (Hunt et al., 2017), is relatively high. However, during summer, the
69 input of solar radiation causes thermal stratification, creating a warm surface water layer separated
70 from the deeper cold-water mass. The upper water layer becomes depleted in nutrients, and the deep
71 water becomes light-limited (Mignot et al., 2014). Consequently, phytoplankton biomass drastically
72 decreases by one to two orders of magnitude (0.027 mg Chl-a m⁻³ in Mena et al., 2019). This period
73 typically follows a spring phytoplankton bloom and is sometimes succeeded by smaller blooms in
74 autumn (Siokou-Frangou et al., 2010). Therefore, most of the carbon export to the seafloor occurs
75 outside the summer period (Miquel et al., 1994).

76 The ecological functions in these oligotrophic systems are significantly influenced by the size structure
77 and taxonomic diversity of phytoplankton communities (Mena et al., 2019). Different size fractions are
78 associated with varying elemental compositions (Ward et al., 2012), and there is a substantial increase
79 in carbon and nitrogen stable isotope ratios between pico-, nano-, and micro-particle size fractions

80 (Hunt et al., 2017). Notably, in the northwestern Mediterranean, the contribution of picophytoplankton
81 is maximized when the total chlorophyll-a biomass is low, with picophytoplankton accounting for over
82 60% of the total biomass in late summer (Charles et al., 2005; Lantoine, 1995; Mena et al., 2019).

83 Within the marine food web, the stable isotope composition of consumers reflects that of their primary
84 food source (Michener and Lajtha, 2007; Rau et al., 1981). Carbon isotope composition in consumers
85 provides insights into the primary food source, while nitrogen isotope composition indicates their
86 trophic position in the food web (Post, 2002). Given the isotopic differences between terrestrial and
87 marine organic matter and the isotopic heterogeneity among different size classes of marine organic
88 particles (Rau et al., 1990), changes at the base of the food web are expected to influence the stable
89 isotope composition of consumers.

90 Combining studies on benthic food webs in and around the Gulf of Lions reveals several key trends. The
91 complexity of these networks remains consistent across diverse habitats (Carlier et al., 2009, 2007a,
92 2007b; Charles et al., 2017; Darnaude et al., 2004; Fanelli et al., 2013, 2011; Nahon et al., 2012). Even
93 in areas influenced by terrestrial inputs, benthic communities exhibit a dependence on pelagic primary
94 production (Carlier et al., 2007b; Cresson et al., 2020; Darnaude et al., 2004). The structure of benthic
95 food webs is intricately influenced by distance from the coast and depth (Cresson et al., 2020; Darnaude
96 et al., 2004; Fanelli et al., 2011). Moreover, seasonality emerges as a key factor influencing food webs
97 across habitats (Carlier et al., 2007a; Coma et al., 2009; Fanelli et al., 2011; Mena et al., 2019). In light
98 of these observations, conducting thorough seasonal investigations in an area heavily impacted by
99 intensive trawling (Jac et al., 2021) and currently under consideration for a floating offshore wind farm
100 is imperative. The anticipated modifications to benthic communities with the installation of wind
101 turbines (Raoux et al., 2017) underscore the need for comprehensive contextualization of future
102 changes. This becomes particularly crucial in a region already dealing with the repercussions of ongoing
103 climatic shifts (Tramblay and Somot, 2018; Zittis et al., 2019).

104 The primary objective of this study is thus to investigate the impact of the seasonal thermal stratification
105 on the structuring of the coastal terrigenous mud community (UNEP/MAP, 2019). We aim to achieve
106 this by conducting stable carbon and nitrogen isotope analyses on suspended particulate organic
107 matter, sediments, and benthic fauna during two distinct seasons. Through this research, we seek to
108 enhance our understanding of how seasonal thermal stratification influences the trophic dynamics of
109 this ecosystem.

110

111

112 2. Material and methods

113 This study was conducted within the framework of the APPEAL research program (Approches socio-
114 écosystémiques de l'impact des parcs éoliens flottants), which is dedicated to investigating the impact
115 of Floating Offshore Wind Farms (FOWF) prior to pilot site establishment. The overarching goal was to
116 define the environmental, ecological, and socio-economic baseline, encompassing usage patterns,
117 perceptions, and acceptability at future FOWF installation sites.

118

119 2.1. Study area

120 This study was conducted in the Gulf of Lions, located in the Mediterranean Sea, France (Figure 1). In
121 this region, the continental shelf spans over 15,000 km², with a depth interruption at 110-120 m and a
122 variable width ranging from 5 to 70 km. The outer edge features several submarine canyons. The
123 biogeochemical functioning processes of the Gulf of Lions are notably influenced by the Rhone River,
124 serving as the primary source of freshwater and nutrients for the Mediterranean Sea (Sempéré et al.,
125 2000). Sampling occurred within the Parc Naturel Marin du Golfe du Lion, situated 14.4 km off Le
126 Barcarès (7.7 nautical miles), at a depth of 74 m (42°42'59" N; 3°13'10" E) within an area designated for
127 a future pilot FOWF.

128

129 2.1. Water column

130 We conducted measurements of salinity and temperature at the study site during both sampling
131 periods, which occurred in April and September 2018, using the Sea-Bird Scientific (USA) SeaCAT CTD
132 SBE 19plus V2 profiler. Additionally, we collected monthly temperature profiles retrieved from the
133 nearest long-term observation site on the Gulf of Lions shelf, known as the "Plateau Observatory
134 Laboratoire Arago" station. The POLA station is located at coordinates 42°28'18" N and 03°15'30" E,
135 approximately 27.3 km (or about 14.8 nautical miles) away from our study site, positioned at a depth of
136 95 meters and situated 5 nautical miles from the coast. More detailed information about this
137 observatory site can be found at <https://www.obs-banyuls.fr/en/observe/observation-sites.html>.

138

139 2.2 Sampling of food sources and consumers

140 We conducted sampling on April 20th and September 19th, 2018. To analyze the stable isotope
141 composition of suspended particulate organic matter (SPOM) accessible to benthic primary consumers,

142 we collected water samples about 2 m above the sediment using a 10L-Niskin® container. These samples
143 were subsequently filtered through 200 µm mesh to eliminate most zooplanktonic organisms and large
144 detritus. SPOM was isolated by filtering the samples through pre-combusted Whatman GF/F filters (25
145 mm in diameter, 0.7 µm pore size). The filtered materials were then placed in individual Petri dishes and
146 dried in an oven at 50°C overnight. Following drying, the filters were stored in a dark environment inside
147 a desiccator until further analysis.

148 We collected sediment organic matter (SOM) using a Van Veen grab. A sample of the upper undisturbed
149 sediment layer (i.e. <1 cm thick) was collected in three grabs. These samples were then frozen and
150 freeze-dried using a Christ Alpha 1-4LD freeze-dryer. Afterwards, the dried samples were finely ground
151 using a mortar and pestle.

152 We collected demersal fish and epibenthic invertebrate megafauna using a 2-meter beam trawl
153 equipped with a chain and a 20 mm mesh net. For benthic infauna, we employed a Charcot dredge with
154 an opening of 59 x 23 cm (width x height) and a bag mesh size of 0.5 mm. Each gear underwent three
155 10-minute hauls. Back in the laboratory, organisms were identified to the lowest possible taxonomic
156 level.

157 Given that trophic level and body size are strongly correlated in marine environments and because
158 ontogenetic trophic niche shifts may occur (Hammerschlag-Peyer et al., 2011; Methou et al., 2020;
159 Potapov et al., 2019), we consider this variable when collecting specimens for stable isotope analyses.
160 Using a ruler, we measured the longest dimension of the entire animals collected on both sampling
161 dates. We extracted part of the dorsal muscle of fish, while other animals were temporarily placed in
162 filtered seawater (GF/F) overnight to facilitate the emptying of their digestive tracts. Bivalves and
163 gastropods were subsequently de-shelled. All samples were individually stored, initially frozen at -20°C
164 and subsequently subjected to freeze-drying. Once dried, the samples were ground into a homogeneous
165 powder using a TissueLyser II (Qiagen).

166 We categorized taxa into five feeding groups (FG) using information sourced from databases like the
167 Biological Traits Information Catalogue developed by the Marine Life Information Network (Marlin,
168 2006); reviews on feeding behaviors (e.g. Jumars et al., 2015; Macdonald et al., 2010; Riisgård and
169 Larsen, 2000); primary literature detailing species' feeding behaviors; insights into feeding structures
170 morphology, and expert knowledge. Based on this assessment, we defined active suspension feeders
171 (AS) as species that actively pump surrounding water to feed on suspended micro-organisms and
172 detritus. They generate water current to direct food particles towards their feeding appendages
173 (Riisgård and Larsen, 2000; MarLIN, 2006; Jumars et al., 2015). Passive suspension feeders (PS) were
174 classified as species that passively capture suspended particles, relying on natural water flow or particle
175 motion to bring particles into contact with their feeding structures (Riisgard and Larsen, 2000; MarLIN,
176 2006; Jumars et al., 2015). Surface deposit feeders (SD) were identified as species that feed on

177 fragmented particulate organic matter found on the surface of the substratum (Macdonald et al., 2010;
 178 Marlin, 2006, 2006). Sub-surface deposit feeders (SSD) were defined as species that feed on fragmented
 179 particulate organic matter within the substratum (MarLIN, 2006). Finally, carnivores (C) were mobile
 180 predator and scavenging species that feed on prey and/or dead organisms (MarLIN, 2006).

181

182 2.3 Stable isotope analysis

183 Stable isotope analyses were performed with a continuous flow mass spectrometer (Delta V+ with a
 184 conflo IV interface, Thermo Scientific, Bremen, Germany) coupled to an elemental analyzer (Flash EA
 185 2000, Thermo Scientific, Milan, Italy) at the Pôle Spectrométrie Océan (Plouzané, France). Results were
 186 expressed in standard δ notation based on international standards, Vienna Pee Dee Belemnite (VPDB)
 187 for $\delta^{13}\text{C}$ and atmospheric nitrogen (Atmos. N_2) for $\delta^{15}\text{N}$ following the formula:

188

$$189 \quad \delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3 \quad (\text{in } \text{‰})$$

190

191 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,
 192 USGS-62 and USGS-63. Analytical error was estimated by replicate measurements (every six samples)
 193 of an internal standard Thermo –Acetanilide. Measurement uncertainty was estimated $\pm 0.08 \text{ ‰}$ and \pm
 194 0.11 ‰ for Nitrogen and Carbon respectively.

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

200

201 2.4 Data treatment

202 For each sampling date, taxa were presented as a cluster of points in the δ plane, where $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
 203 values determining their positions on the horizontal and the vertical axis, respectively. We assessed the
 204 association between mean $\delta^{15}\text{N}$ measurements and consumers size by calculating correlation and
 205 testing the significance of the correlation using a Pearson correlation test on data collected during both
 206 sampling dates. To quantitatively compare the distribution of points within the δ plane between the
 207 sampling dates, we applied the “community-wide” metrics introduced by Layman et al. (2007). These
 208 metrics included the calculation of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ value ranges (CR and NR, respectively), which
 209 represented the difference between the highest and lowest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Additionally, the total
 210 area (TA), was determined as the area enclosed by the minimum convex envelope that encompassed
 211 all data points. The mean distance to the centroid (CD) indicated the average Euclidean distance from

212 each point to the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value of all points. Moreover, the mean nearest neighbor distance
213 (MNND) was computed as the average Euclidean distance to the nearest neighboring point, with SDNND
214 representing the standard deviation to this mean. As the calculation of these metrics depends on species
215 richness, and the number and types of species collected varied between sampling sessions (i.e., April
216 and September), we computed metrics exclusively for taxa present during both dates.

217 For each of these taxa, we calculated the trophic seasonal trajectory, including its length and direction.
218 This trajectory was determined as the Euclidean vector defined by the displacement of the taxon's
219 position within the δ plane between the two sampling dates, following the approach proposed by
220 Sturbois et al. (2022).

221 We conducted two-factor analyses of variance to simultaneously evaluate the impact of sampling date
222 and factors related to taxa or feeding groups on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. To assess the difference in mean
223 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between the two sampling dates, we conducted permutation Student's t-tests for
224 each taxon and feeding group. All data analyses were carried out using the R software environment
225 3.4.3 (R Core Team, 2020), employing generalized linear models and the 'perm.t.test' function, with
226 1000 permutations, from the Student's t-test in the R package 'RVAideMemoire' ([https://cran.r-](https://cran.r-project.org/package=RVAideMemoire)
227 [project.org/package=RVAideMemoire](https://cran.r-project.org/package=RVAideMemoire)). A p-value below 0.05 indicated the rejection of the null
228 hypothesis, i.e., either no difference between means or no interaction between factors.

229

230 **3. Results**

231 **3.1 Seasonal thermal stratification**

232 Irrespective of the date, whether in April or September, salinity consistently remained around 38.2
233 throughout the entire water column's depth (Figure 2a). We observed the development of a 10-20 m
234 thick summer thermocline (Figure 2b, 2c). Between May to October, this stratification partitioned the
235 water column into a lower layer with a temperature close to 13°C and an upper layer with an average
236 temperature between 20 and 24°C. Conversely, from late autumn to April, the water column was
237 thoroughly mixed, maintaining an average temperature near 13°C. The sampling dates defined the
238 stratification period of the water column on the Gulf of Lion continental shelf.

239

240 **3.2 Sample collection**

241 All fish, the majority of crustaceans, echinoderms, cnidarians and mollusks were captured using a beam
242 trawl. The Charcot dredge was employed to sample small crustaceans, sub-surface deposit feeders and
243 almost all annelids. In total, we identified 54 taxa, with 43 observed in April, 38 in September and 28
244 found in both sampling periods (Table 1 and Table 2). We collected more species in April than in
245 September, but many taxa were represented by just one individual (Table 2). Therefore, statistical tests,

246 Layman metrics and trophic trajectories were conducted on taxa collected during both sampling
247 campaigns and represented by several individuals (Table 1).

248

249 3.3 Stable isotope analysis

250 3.3.1 Basal food sources

251 The sole noteworthy temporal alteration in the isotopic composition of food sources between the two
252 sampling dates was observed in the $^{13}\text{C}/^{12}\text{C}$ ratio of suspended particulate organic matter (SPOM). In
253 April, the SPOM showed a significant ^{13}C depletion ($-24.6 \pm 0.5 \text{‰}$) compared to September (-23.7 ± 0.2
254 ‰) (Permutation Student's t-tests, $p = 0.002$). The $\delta^{15}\text{N}$ values exhibited variability on both dates (4.4
255 to 6.9 ‰ in April, 4.5 to 8.1 ‰ in September) and no significant difference was detected. Stable isotope
256 compositions of SOM were consistent (Table 1, Figure 3) across the two dates of sampling (mean $\delta^{13}\text{C} =$
257 -21.8‰ , mean $\delta^{15}\text{N} = 4.4 \text{‰}$).

258

259 3.3.2 Consumers

260 Collecting size data, particularly for vermiform animals (e.g., worms or synaptids), posed challenges due
261 to the occasional presence of specimens in pieces or incomplete. Nevertheless, the results demonstrate
262 that isotopic ratio measurements were consistently taken for a given taxon on specimens with similar
263 sizes in both seasons. (Tables 1 and 2). Stable nitrogen isotope ratios exhibited a positive correlation
264 with consumer size measurements. The correlation coefficients (Pearson's r) revealed a moderate to
265 strong linear relationship between the variables, with r values of 0.682 ($p < 0.002$) in April and 0.757 (p
266 < 0.001) in September. Figure 3 shows the positions of the consumers in the $\delta^{13}\text{C} - \delta^{15}\text{N}$ plane for all
267 species collected on both sampling dates. The relative position of the feeding groups to each other
268 remained unchanged between April and September. The lowest trophic levels were active suspension
269 feeders (blue dots, e.g. *Acanthocardia echinata*, *Ampelisca* spp.) and surface deposit feeders (yellow
270 dots, e.g. *Alpheus glaber*, *Goneplax rhomboides*, *Tuberapseudes echinatus*, *Maera grossimana*).
271 Compared to these groups, passive suspension feeders (pink dots), mainly cnidarians (*Alcyonium*
272 *palmatum*, *Pennatula phosphorea*, *Veretillum cynomorium*) and echinoderms (*Ocnus planci*, *Antedon*
273 *bifida*), occupied a higher trophic position. The overall high $\delta^{15}\text{N}$ values of sub-surface suspension
274 feeders (green dots, e.g. *Oosteregrenia digitata*, *Sternaspis scutata*, *Notomastus* sp., *Glandiceps* sp.) were
275 close to the median value recorded for carnivores (red dots). Across all dates and taxa, the carnivorous
276 annelid *Scoletoma* sp. had the highest $\delta^{15}\text{N}$ value (i.e. 12.1 ‰). Otherwise, the highest trophic levels
277 were occupied by fish. The distribution of consumer positions in the $\delta^{13}\text{C} - \delta^{15}\text{N}$ niche space appeared
278 to contract between April and September.

279 Two-factor controlled analyses of variance indicated that differences in $\delta^{13}\text{C}$ values were significant
280 between taxa and between feeding groups (taxa, $df = 16$, $F = 20.04$, $p < 0.001$; feeding groups, $df = 4$, $F =$

281 7.15, $p < 0.001$) but not between sampling dates. In contrast, the effect of the sampling date on $\delta^{15}\text{N}$
282 (Figure 4) was different depending on the identity of the taxa (time x taxa, $df = 16$, $F = 8.88$, $p < 0.001$)
283 and feeding groups (time x feeding groups, $df = 4$, $F = 3.68$, $p = 0.007$). Concerning active suspension
284 feeders and surface deposit feeders, mean $\delta^{15}\text{N}$ values significantly increased between April and
285 September (permutation Student's t-tests, $p < 0.002$, for both feeding groups). No temporal change was
286 observed for the passive suspension feeder *O. planci* (permutation Student's t-tests, $p = 0.198$) and the
287 sub-surface deposit feeders, *O. digitata* and *S. scutata* (permutation Student's t-tests, $p = 0.587$ and
288 $p = 0.231$, respectively). Among carnivores, $\delta^{15}\text{N}$ increase was mainly observed in *Liocarcinus depurator*
289 and *Astropecten aranciacus* (permutation Student's t-tests, $p = 0.011$ and $p = 0.007$, respectively) and to
290 a lesser extent for the fish, *Trigla lyra* (permutation Student's t-tests, $p = 0.045$). Changes for other
291 carnivores (i.e., *Galeodea rugosa*, *Lumbrineris* sp, *Labioleanira ylheni* and *Nephtys fallax*) were not
292 statistically significant between the two sampling dates.

293

294 3.3.3 Layman's community-wide metrics

295 Layman's metrics (Table 3) were computed using the benthic community, considering only taxa
296 represented by several individuals and collected on both sampling dates. Trophic level diversity (NR),
297 defined as the difference between the maximum and minimum values of $\delta^{15}\text{N}$, declined from 6.9 ‰ in
298 April to 5.0 ‰ in September. The diversity of basal food sources, measured by $\delta^{13}\text{C}$ range (CR), similarly
299 decreased from 4.5 ‰ in April to 3.1 ‰ in September, although it remained relatively narrow. Between
300 April and September, the trophic diversity extent, total area (TA), occupied by consumers in the $\delta^{13}\text{C}$ -
301 $\delta^{15}\text{N}$ plane decreased from 20.2 to 13.8 (Table 3, Figure 5); the average distance from each point to the
302 centroid of all samples (CD) suggests a reduction in diversity from 2.5 to 1.9 ‰; species spacing (MNND)
303 and evenness of species packing (SDNND) decreased from 0.32 to 0.23 ‰ and from 0.27 to 0.19 ‰,
304 respectively. The most notable contrast observed between the two sampling campaigns was the
305 contraction in the dispersion of consumer positions in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ niche space.

306

307 3.3.4 Trophic trajectories

308 The trajectories of food sources and taxa in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ plane are depicted in Figure 5. The extent of
309 movement varied among different taxa. The most extensive trajectories were observed among active
310 suspension feeders, the majority of surface deposit feeders and low trophic level carnivores. The
311 trajectories indicated an enrichment in both ^{15}N and ^{13}C between the two dates of sampling. The
312 positions of taxa at higher trophic levels and those that feed on sub-surface deposits either remained
313 the stable or exhibited slight changes.

314

315

316 **4. Discussion**

317 Vertical temperature profiles confirmed that the sampling campaigns took place during two
318 periods characterized by very contrasting conditions. Stable isotope analysis revealed changes in the
319 structure of the benthic food web in response to the seasonal stratification of the water column.
320 Specifically, the niche space contracted during the warm conditions, predominantly affecting low
321 trophic level consumers.

322

323 *Changes in the benthic food web*

324 The difficulty of collecting multiple individuals of the same species on both sampling dates
325 suggests modifications within the benthic community. Changes in the abundance and composition of
326 benthic communities have been already observed on continental shelf regions dominated by major river
327 discharges (Aller and Stupakoff, 1996; Harmelin et al., 2009). However, the timeframe for Rhône River
328 floods does not coincide with the summer stratification period of the waters in the Gulf of Lion. As a
329 result, the variations in benthic fauna sampling between the two dates are more likely to result from a
330 disturbance resembling the impact of trawling. The sampled area is indeed recognized as one of the
331 most intensively abraded by bottom-contacting fishing gears in the Gulf of Lions
332 (<http://dx.doi.org/8bed2328-a0fa-4386-8a3e-d6d146cafe54>). Furthermore, during the September
333 sampling campaign, numerous trawling vessels were observed actively operating in the waters near our
334 study site. In support of our observations, Labrune et al. (in preparation) conducted parallel quantitative
335 sampling of endofauna, confirming a noticeable decrease in species richness and abundances between
336 April and September.

337 To highlight any notable seasonal impact on the stable isotope composition of the benthic
338 fauna, our analysis focused on species represented by multiple individuals during both sampling dates.
339 Layman's metrics applied to this set of taxa confirm the trend observed in the overall dataset, indicating
340 a contraction in the community's niche space from the beginning to the end of the stratification period.
341 Diversity of the trophic levels, total extent and degree of species spacing decreased between April and
342 September. Our results revealed shift in nitrogen isotope composition among feeding groups. Thus, the
343 $\delta^{15}\text{N}$ of carnivores increased proportionally with the $\delta^{15}\text{N}$ of their prey. The $\delta^{15}\text{N}$ of the sea star
344 *Astropecten aranciacus* or the swimming crab *Liocarcinus depurator*, which feed on active suspension
345 feeder bivalves and surface deposit feeders (Chartosia et al., 2010), increased. In contrast, the $\delta^{15}\text{N}$
346 value of the gastropod *Galeodea rugosa*, a consumer of subsurface deposit feeders (Hughes, 2008),

347 remained unchanged. High trophic level carnivores exhibited no or only slight changes, possibly
348 because the tissue isotopic turnover rate of ectotherms decreases with body (Vander Zanden et al.,
349 2015). This could explain why the observed seasonal effect in low trophic level carnivores was
350 attenuated in their higher trophic level counterparts. The reduction in the dispersion of trophic
351 positions among benthic consumers aligns with the decrease in trophic positions across different size
352 classes of zooplankton during nutrient-depleted periods in summer-autumn and in oligotrophic areas
353 (Bănaru et al., 2014; Hunt et al., 2017; Tesán-Onrubia et al., 2023). The scarcity of food resources during
354 summer likely intensifies competition interactions and omnivorous behaviors, leading to lower stable
355 isotope fractionation in higher trophic levels and increased of trophic niche overlap (Bănaru et al., 2014).
356 As documented in prior studies (Jennings et al., 2002; Potapov et al., 2019; Tesán-Onrubia et al., 2023),
357 we observed a correlation between stable nitrogen isotope ratios and the body size of consumers. Size
358 measurements indicate that temporal variations in stable isotope ratios could not be attributed to
359 ontogenetic changes in the sampled organisms between the two dates. Thus, the seasonal changes in
360 stable isotope composition across the food web resulted from seasonal variations in the composition of
361 the primary food sources.

362

363

364 *Sources of food web changes*

365 The stable isotope composition of sedimentary organic matter (SOM) remained consistent
366 between the sampling dates. The $\delta^{13}\text{C}$ value, -21.8 ‰, exceeded the reported SOM values in the region
367 directly influenced by the Rhone River, ranging from -27.2 to -24.2‰ (Bourgeois et al., 2011). This
368 discrepancy implies that SOM at our study site primarily originated from a marine source. The $\delta^{13}\text{C}$
369 values of suspended particulate organic matter (SPOM), measuring -24.6‰ in April and -23.7‰ in
370 September, closely resembled values reported for fresh marine phytoplankton, ranging from -23 to -
371 19‰ (Darnaude et al., 2004; Druffel et al., 1992; Fry and Sherr, 1989; Harmelin-Vivien et al., 2008). The
372 ^{13}C -depletion observed in April a probable contribution of continental material during that period
373 (Harmelin-Vivien et al., 2008). This is consistent with the observation that during spring, rivers, especially
374 the Rhone River, spread fine organic particles strongly depleted in ^{13}C over a large part of the Gulf of
375 Lions (Auger et al., 2011; Cauwet et al., 1990), whereas during summer the contribution of continental
376 sources is extremely low because river flows are at their lowest (Durrieu de Madron et al., 2008).

377 Establishing a robust baseline is the primary challenge in food web studies relying on stable
378 isotope ratios (Harmelin et al., 2009). In this context, nitrogen stable isotope ratios for SPOM, measured
379 at 5.7‰ in April and 6.0‰ in September, were notably elevated and did not capture the signature of
380 the phytoplankton primary source. Instead, they likely reflect a combination of phytoplankton cells and

381 phyto-detritus along with small organisms and remnants of zooplankton (Hunt et al., 2017; Tesán-
382 Onrubia et al., 2023). The downward export of carbon and nutrients from the euphotic zone involves
383 both passive and active fluxes (Schnetzler and Steinberg, 2002; Steinberg et al., 2000). Sinking organic
384 material comprises a variety of energy and nutrient sources, such as phytoplankton cells, phytodetritus,
385 fecal pellets, zooplankton remains, and aggregates of organic particles from diverse origins (Turner,
386 2015; Urrère and Knauer, 1981). The passive descent of these particles is coupled with zooplankton
387 vertical migrations, significantly contributing to the transfer of energy and nutrients to benthic
388 ecosystems. The daily vertical movement of zooplankton through the water column (Bandara et al.,
389 2021), driven by the need to optimize feeding and avoid predators, with nocturnal ascent to feed on
390 surface phytoplankton and daytime descent to evade visual predators, implies that our sampling near
391 the seafloor during daylight hours resulted in a biased representation of the food sources at the base of
392 the food web.

393 In a recent comprehensive analysis of stable isotope ratios in size-fractionated plankton across
394 the Mediterranean Sea, Tesán-Onrubia et al (2023) reported $\delta^{15}\text{N}$ values at two stations that closely
395 match our study site in terms of depth and distance from the coast. The reported $\delta^{15}\text{N}$ values range
396 from 0.5‰ for phytoplankton to 3.7‰ for small zooplankton collected within the deep chlorophyll
397 maximum. Additionally, Bănaru et al. (2014) demonstrated that the planktonic size-fraction smaller than
398 200 μm exhibits seasonal $\delta^{15}\text{N}$ variations, increasing from 1.4‰ in the cold season to nearly 4‰ in
399 summer. Therefore, the rise in $\delta^{15}\text{N}$ values observed in active suspension feeders and surface deposit
400 feeders from April to September aligns with the seasonal transition in the composition and isotopic
401 signature of their primary food sources. Indeed, this shift reflects alterations in phytoplankton growth
402 dynamics during the summer conditions marked by high temperature, low oxygen, and nutrient-
403 depleted waters (Chen et al., 2019). Plankton, nutrient fluctuations, and seasonal changes are intricately
404 interrelated (Bănaru et al., 2014; Chen et al., 2019; Hunt et al., 2017; Mena et al., 2019). Our study
405 extends the understanding of the trophic network beyond the observed patterns in the zooplankton
406 community to encompass benthic communities.

407 During warm season, the majority of the phytoplankton biomass, primarily composed of
408 picoplankton cells is concentrated within a deep chlorophyll maximum (DCM) situated below the
409 thermocline (Lantoine, 1995; Mena et al., 2019). Phytoplankton are preyed upon by zooplankton,
410 leading the entire pelagic food chain to adopt a distribution pattern based on the peak abundance of
411 prey within a spatial scale of a few meters (Röpke et al., 1993). Sinking organic material predominantly
412 comprises decaying particles. The organic material for primary consumers undergoes a dual reduction,
413 both in quantity and digestibility (Coma et al., 2009). Consequently, the trophic conditions resemble
414 those encountered by sub-surface deposit feeders, specialists in consuming poorly digestible and highly
415 diluted sedimentary organic matter. In benthic food webs, sub-surface deposit feeders have $\delta^{15}\text{N}$ values

416 close to those of above-sediment secondary consumers. Expanding on the insights from Romero-
417 Romero et al (2021) concerning deep-sea deposit feeders, microbial communities may convert detrital
418 food sources into compounds that are more readily assimilated by primary consumers—a phenomenon
419 known as microbivory. This process has been demonstrated to substantially elevate the $\delta^{15}\text{N}$ content of
420 consumers suggesting that detritivory may functionally be omnivory (Steffan et al., 2017). The increase
421 in $\delta^{15}\text{N}$ values in consumers may also result from fasting. Supporting evidence from previous studies
422 (Doi et al., 2017; Kaufman et al., 2008) illustrates how restricted access to food in marine invertebrates
423 can lead to a notable rise in $\delta^{15}\text{N}$ values. However, fasting is not the most likely process driving the
424 contraction of trophic levels in the benthic food web at the studied site, particularly considering its
425 location on a continental shelf.

426

427 5. Conclusion

428 Further investigations are necessary to provide a comprehensive description and understanding
429 of the dynamics and structure of the benthic food web. For instance, documenting passive suspension
430 feeders, which have proven challenging to sample, and conducting more exhaustive sampling of primary
431 food sources would be valuable. Nevertheless, the observed seasonal contraction in the dispersion of
432 trophic positions among benthic consumers aligns with a similar contraction observed at the basis of
433 pelagic food chain (Tesán-Onrubia et al., 2023). Both phenomena are correlated with changes in
434 phytoplankton community structure driven by summer vertical stratification (Mena et al., 2019).

435 Our results emphasize the significance of accounting for both natural seasonal fluctuations and
436 pre-existing disturbances linked to human activities on the continental shelf. In this context, it is
437 essential to address the potential outcomes of future river flow patterns, especially in light of the
438 anticipated increase in precipitation deficits in the Mediterranean (Tramblay and Somot, 2018; Zittis et
439 al., 2019). Climate change effects might result in a reduction of continental-derived inputs and an
440 extension of the summer thermal stratification period (Coma et al., 2009). This, in turn, might intensify
441 the seasonal changes in marine food webs.

442 Furthermore, the present study establishes a baseline for a site that will host a pilot
443 Mediterranean floating offshore wind farm. Installing wind turbines in a heavily trawled area holds the
444 potential to enhance species diversity, acting as fish aggregation devices (Girard et al., 2004) and serving
445 as artificial reefs conducive to the colonization of sessile organisms (Bergström et al., 2014) potentially
446 including propagules from non-indigenous species (De Mesel et al., 2015). The organisms that attach to
447 the submerged structures of wind turbines may modify the downward flow of organic matter (Ivanov
448 et al., 2021) and facilitate the evolution of a more intricate benthic food web (Wilson and Elliott, 2009).

449 The anticipated effects may be most prominent during periods of summer stratification, characterized
450 by naturally reduced material fluxes and constraints on benthic fauna due to limited food availability.

451

452

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707 Captions of the tables and figures

708

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

715

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

720

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

723

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

726

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

730

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

736

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

742

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

749

750 Table 1 (revised)

751

Sources/phylum	Taxa	code	FG	April				September							
				$\delta^{13}\text{C}$	(sd)	$\delta^{15}\text{N}$	(sd)	Body size range (mm)	n	$\delta^{13}\text{C}$	(sd)	$\delta^{15}\text{N}$	(sd)	Body size range (mm)	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)	24 - 52	5	-20.0	(0.4)	4.2	(0.2)	33 - 50	5
Arthropoda	<i>Ampelisca</i> sp.	<i>Amp</i>	AS	-21.9	-	2.6	-	7	11	-21.4	-	4.0	-	7	6
Echinodermata	<i>Astropecten aranciacus</i>	<i>Ast</i>	C	-19.7	(0.5)	4.2	(0.1)	50 - 90	5	-19.0	(0.8)	6.0	(0.6)	33 - 80	5
Mollusca	<i>Galeodea rugosa</i>	<i>Gal</i>	C	-19.5	(0.4)	6.5	(0.0)	44 - 60	4	19.2	(0.9)	6.6	(0.2)	48 - 52	3
Annelida	<i>Glycera fallax</i>	<i>Gly</i>	C	-19.4	-	9.3	-	70	6	-18.6	(0.4)	9.6	(0.6)	70 - 120	5
Annelida	<i>Labioleanira ylheni</i>	<i>Lab</i>	C	-18.3	(0.3)	7.1	(0.2)	44 - 58	3	-18.3	(0.7)	7.2	(0.4)	44 - 90	3
Arthropoda	<i>Liocarcinus depurator</i>	<i>Lio</i>	C	-21.2	(0.4)	4.8	(0.3)	21 - 40	5	-20.9	(0.8)	7.2	(0.3)	22 - 40	5
Annelida	<i>Lumbrineris</i> sp	<i>Lum</i>	C	-19.8	(0.3)	8.4	(0.3)	60 - 80	12	-19.8	(0.3)	7.8	(0.4)	70 - 85	25
Annelida	<i>Nephtys kersivalensis</i>	<i>Neph</i>	C	-18.0	(0.5)	7.6	(0.6)	70	5	-18.0	(0.4)	7.7	(0.4)	100 - 150	5
Actinopterygii	<i>Trigla lyra</i>	<i>Tri</i>	C	-19.0	(0.1)	8.5	(0.5)	96 - 157	5	-18.9	(0.4)	9.2	(0.4)	83 - 190	4
Echinodermata	<i>Ocnus planci</i>	<i>Ocn</i>	PS	-17.6	(1.2)	6.4	(0.4)	85 - 113	3	-19.2	(0.6)	5.7	(0.7)	95 - 130	4
Arthropoda	<i>Alpheus glaber</i>	<i>Alp</i>	SD	-21.6	(0.3)	4.2	(0.6)	28 - 36	4	-20.9	(0.1)	5.7	(0.5)	22 - 40	5
Annelida	<i>Cirratulidae</i>	<i>Cir</i>	SD	-21.1	-	4.7	-	20	5	-21.1	(0.3)	5.5	(0.0)	20	6
Arthropoda	<i>Goneplax rhomboides</i>	<i>Gon</i>	SD	-22.3	(1.1)	4.3	(1.0)	5 - 12	5	-21.6	(0.1)	5.4	(0.5)	5 - 15	5
Echinodermata	<i>Leptopentacta elongata</i>	<i>Lep</i>	SD	-17.9	(1.3)	4.5	(0.9)	59 - 90	5	-17.5	(0.7)	5.6	(1.1)	66 - 90	5
Arthropoda	<i>Maera grossimana</i>	<i>Mae</i>	SD	-21.5	(0.3)	3.1	(0.8)	10	18	-21.4	-	4.5	-	10	16
Arthropoda	<i>Tuberapseudes echinatus</i>	<i>Tub</i>	SD	-21.1	(0.4)	2.6	(0.1)	10 - 14	3	-21.2	-	4.3	-	10 - 14	10
Echinodermata	<i>Oestergrenia digitata</i>	<i>Oes</i>	SSD	-18.6	(0.2)	7.1	(0.3)	140 - 170	5	-18.3	(0.5)	7.3	(0.4)	145 - 170	5
Annelida	<i>Sternaspis scutata</i>	<i>Ste</i>	SSD	-18.5	(0.7)	6.2	(0.2)	20 - 50	6	-18.7	(1.2)	5.8	(0.5)	30	8

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755

756

757 Table 2 (revised)

Phylum	Taxa	FG	April				September							
			$\delta^{13}\text{C}$	(sd)	$\delta^{15}\text{N}$	(sd)	Body size range (mm)	n	$\delta^{13}\text{C}$	(sd)	$\delta^{15}\text{N}$	(sd)	Body size range (mm)	n
Actinopterygii	<i>Arnoglossus laterna</i>	C	-18.6	-	10.3	-	150	1	-	-	-	-	-	-
Actinopterygii	<i>Callionymus lyra</i>	C	-	-	-	-	-	-	18.9	(0.1)	8.0	(0.1)	84 - 95	2
Actinopterygii	<i>Gobius paganellus</i>	C	-17.6	-	10.7	-	124	1	18.7	(0.1)	9.9	(0.1)	72 - 77	3
Annelida	<i>Goniadidae</i>	C	-19.2	-	9.8	-	110	1	19.7	-	9.1	-	122	1
Annelida	<i>Harmothoe</i> sp.	C	-20.2	-	4.3	-	45	1	-	-	-	-	-	-
Annelida	<i>Marphysa bellii</i>	C	-17.4	-	8.6	-	83 - 96	1	18.5	(0.3)	7.2	(0.3)	80 - 113	5
Actinopterygii	<i>Merluccius merluccius</i>	C	-	-	-	-	-	-	19.3	-	8.8	-	210	1
Actinopterygiens	<i>Microchirus variegatus</i>	C	-18.1	-	9.6	-	150	1	19.4	(0.4)	7.4	(0.6)	52 - 108	2
Nemertini	<i>Nemertea</i>	C	-19.3	-	6.4	-	80	1	-	-	-	-	-	-
Arthropoda	<i>Processa</i> sp.	C	-20.9	-	4.1	-	45	1	19.9	(1.0)	6.9	(0.5)	43 - 48	6
Annelida	<i>Scoletoma</i> sp.	C	-17.6	-	12.1	-	153	1	-	-	-	-	-	-
Actinopterygii	<i>Serranus hepatus</i>	C	-18.4	-	9.7	-	-	1	18.6	-	9.8	-	103	1
Arthropoda	<i>Solenocera membranacea</i>	C	-	-	-	-	-	-	19.5	(0.3)	7.9	(0.4)	48 - 52	5
Actinopterygii	<i>Trachinus draco</i>	C	-18.3	-	10.3	-	53	1	-	-	-	-	-	-
Actinopterygii	<i>Trisopterus minutus</i>	C	-	-	-	-	-	-	18.9	(0.2)	9.4	(0.5)	84 - 91	2
Cnidaria	<i>Alcyonium palmatum</i>	PS	-17.2	-	4.8	-	75	1	16.1	(0.7)	6.3	(0.4)	70 - 118	5
Cnidaria	<i>Andresia</i> sp.	PS	-22.2	(0.2)	4.9	(0.3)	42 - 45	4	-	-	-	-	-	-
Echinodermata	<i>Antedon bifida</i>	PS	-	-	-	-	-	-	21.2	(0.5)	5.5	(0.3)	72	5
Cnidaria	<i>Pennatula phosphorea</i>	PS	-18.5	-	6.0	-	170	1	19.0	(0.3)	6.4	(0.2)	152 - 173	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)	145 - 150	3
Annelida	<i>Ampharetidae</i>	SD	-20.8	-	3.9	-	11 - 14	11	-	-	-	-	-	-
Echinodermata	<i>Amphiura filiformis</i>	SD	-20.5	(1.3)	4.9	(2.6)	5 - 10	2	-	-	-	-	-	-
Arthropoda	<i>Inachus dorsettensis</i>	SD	-21.6	-	3.0	-	20	1	-	-	-	-	-	-
Arthropoda	<i>Macropodia longipes</i>	SD	-21.5	(0.6)	3.6	(0.1)	15	2	-	-	-	-	-	-
Annelida	<i>Magelona</i> sp.	SD	-21.3	-	3.9	-	31	1	-	-	-	-	-	-
Annelida	<i>Pista</i> sp.	SD	-	-	-	-	-	-	21.0	-	6.0	-	50	1
Annelida	<i>Spionidae</i>	SD	-20.1	-	5.5	-	25	1	20.3	(0.6)	4.0	(0.2)	20 - 25	4
Annelida	<i>Terebellides</i> sp.	SD	-20.0	-	4.5	-	35-42	4	-	-	-	-	-	-
Annelida	<i>Capitella</i> sp.	SSD	-16.3	-	9.4	-	98	1	-	-	-	-	-	-
Prochordata	<i>Glandiceps</i> sp.	SSD	-	-	-	-	-	-	18.6	-	8.7	-	150	1
Annelida	<i>Maldanidae</i>	SSD	-	-	-	-	-	-	19.1	(0.2)	7.9	(0.3)	40	4
Annelida	<i>Notomastus</i> sp.	SSD	-17.8	-	7.0	-	110	1	-	-	-	-	-	-
Mollusca	<i>Nucula</i> sp.	SSD	-	-	-	-	-	-	19.0	(0.6)	5.5	(0.4)	5 - 10	2

759 Table 3

760

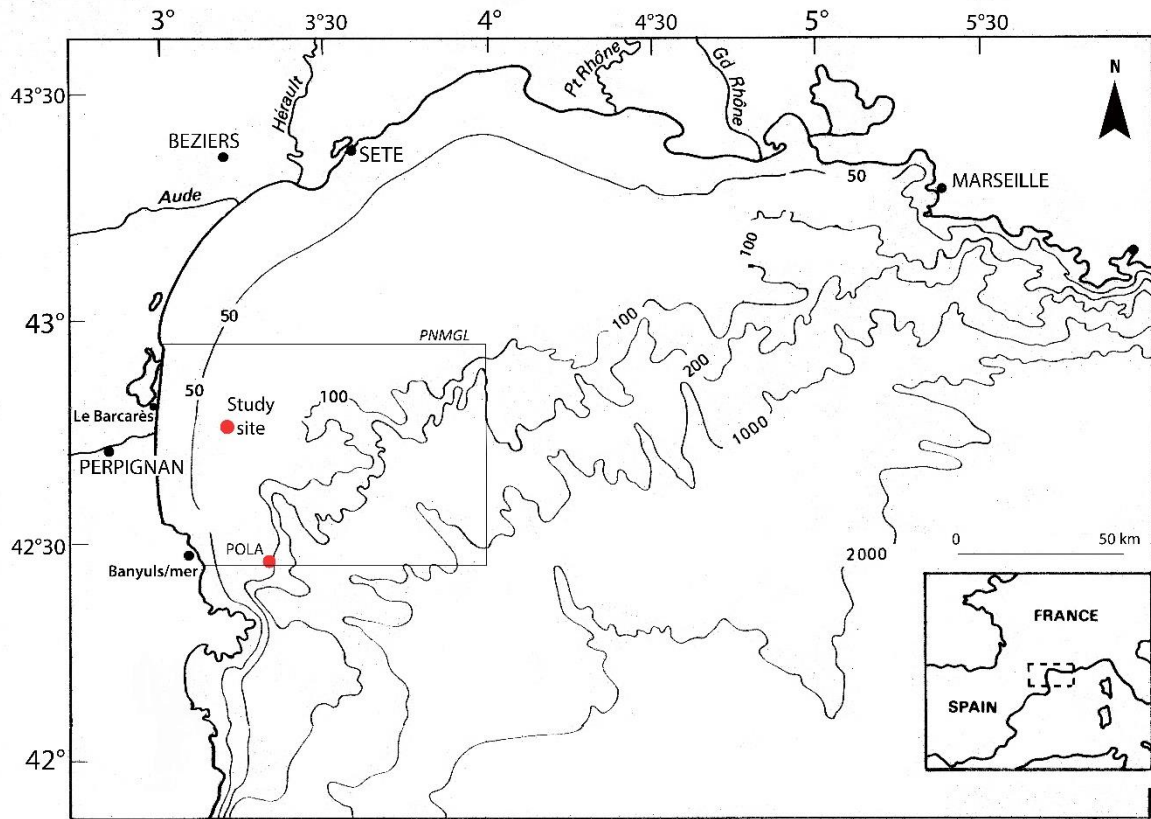
Metric, information	April	September
$\delta^{15}\text{N}$ range (NR), <i>diversity of trophic levels</i>	6.9	5.0
$\delta^{13}\text{C}$ range (CR), <i>diversity of basal resources</i>	4.5	3.1
Total area (TA), <i>extent of trophic diversity</i>	20.2	13.8
Mean distance to centroid (CD), <i>degree of trophic 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

761

762

763 Figure 1

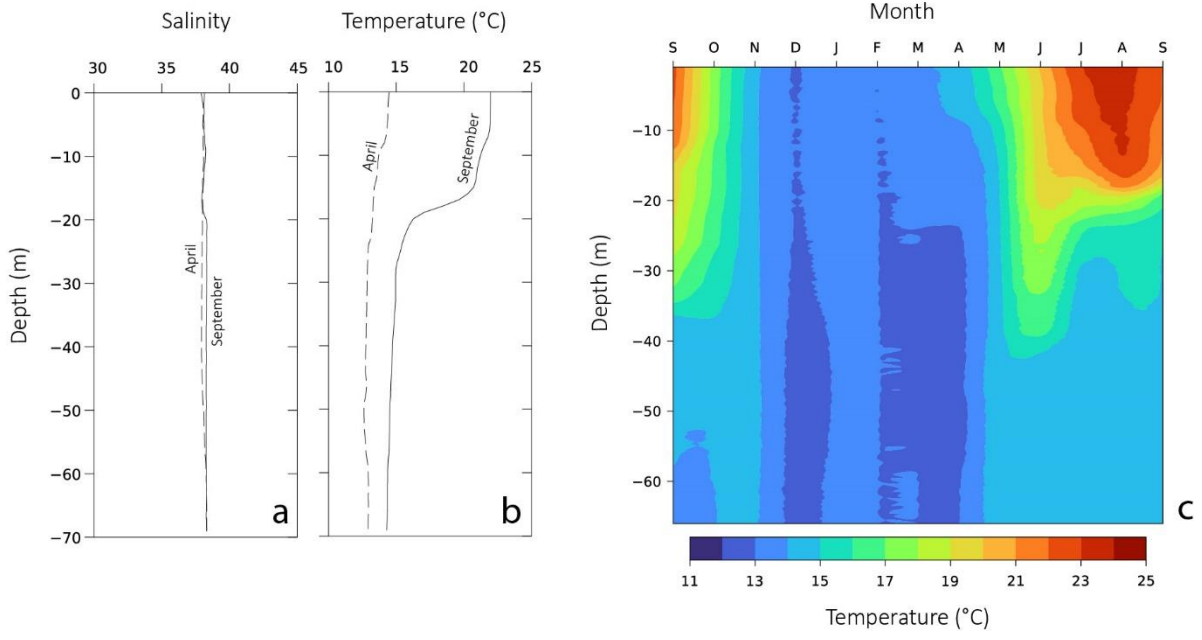
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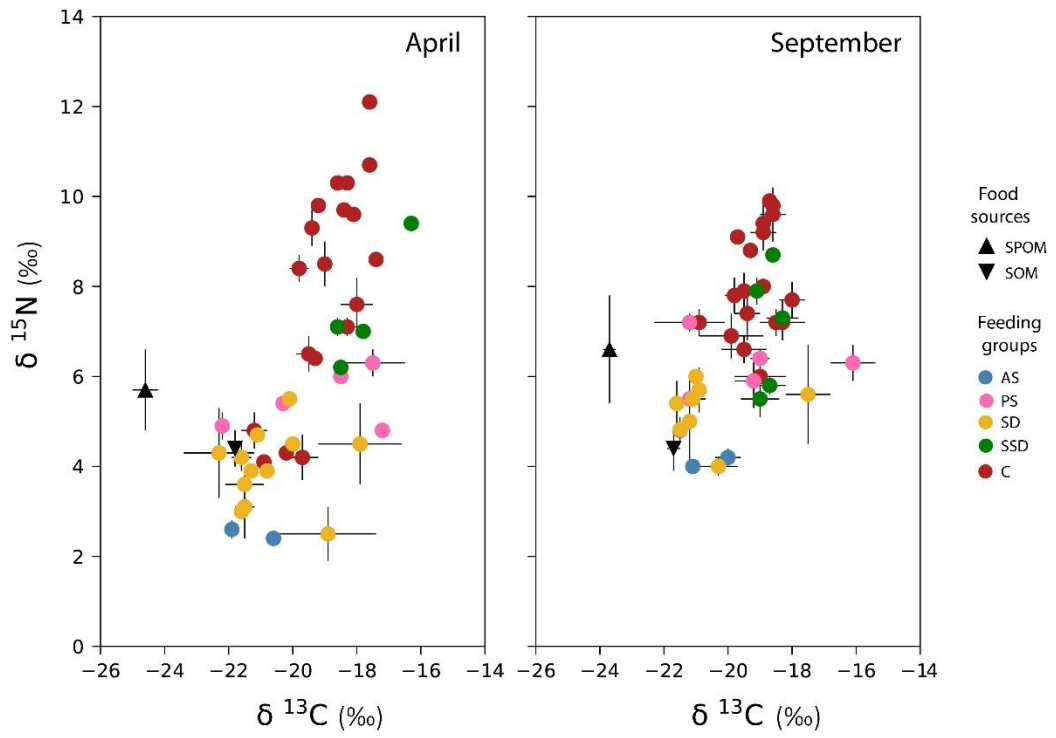
766

767 Figure 2



768

769 Figure 3 (revised)



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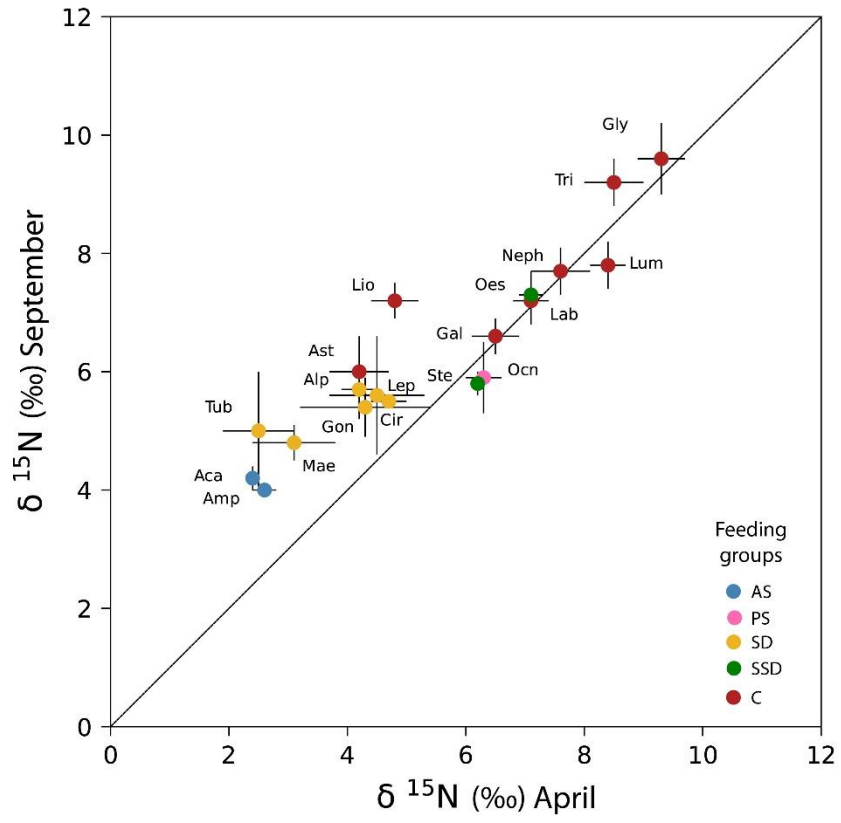
771

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774 Figure 4 (revised)

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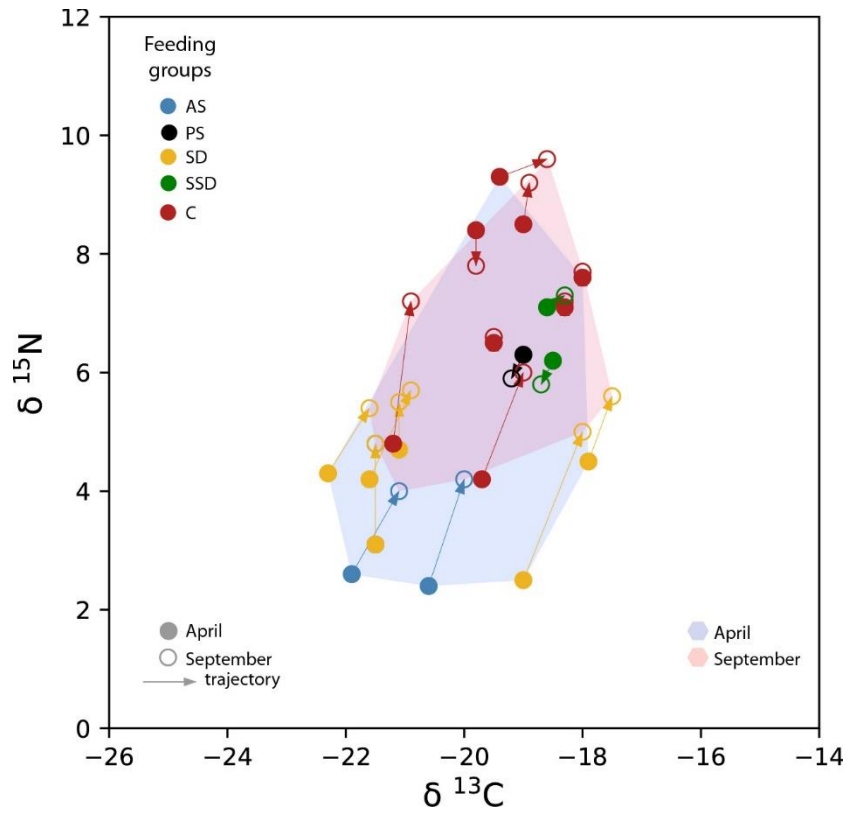


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777 Figure 5 (revised)

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