



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

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► To cite this version:

François Charles, Céline Labrune, François Lantoiné, François Le Loc'h, Lyvia Lescure, et al.. Seasonal stratification leads to changes within the benthic food web of the Gulf of Lions (northwestern Mediterranean). 2023. hal-03924675

HAL Id: hal-03924675

<https://hal.science/hal-03924675>

Preprint submitted on 10 Jan 2023

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19 Seasonal change within benthic food web

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Abstract

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

Keywords

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

1. Introduction

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

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

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

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

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

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

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

2. Material and methods

2.1. Study area

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

2.1. Water column

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

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

2.2 Sampling of food sources and consumers

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

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

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

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

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

2.3 Stable isotope analysis

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

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

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

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

2.4 Data treatment

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

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

Two-factor analyses of variance were performed to simultaneously assess the effect of sampling date 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 values between dates was then tested for each taxon and each feeding group, by running permutation Student's t-tests. All data were analyzed using the R software environment 3.4.3 (R Core Team, 2020), with the glm: fitting generalized linear models and the 'perm.t.test' function, 1000 permutations, from the Student's t-test in the R package 'RVAideMemoire' (<https://cran.r-project.org/package=RVAideMemoire>). A p-value of less than 0.05 meant that the null hypothesis 'no difference between means' or 'no interaction between factors' was rejected.

3. Results

3.1 Seasonal thermal stratification

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

3.2 Sample collection

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

3.3 Stable isotope analysis

3.3.1 Basal food sources

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

3.3.2 Consumers

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

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

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

3.3.3 Layman's community-wide metrics

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

3.3.4 Trophic trajectories

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 move was different for different taxa. The longest trajectories were for active suspension feeders, most surface deposit feeders and low trophic level carnivores. The direction of the trajectories showed an enrichment in ^{15}N and ^{13}C between the two dates of sampling. The positions of high trophic level taxa and taxa that feed on sub-surface deposits remained the same or changed slightly.

4. Discussion

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

Changes in the benthic food web

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

Sources of food web changes

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

part of the Gulf of Lions (Auger et al., 2011; Cauwet et al., 1990), whereas during summer the contribution of continental sources is extremely low because river flows are at their lowest (Durrieu de Madron et al., 2008). Regarding nitrogen stable isotope ratios, values, 5.7‰ in April and 6.0‰ in September, did not explain the differences in $\delta^{15}\text{N}$ values of primary consumers. Therefore, the increase of $\delta^{15}\text{N}$ values in active suspension feeders and surface deposit feeders between April and September resulted from either a change in the trophic status (Romero-Romero et al., 2021) or a fasting effect (Doi et al., 2017). Fasting in marine invertebrates induces a significant 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., 2008). During summer thermal stratification period, flow of matter to the benthos are lower than in winter or spring (Miquel et al., 1994). Stratification of the water column leads to a general decrease in phytoplankton productivity (Mignot et al., 2014). Most of the phytoplankton biomass, mainly picoplankton cells (Lantoiné, 1995), is concentrated in a deep chlorophyll maximum located below the thermocline. Picoplankton are grazed by zooplankton and the entire pelagic food chain adopts the distribution of peak prey abundance on a spatial scale of few meters (Röpke et al., 1993). The vertical downward flow of material available to benthic primary consumers drastically decreases (Coma et al., 2009). Moreover, sinking organic particles consist of fecal pellets. As a result, organic material available to primary consumers is not only more diluted but also becomes less digestible. A set of trophic conditions similar to those faced by sub-surface deposit feeders that feed on poorly digestible and highly diluted sedimentary organic matter. Within benthic food webs, sub-surface deposit feeders are at the trophic level of secondary consumers. It is therefore likely, as shown by Romero-Romero et al. (2021) for abyssal deposit feeders, that microbial communities transformed primary food sources (SPOM and SOM) into compounds more easily digested by primary consumers. Microbivory, which is ubiquitous among detritus feeders, can significantly elevate the trophic position of the fauna (Steffan et al., 2017). This pathway of transformation and transfer of poorly digestible material may also explain why active suspension feeders and surface detritus feeders moved from being primary to secondary consumers during the stratification period.

5. Conclusion

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

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

Acknowledgements

We thank the captain and crew of the RV Nereis II for their technical assistance during the sampling. We benefited from the technical means of temperature data collection of the Mediterranean Ocean Observing System for the Environment (MOOSE) program. This study was supported by France Energies Marines (FEMs) and the French National Research Agency through APPEAL project (ANR-10-IEED-0006-25) and funded by the Parc Naturel Marin Golfe du Lion (PNMGL) and the French Agency for Biodiversity (OFB). We thank Noémie Michez of the PNMGL for her support. For the purpose of Open Access, a CC-BY public copyright licence has been applied by the authors to the present document and will be applied to all subsequent versions up to the Author Accepted Manuscript arising from this submission.

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Captions of the tables and figures

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

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

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

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

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

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

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

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

582 Table 1

583

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

584

585 Table 2

586

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

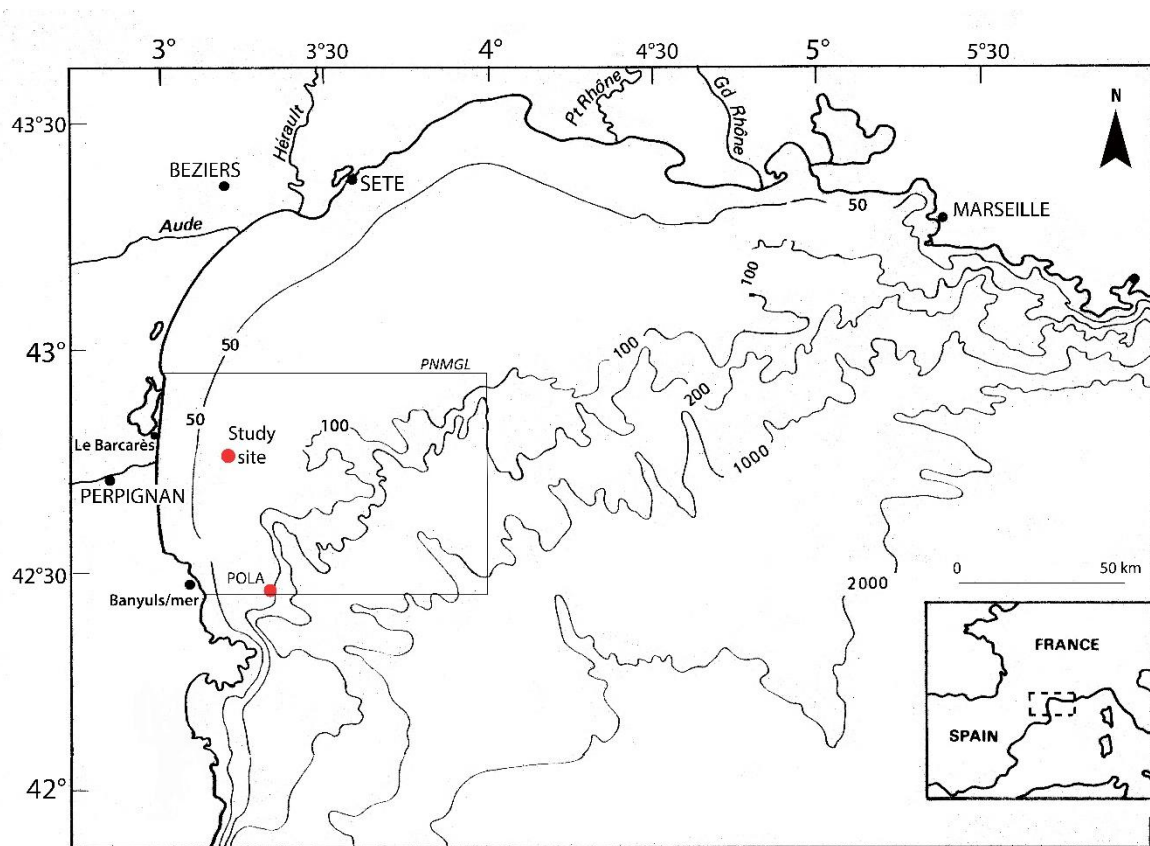
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Metric, <i>information</i>	April	September
$\delta^{15}\text{N}$ range (NR), <i>diversity of trophic levels</i>	6.9	5.0
$\delta^{13}\text{C}$ range (CR), <i>diversity of basal resources</i>	4.5	3.1
Total area (TA), <i>extent of trophic diversity</i>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

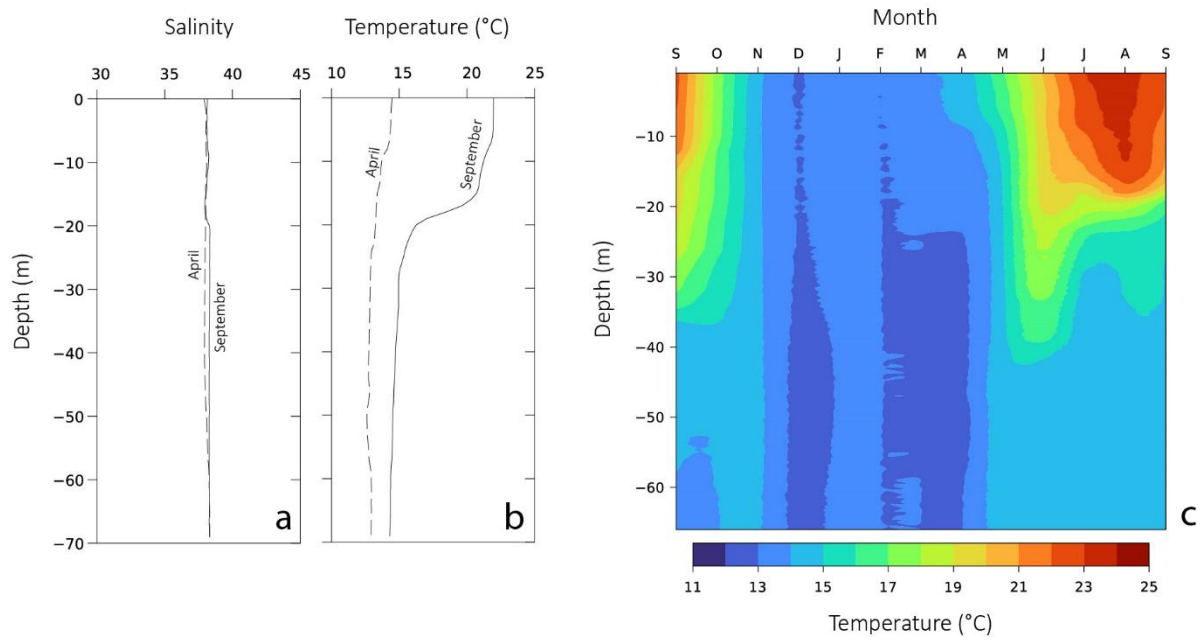
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Figure 1



596 Figure 2

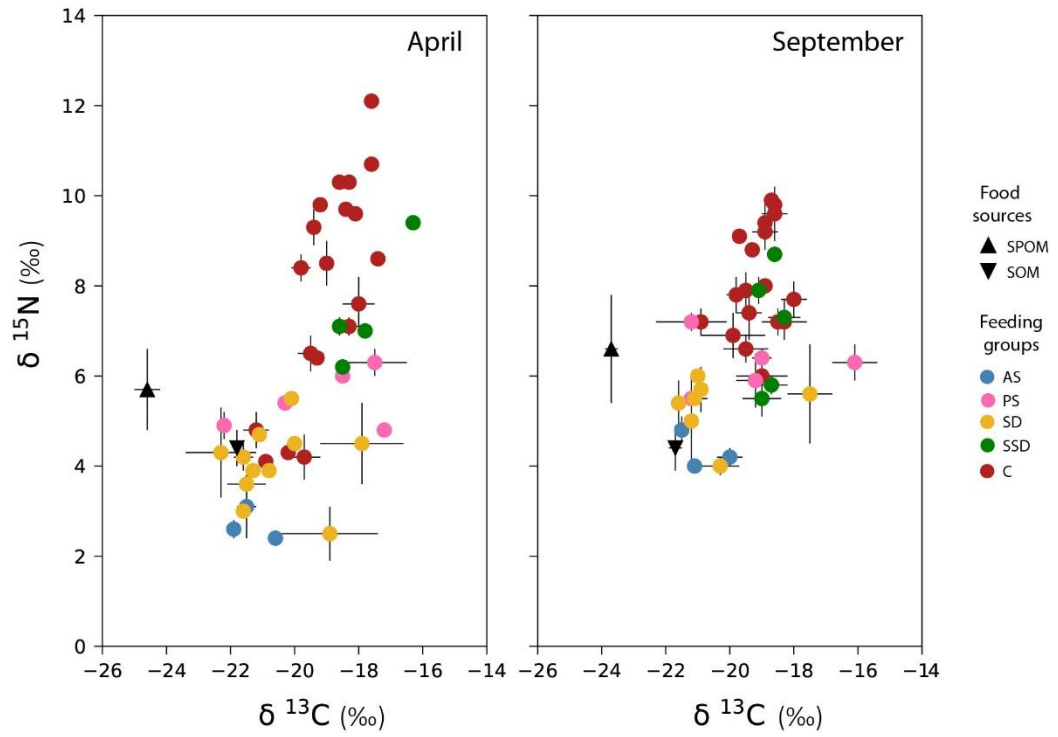


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598 Figure 3

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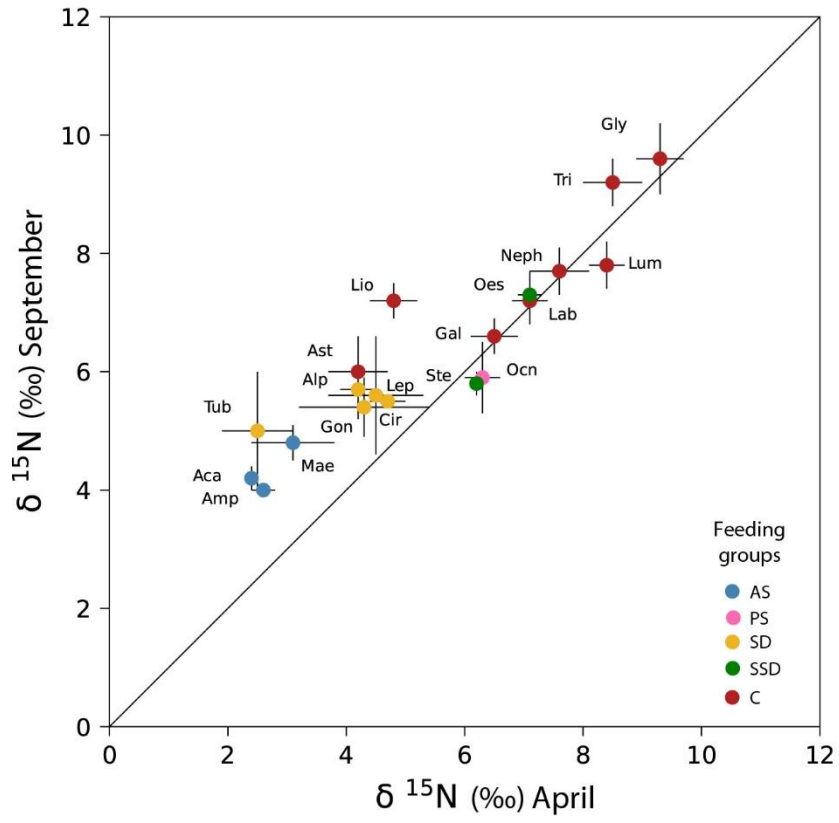


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603 Figure 4

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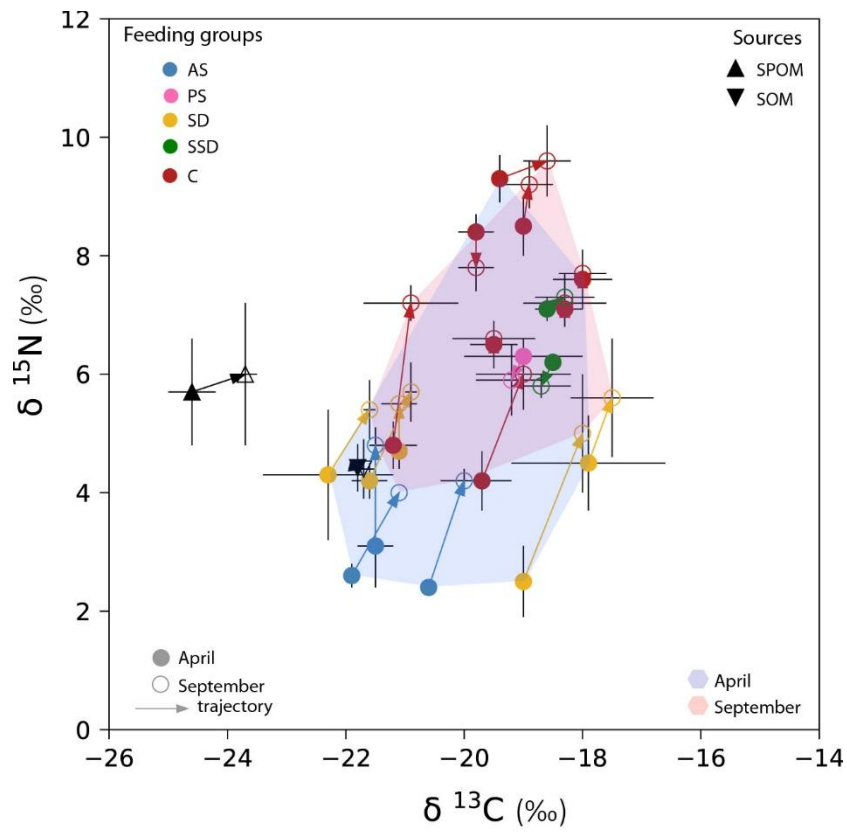


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606 Figure 5

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