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Fish food-web structure of a southern Mediterranean lagoon (El Mellah Lagoon, Algeria): what we can learn from stable isotope analysis

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Abstract

The structure of a fish food-web was described for the first time in a coastal lagoon in the southern Mediterranean Sea by analysing stable carbon and nitrogen isotopes of fish species and their potential food sources. The El Mellah Lagoon (EML) located in extreme north-eastern Algeria, is the only coastal lagoon in the southern Mediterranean with low human pressure due to few human activities and its protected status under the Ramsar Convention. We investigated the structure of the fish food-web in the spring at four stations in the lagoon that differed in their proximity to rivers and the channel, which connects to the sea. The results provided insight into ecological functions of EML as a feeding area for all fish species caught in the lagoon, in particular marine migrant juveniles and resident species. The $\delta^{13}C$ results highlighted the importance of marine organic matter on the functioning of the EML fish food-web, to which organic matter in marine sediments and likely microphytobenthos contribute most. Our study also revealed the importance of seagrass (*Ruppia* sp.) for detritivorous fish (i.e., Mugilidae species) and for their potential to shelter a wide variety of benthic invertebrates that are potential food sources for benthivorous fish. Our study revealed the small influence of freshwater inputs on the functioning of the EML food-web and that juvenile marine fish may use the lagoon for reasons other than feeding, most likely to avoid predation and obtain physiological advantages.

Keywords: stable isotopes; niche overlap; trophic position.

Introduction

Coastal lagoons provide ecological functions as nursery and feeding areas, as well as essential migration routes for diadromous fish species (Franco *et al.*, 2008; Pérez-Ruzafa & Marcos, 2012). These interface ecosystems attract many aquatic species due to their variety of habitats, which enable the species to grow (Costanza *et al.*, 1997). The fish populations in these paralic environments include marine and continental species that enter the lagoon at different stages of development (Embarek *et al.*, 2017). Lagoon fish communities consist of mature individuals, which come to reproduce obligatorily, regularly, or occasionally, and juveniles, which use the environment to feed. Thus, the fish communities are structured by the life cycles of the species they contain, the biotic capacity of the environment and the relationships among species. Lagoons at the interface of continental and marine environments are also subject to considerable threats from human impacts, such as major fisheries, aquaculture farms, and urban and industrial pollutions. Due to lack of management, these factors contribute to degradation of these sensitive habitats, which modifies their structure and functioning (Pérez-Ruzafa & Marcos, 2012).

The aquatic environment of lagoons also has high spatial and temporal variability, plays a crucial role in feeding adult and juvenile fish. In these ecosystems, production is generated by freshwater inputs of particulate and dissolved organic matter, nutrients and primary production while the connection with the sea directly influences water quality, which influences the amount of food available (Elliott *et al.*, 2002). For example, for oligotrophic seas such as the Mediterranean, freshwater inputs increase the development of marine communities (Caddy, 1993; 2000). This relatively high primary and secondary production (Largier, 1993) at the base of the food web stimulates productivity of the many trophic compartments (Salen-Picard *et al.*, 2002), which increase the amount of resources available in coastal fisheries (Kerr & Ryder, 1992; Lloret *et al.*, 2001; Darnaude *et al.*, 2004). Environmental changes are thus likely to influence ecosystem functioning and subsequent ecological processes, such as trophic transfer through the food web and nutrient cycling, which are fundamental for management issues. Understanding trophic interactions is particularly important in transitional environments such as coastal lagoons.

Stable isotope analysis provides information on long-term assimilation of organic matter, unlike the snapshot of it revealed by stomach contents (Fry, 2006; Parnell *et al.*, 2010), and is also a reliable approach to address questions about aquatic food-web ecology. Carbon and nitrogen stable isotopes are a relevant tool to reconstruct the diet of many species and determine the contribution of producers and trophic pathways to food-web communities (Fry, 2006; Boecklen *et al.*, 2011). The stable nitrogen and carbon isotope compositions of consumers depend on those of their food sources and isotopic fractionation during feeding. In general, stable nitrogen and carbon isotope compositions are expressed as $\delta^{15}N$ and $\delta^{13}C$, respectively, and usually increase from prey to consumers by 3.4‰ and 1.0‰ respectively (DeNiro & Epstein, 1981; Minagawa & Wada, 1984). Thus, $\delta^{15}N$ can indicate the trophic position of an organism within at food web. In addition, the $\delta^{13}C$ values of food sources (e.g., primary producers) also result in differences in those of their consumers (Riera *et al.*, 1999), which distinguishes benthic vs. pelagic food webs or freshwater vs. marine food sources (Fry, 2006). Consequently, $\delta^{13}C$ can be used to tracer of trophic food sources for consumers (Peterson, 1999).

Stable isotopes analysis has been widely used to explore food webs of coastal ecosystems such as lagoons and estuaries. In the northern Mediterranean, studies have explored spatial heterogeneity in the food web of strongly human-impacted lagoons (Salses-Leucate, in France; Carlier *et al*., 2009) or those less impacted (Lapalme, in France; Carlier *et al*., 2008), the influence of salinity on the structure of the fish food-web (coastal lagoons of the Ebro Delta, in Spain; Prado *et al*., 2014), the trophic pathway of organic matter (Mauguio Lagoon, in France; Vizzini *et al*., 2005), temporal dynamics of trophic positions of secondary consumers (Cabras Lagoon, in Italy; Como *et al*., 2018), the feeding behaviour of economically important and threatened fish species (Italian lagoons; Sporta Caputi *et al*., 2020), the trophic impact of invasive species (*Mnemiopsis leidyi* in Berre Lagoon, in France; Marchessaux *et al*., 2021), and the sources and pathways of primary production (Mar Menor Lagoon, in Spain; Pérez-Ruzafa *et al*., 2020). To date, no studies have used stable isotope analysis to explore the trophic structure and functioning of a coastal lagoon in the southern Mediterranean (North Africa).

The present study is the first to use stable nitrogen and carbon isotope compositions to explore spatial variation in the food-web structure of a North African coastal lagoon, using El Mellah Lagoon (EML) in northern Algeria as a case study. EML is interesting to study as its biodiversity has been extensively inventoried since 1907 (Bounhiol, 1907), most recently in 2017 (Embarek *et al.*, 2017). The inventories have revealed progressive and continuous silting up of the channel, EML's only connection to the sea, as well as a decrease in species richness. Since 2004, EML has been protected by the Ramsar Convention and is an integral reserve of El Kala National Park.

The main objectives of the present study were to (i) assess the fish community structure of EML as a function of hydro-morpho-sedimentary parameters, (ii) determine stable isotope compositions (i.e., $\delta^{15}N$ and $\delta^{13}C$) of the dominant fish and identify their potential food sources (i.e., particulate organic matter (POM), sediment organic matter (SOM), and benthic and pelagic invertebrates), and (iii) characterise the EML's fish food-web.

Materials and Methods

Study area

EML is located in extreme north-eastern Algeria (36°54' N and 8°20' E), which border the south-western Mediterranean Sea. This expanse of brackish water is roughly ovoid, extending 4.5 km north to south and 2.5 km east to west (Guelorget & Perthuisot, 1983) (Fig. 1), with an area of ca. 8.6 km^2. With an mean depth of 3.5 m (Messerer, 1999; Draredja, 2007), EML connects to the sea via a channel ca. 870 m long, 20 m wide, and 0.5-2.0 m deep (Draredja, 2007). It receives freshwater from three intermittent rivers (wadis): El-Mellah and Bélaroug in the south and R'Kibet in the north-west.

EML has low human pressure but significant economic interest for fishing, aquaculture and tourism (Draredja, 2007). Due to limited exchange between EML and the sea, the EML's hydrology is strongly influenced by precipitation, evaporation and freshwater inputs (Guelorget *et al.*, 1989; Ounissi *et al.*, 2002).

The hydrological regime of the catchment around EML is influenced primarily by freshwater inflow due to precipitation (Refes, 1994) and marine water from the sea that passes through the channel, especially during the dry season (i.e., March-November). Water in EML flows from north to south during high tide and from south to north during low tide (Messerer, 1999). During the dry season, the temperature and salinity of EML vary little. The temperatures at the surface and the bottom of EML differ by no more than 1°C (Draredja, 2007). A fine sand, often covered by seagrass (*Ruppia* sp.), covers the edge of EML, and the fine fraction tends to increase as depth increases, forming a pure fluid silt in the centre of EML (Draredja *et al.*, 2020).

Sampling

Hydro-morpho-sedimentary parameters, POM, SOM, as well as fish and their main potential prey (i.e., benthic and pelagic invertebrates) were measured and collected in spring (i.e., April) 2019 at four sampling stations in EML along a spatial gradient from the channel to the

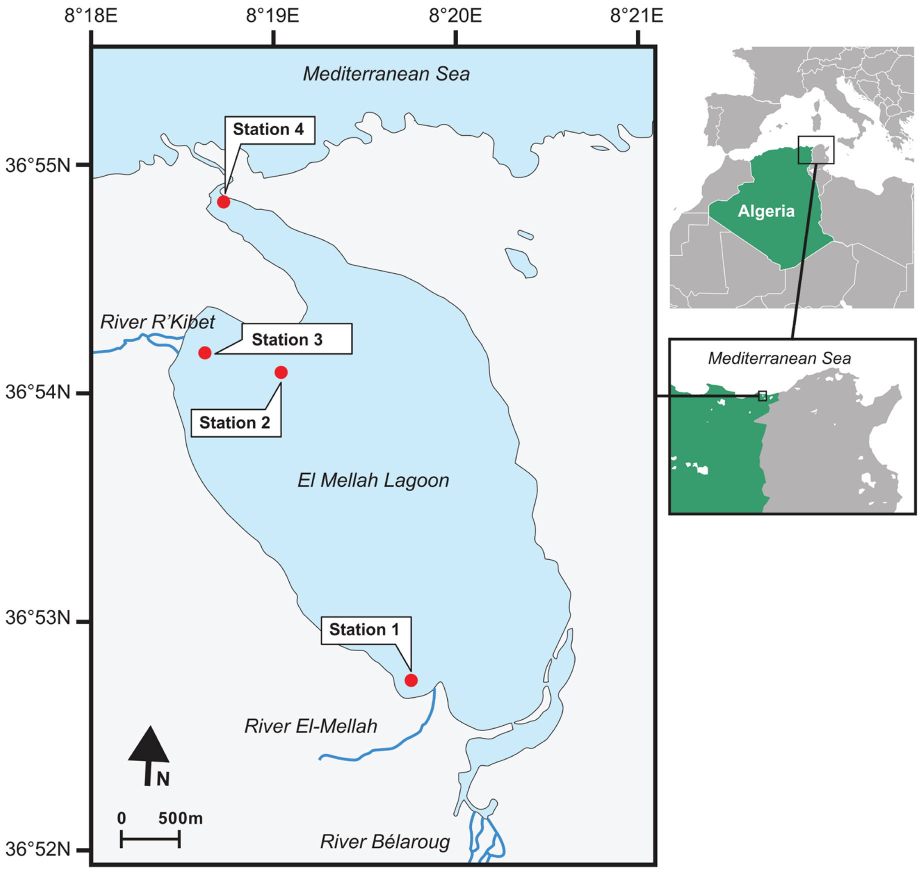


Fig. 1: Location of the four sampling stations in El Mellah Lagoon located in the southern Mediterranean.

R'Kibet, El-Mellah and Bélaroug Rivers (Fig. 1). We focused on the spring because it is when fish visit EML the most (Embarek *et al.*, 2017).

Hydro-morpho-sedimentary parameters

We measured five hydro-morpho-sedimentary parameters: depth, distance to the channel, distance to the nearest river, water transparency, and sediment characteristics. Distances to the channel and nearest river (km) were used as a proxies for salinity to determine the influence of seawater and freshwater in EML, respectively. For each station, distance to the channel was estimated as that to the outlet of the channel, while distance to the river was measured to the nearest river (R'Kibet, El-Mellah or Bélaroug) using Google Maps© (Fig. 1). Water transparency (m) was assessed using a Secchi disk. Sediments characteristics were determined via particle size analysis according to Draredja (2007). We defined three subtract categories: "sands" (> 90% sand), which is characteristic of shallow areas; "silty sand" (50-90% sand), located in the south-western section of EML, where depth range from 1.5-3.5 m; and "sandy silt" (50-90% silt), in areas more than 2.5 m deep.

POM and SOM sampling

To sample POM, water was collected using sterile bucket and conserved in a cooler box. In the laboratory, the water was filtered through pre-combusted Whatman GF/F filters (0.45 µm pore size, 47 mm diameter), with three replicates per station. The sediment was sampled using a Van Veen grab, while SOM was collected by scraping the top 1 cm of the sediment. Three replicates were performed at each station. The POM and SOM samples were conserved at -20°C in the laboratory until lyophilisation.

Benthic and pelagic invertebrate sampling

Pelagic invertebrates were sampled using a WP2 net (200 µm mesh; Tranter & Smith, 1996) trawled for 10 min 1 m below the water surface. They were preserved at -20°C in the laboratory until sorting and lyophilisation. Benthic invertebrates were collected using a Van Veen grab (sampling an area of 0.1 m^2), with three replicates per station. Samples were sieved through a 1 mm mesh and then washed again with distilled water. In the laboratory, benthic invertebrates were sorted and identified to species.

Fish sampling

Fish were collected using a beach seine net (L = 14 m, H = 2 m, mesh size = 3 cm). The gear is suitable for catching small fish such as juveniles, which are abundant in shallow waters. The fish were caught during daylight hours in water less than 1.5 m deep. At each station, 2-4 replicates were performed in a sampling area of 40 m² during each collection. The fish caught were kept cool on ice. In the laboratory, fish specimens were identified to species, which for Mugilidae species required examining the pyloric caeca. Once identified, each fish was measured (total length) to the nearest cm and weighed to the nearest 0.1 g using an electronic scale. Fish abundance was calculated as the number of individuals per 100 m² (ind. 100 m^{-2}) based on the number of individuals of a fish species collected in the sampled area (i.e., 40 m²). Functional groups of fish species based on ecological guilds and feeding mode were determined according to Franco *et al.* (2008). For stable isotope analysis, the most abundant species were selected to summarize the trophic structure of communities.

Stable isotope analysis

As lipids contain less ^{13}C than carbohydrates and proteins do (DeNiro & Epstein, 1978; Griffiths, 1991), fatty tissues tend to be isotopically lighter than lean tissue. Consequently, trophic interpretations based on δ^{13}C composition may be confounded by lipid effects (Wada *et al.*, 1987; Bodin *et al.*, 2007). To minimise these effects for mega- and macro-fauna (except polychaetes), low-lipid muscle tissue was used for stable isotope analysis. The valve muscle of bivalves, the abdomen muscle of shrimp, the muscle in the forceps of crabs, and the white dorsal muscle of fish (including small fish) were dissected and analysed for stable isotope composition. For polychaetes, the entire organism was analysed after removing the digestive tracts, jaws, and cerci. The tissues were then washed with milli-Q water to prevent contamination (Kharlmamenko *et al.*, 2001; O'Reilly *et al.*, 2002) and then freeze-dried and ground before being encapsulated. For small benthic invertebrates (e.g., *Serpula vermicularis*), each sample was a pool of three individuals.

As fish size may influence isotope composition, especially δ^{15}N (Wilson *et al.*, 2009), we carefully selected individuals of similar length across the species analysed. Prior to δ^{13}C analyses, POM filters were divided into two subsamples: one was exposed to HCl vapour for 4 h to remove residual carbonates (Cresson *et al.*, 2012) before placed in tin cups (Lorrain *et al.*, 2003), whereas the other was left untreated and used to measure δ^{15}N. Sediment samples were dried at 60°C for 24 h. They were divided into two subsamples: one was treated with HCl, ground to a fine and homogeneous powder, and then encapsulated, whereas the other was encapsulated immediately after drying.

The δ^{13}C and δ^{15}N were determined using an elemental analyser (Flash EA 2000, Thermo Scientific) coupled with an isotope ratio mass spectrometer (Delta V+, Thermo Scientific) with a conflo IV interface at the Plateforme Ocean Spectrometry pole in Plouzané, France. Replicate analyses of international IAEA and laboratory standards yielded analytical errors of less than 0.1% and 0.2% for carbon and nitrogen, respectively. Stable isotope ratios were expressed in relative δ notation (parts per mil (‰)) based on the Pee Dee Belemnite standard for carbon and atmospheric N_2 for nitrogen (Eq. 1):

$$\delta X = [(\frac{R_{sample}}{R_{standard}} - 1] \times 1000 \qquad (1)$$

where δX is δ^{13}C or δ^{15}N, and R is the ratio of ^{13}C:^{12}C or ^{15}N:^{14}N.

C:N ratios greater than 4 indicate that tissues had high lipid contents, which would have biased the δ^{13}C; thus, they were excluded from further analysis.

Statistical analysis

Environmental and biological characterisation of EML

Environmental and biological variations in EML were analysed using principal component analysis (PCA) to determine spatial differences in hydro-morpho-sedimentary parameters (i.e., depth, distances to the channel and nearest river, water transparency, and sediments) and benthic invertebrate (e.g., presence of Bivalvia, Polychaeta, and Malacostraca) among the four stations. The hydro-morpho-sedimentary variables were log-transformed (log + 1) to reduce their skewness, and then centred and reduced before analysis. PCA was used to summarise the variables into principal components and the relationship between variables was measured using the Pearson correlation coefficient. The distance between observations was Euclidean. PCA was performed using the *FactoMineR* package (Husson *et al.*, 2017) of R software (R Core Team, 2020).

Fish community structure

Fish length was compared using the non-parametric Kruskall-Wallis test, as the data were not normal (Shapiro-Wilk test) or homoscedastic (Levene's test). Dunn's test was used for post-hoc comparisons. The Shapiro–Wilk, Levene's, Kruskall-Wallis, and Dunn's tests were performed using the *stats* package of R.

Correspondence analysis (CA) was used to determine spatial variation in fish communities in EML, based on fish abundance at the four stations. CA uses the chi-square metric, which weights each gap between rows and columns as a function of the total number of rows and columns. The influence of descriptors and individuals on structuring the axes is determined by analysing the relative contributions to the total inertia of the axes (%), cosine-square values (from 0-1), and correlation coefficients (r). CA was performed using the *vegan* (Oksanen *et al.*, 2013)*, FactoMineR* (Lê *et al.*, 2008) and *stats* packages of R.

Stable isotope compositions of fish and their potential food sources

Dual $\delta^{13}C$-$\delta^{15}N$ plots were used to graphically represent isotope compositions with associated standard deviations of all compartments of the entire food web at each station. We first tested the hypothesis that isotope compositions of potential food sources for fish differed significantly along the spatial gradient. For all samples, non-parametric Kruskal-Wallis tests were performed separately for each isotope ratio. Student's t-test was used to test whether the fish collected had a similar length among the stations. As significant differences in $\delta^{13}C$ and $\delta^{15}N$ in a specific compartment between stations does not necessarily imply a significant difference in the joint $\delta^{13}C$ and $\delta^{15}N$ isotope composition, permutational multivariate analysis of variance (PERMANOVA) using a Euclidean distance similarity index was performed to discriminate compositions better. The PERMANOVA and pairwise tests were performed using the *vegan* (Oksanen *et al.*, 2013) and *RVAideMemoire* packages (Hervé & Hervé, 2020) of R.

Structure of the fish food-web

To determine the structure of the fish food-web of EML, we estimated the trophic positions and widths of isotopic niches of fish and their potential prey, both within EML and among the stations. Isotopic niche overlaps were also calculated to determine the similarity of fish niches.

Trophic positions (Cabana & Rasmussen, 1996) were calculated as follow (Eq. 2):

$$Trophic\ positions = TP_{base} + \frac{\delta^{15}N - \delta^{15}N_{base}}{TDF} \qquad (2)$$

where TP_{Base} is the trophic position of the isotopic baseline, $\delta^{15}N_{Base}$ is the $\delta^{15}N$ of the baseline, and TDF is the trophic discrimination factor.

We set $\delta^{15}N_{Base}$ to that of the suspension-feeders bivalve *Mytilaster marioni*, which was found at all stations; TP_{Base} to 2, the theoretical trophic position of suspension-feeders; and TDF to 3.4‰ (Post, 2002).

We estimated isotopic niches by calculating their three Layman metrics (nitrogen range (NR), carbon range (CR), total area (TA)) and using them in a Bayesian approach based on multivariate ellipse-based metrics (Jackson *et al.*, 2011). The centroid of each niche is its centre in isotopic space. Differences in centroid location among stations were first tested using nested linear models and residual permutation procedures (see Turner *et al.* (2010) for statistical details). The spread of the data points was described using the parameters developed by Layman *et al.*, (2007). Convex hulls were constructed to estimate the smallest TA that contained all individuals in the isotopic space. The TA represents the total isotopic niche of a population (Layman *et al.*, 2007). The width of the niche was estimated for each station using multivariate ellipse-based metrics (Jackson *et al.*, 2011). The analysis generates standard ellipse areas (SEA) which are bivariate equivalents of standard deviations in univariate analysis. SEA values corrected for a small sample size (SEA_C) were calculated to estimate niche overlap. Finally, we generated Bayesian estimates of SEA to test for differences in niche width by comparing their 95% credible intervals. All analyses were performed using the *SIBER* package (Jackson *et al.*, 2011) of R.

Isotopic niche overlaps of fish were estimated using a probabilistic method that calculates niche regions and pairwise niche overlap without considering the sample size. The $\delta^{13}C$ and $\delta^{15}N$ of each fish were used to calculate the mean overlap between niche regions with 95% Bayesian credible intervals based on 10,000 iterations in bivariate dimensions. The uncertainty was estimated in a Bayesian framework considering the sample size (Swanson *et al.*, 2015). The analyses were performed using the *nicheROVER* package (Lysy *et al.*, 2014; Swanson *et al.*, 2015) of R.

Results

Environmental and biological characterisation of EML

The first two axes of the PCA explained 77% of the variance and showed a clear difference in hydro-morpho-sedimentary parameters (i.e., depth, water transparency, distances to the channel and nearest river, and sediment characteristics) and benthic invertebrates (i.e., Bivalvia, Polychaeta, and Malacostraca) among the four sampling stations in EML (Fig. 2A and B). The PCA showed clear differences between eastern and western in depth, distances from the channel and nearest river, and water transparency. The depth varied from 0.7 m at station 4 (near the channel) and to 4.5 m at station 2 (north-western section of EML). Stations 1 and 3 were closest to a river (R'Kibet and El-Mellah, respectively), while stations 2 and 4 were closest to the sea. Water transparency varied from 0 m at station 3 to 4.4 m at station 2 (Table 1, Fig. 1). The sediments and benthic invertebrates were positively correlated with the second axis, which differentiated north and south sections of EML. The sediment of station 4 consisted of silt, while that of stations 1, 2, and 3 a consisted of sand, along with silt at the stations 1 and 2, and *Ruppia* seagrass at stations 1 and 3 (Table 1). Stations 1 and 3 contained benthic invertebrates of classes Bivalvia, Polychaeta, and Malacostraca, while station 2 contained only Malacostraca, and station 4 contained only Bivalvia (Fig. 2A and B).

Fish community structure and spatial variations

Among the four stations, 858 fish individuals of 14 species were collected (Table 2). Mean (± standard error) fish abundance was highest for *Atherina boyeri* (47 ± 23 ind. 100 m^{-2}), *Chelon ramada* (53 ± 30 ind. 100 m^{-2}) and *Chelon auratus* (23 ± 11 ind. 100 m^{-2}), which represented more than 67% of the catches. Most individuals

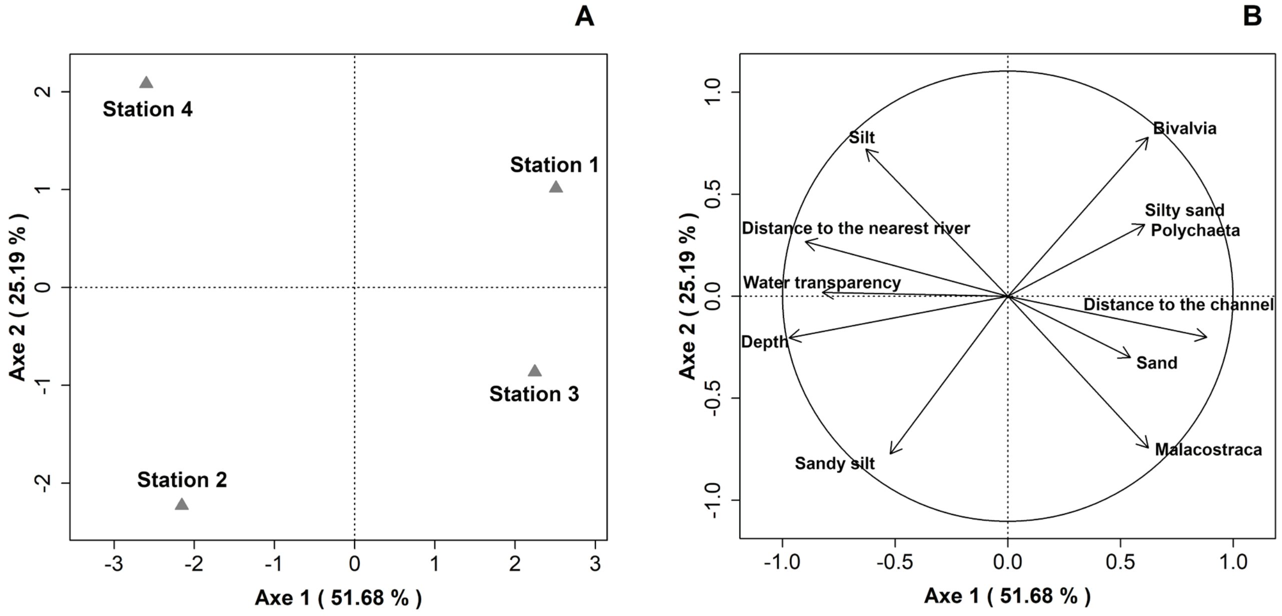


Fig. 2: (A) Observations and (B) correlation circle of the first two axes of the principal component analyses (PCA) on the hydro-morpho-sedimentary parameters (i.e; depth, distance to the channel and nearest river, water transparency and sediments) and benthic invertebrates (presence of Bivalvia, Polychaeta and Malacostraca) in the four sampling stations in El Mellah Lagoon located in the southern Mediterranean during the spring 2019.

Table 1. Hydro-morpho-sedimentary parameters (i.e. depth (m), water transparency (m), distance of the channel and nearest river (km), and sediment) at the four sampling stations in El Mellah Lagoon located in the southern Mediterranean during the spring 2019. * Presence of seagrass *Ruppia*.

Station	Depth (m)	Water transparency (m)	Distance to the channel (km)	Distance to the nearest river (km)	Sediments
1	1.5	1.0	5.2	0.2	Silty sand
2	4.5	4.4	2.6	0.9	Sandy silt*
3	1.5	0.0	3.4	0.1	Sand
4	0.7	0.7	0.7	2.8	Silt*

were juveniles, except for *Aphanius fasciatus* and *Pomatoschistus* spp., which are small fish. The length or weight of a given fish species did not differ significantly among stations, except for *A. boyeri*, *C. auratus*, *Chelons saliens* and other *Chelon* spp. (Kruskall-Wallis, $p < 0.05$). These species were shorter mainly at stations 2 and 3 (north-western section of EML).

The first two axis of the CA, used to analyse the spatial variation in fish abundance among the four stations, explained 89% of the total variance (Fig. 3A). Stations 1 and 3 had higher abundances of lagoon species, such as *Syngnathus abaster*, *A. fasciatus*, *A. boyeri*, *Salaria pavo,* and *Fistularia commersonii* (Fig. 3A and B). In contrast, stations 2 and 4 had higher abundances of migratory marine fish, such as Mugilidae species, *Solea solea* and *Sparus aurata* (Table 2, Fig. 3A and B). Mugilidae species are mainly detritivores, whereas *S. solea* and *S. aurata* are micro- and macro-benthivores. In constrast, the lagoon species are omnivores (*A. fasciatus* and *S. pavo*) or hyperbenthivores (*A. boyeri, S. abaster,* and *F. commersonii*). The diadromous species *Mugil cephalus* and *C. ramada* were caught at stations 2 and 3.

Potential food sources

The mean stable isotope composition of POM ranged from -23.7‰ to -22.6‰ for δ^{13}C and 3.2-4.5‰ for δ^{15}N, which was the lowest δ^{15}N of the food sources sampled (Table 3, Fig. 4A). Mean POM δ^{13}C differed significantly among stations (Kruskall-Wallis, $p < 0.05$), being lowest at station 3 (-23.2‰) and highest at station 4 (-22.8‰) (Table 3, Fig. 5). However, the difference in mean POM δ^{13}C was less than 1‰, which can be considered relatively similar for EML. The mean stable isotope composition of SOM ranged from -22.4‰ to -20.3‰ for δ^{13}C and from 3.5-4.5‰ for δ^{15}N (Table 3, Fig. 4A). Mean SOM δ^{13}C differed significantly among stations (Kruskall-Wallis, $p < 0.05$), being lowest at station 1 (-22.1‰) and highest at station 3 (-20.5‰) (Table 3, Fig. 5). The 2‰ difference in mean SOM δ^{13}C suggests an enrichment of SOM from the south of EML near the rivers northwards to the sea-influenced channel.

Pelagic invertebrates had mean stable isotope compositions that range from -21.6‰ to -19.5‰ for δ^{13}C and 5.1-9.7‰ for δ^{15}N (Table 3, Fig. 4A), but the

Table 2. Number of fish individuals captured (n) and their mean abundance (ind. 100 m^{-2}) ± standard error (se), and mean of total length (cm) and weight (g) ± standard deviation (sd), percentage of dominance, ecological guilds and feeding modes on the four sampling stations in El Mellah Lagoon located in the southern Mediterranean during the spring 2019. For ecological guilds: MM: Marine migrants, LS: Lagoon species, D: Diadromous species. For feeding modes: DV: Detritivores, HZ: Hyperbenthivores/Zooplanktivores, HP: Hyperbenthivores/Piscivores, OV: Omnivores, BMI: Microbenthivores, BMI/BMA: Micro- and Macrobenthivores.

Species	n	Density	Dominance	Length	Weight	Estuarine uses	Feeding modes
Aphanius fasciatus (A.fas)	41	7.1 ± 4.2	0.1	3.3 ± 0.7	0.6 ± 0.4	LS	OV
Atherina boyeri (A.boy)	234	46.8 ± 22.7	9.8	5.3 ± 0.6	1.1 ± 0.4	LS	HZ
Chelon auratus (C.aur)	92	22.6 ± 10.5	4.0	4.7 ± 0.6	1.0 ± 0.4	MM	DV
Chelon labrosus (C.lab)	23	5.2 ± 2.3	26.0	4.4 ± 0.6	1.0 ± 0.7	MM	DV
Chelon ramada (C.ram)	257	52.9 ± 30.4	12.6	4.7 ± 0.6	1.0 ± 0.5	D	DV
Chelon saliens (C.sal)	48	11.4 ± 6.0	2.9	5.2 ± 1.2	1.8 ± 1.7	MM	DV
Chelon spp. (C.spp)	79	17.6 ± 6.2	29.4	4.3 ± 0.6	0.8 ± 0.3	MM	DV
Fistularia commersonii (F.com)	1	0.3 ± 0.3	4.9	6.9	0.3	LS	HP
Mugil cephalus (M.cep)	1	0.2 ± 0.3	6.3	4.9	1.1	D	DV
Pomatoschistus spp. (P.spp)	43	8.9 ± 5.7	0.7	4.5 ± 1.0	1.0 ± 0.8	LS	BMI
Salaria pavo (S.pav)	7	1.3 ± 0.8	0.2	5.0 ± 0.6	1.2 ± 0.5	LS	OV
Solea solea (S.sol)	3	0.6 ± 0.4	0.3	7.3 ± 3.2	4.4 ± 4.3	MM	BMI/BMA
Sparus aurata (S.aur)	13	2.4 ± 2.2	1.4	4.3 ± 0.9	1.1 ± 0.9	MM	BMI/BMA
Syngnathus abaster (S.aba)	16	2.8 ± 1.8	1.5	8.7 ± 0.6	0.4 ± 0.1	LS	BMI

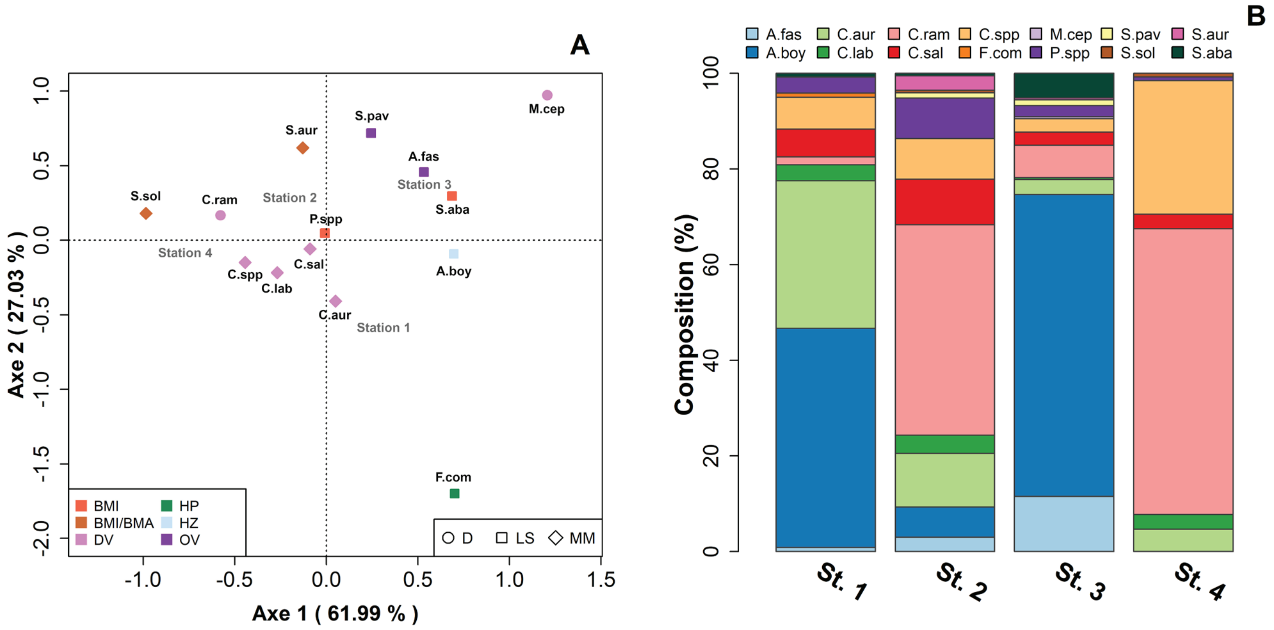


Fig. 3: (A) The first two axes of the correspondence analyses (CA) performed on the abundance of fish species, (B) the percentage of fish composition in the four sampling stations in El Mellah Lagoon located in the southern Mediterranean during the spring 2019. The categories of functional groups of ecological guilds (top right) and feeding mode (bottom right). See Table 2 for fish species abbreviations. For ecological guilds: MM: Marine migrants, LS: Lagoon species, D: Diadromous species. For feeding modes: DV: Detritivores, HZ: Hyperbenthivores/Zooplanktivores OV: Omnivores, HP: Hyperbenthivores/Piscivores, BMI: Microbenthivores, BMI/BMA: Micro- and Macrobenthivores.

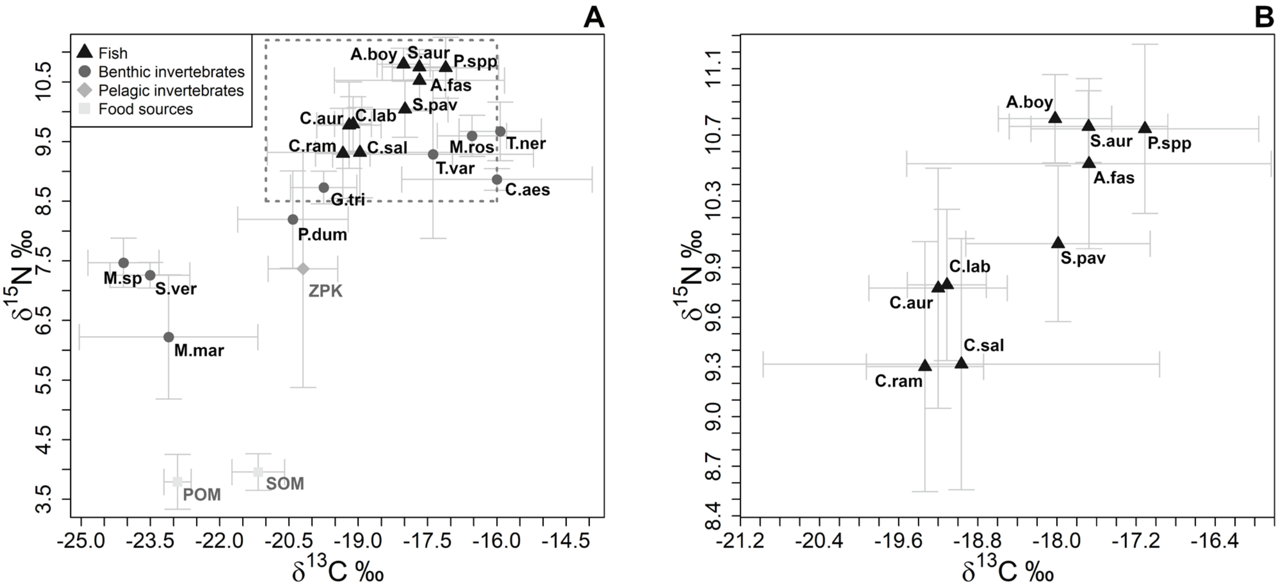


Fig. 4: Biplot of mean ± standard deviation of δ^{13}C and δ^{15}N (‰) of fish, pelagic and benthic invertebrates and food sources collected inside El Mellah Lagoon located in the southern Mediterranean during the spring 2019. A) δ^{13}C and δ^{15}N for all species, B) zoom on the stable isotope values of fish. See Tables 3 for abbreviations.

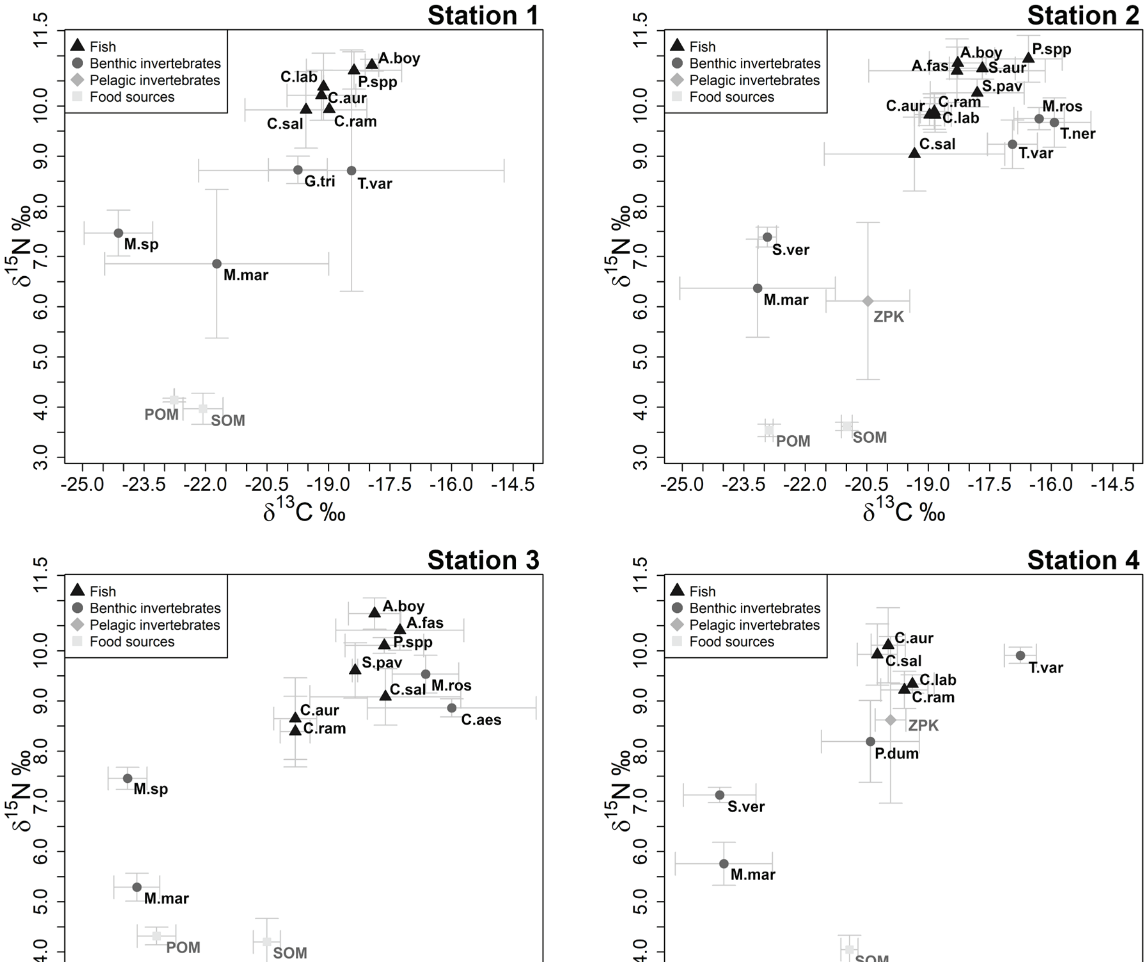


Fig. 5: Biplots of mean ± standard deviation of δ^{13}C and δ^{15}N (‰) of fish, pelagic and benthic invertebrates and food sources collected in the four sampling stations in El Mellah Lagoon located in the southern Mediterranean during the spring of 2019. See Tables 3 for abbreviations.

Table 3. Number of fish individuals analysed (n) and mean ± standard deviation δ^{13}C and δ^{15}N (‰) of fish, pelagic and benthic invertebrates and food sources in the four sampling stations in El Mellah Lagoon located in the southern Mediterranean during the spring 2019. * indicate pool of three individuals.

Species	**station 1**			**station 2**			**station 3**			**station 4**			**All stations**	
	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N
Fish														
Aphanius fasciatus				8	-18.3±2.2	10.7±0.6	12	-17.3±1.6	10.4±0.4				-17.7±1.8	10.5±0.5
Atherina boyeri	10	-7.9±0.2	10.8±0.1	10	-18.3±0.7	10.9±0.3	13	-17.9±0.6	10.7±0.3				-18.0±0.6	10.8±0.3
Chelon auratus	9	-19.2±0.8	10.2±0.5	14	-18.8±0.4	9.8±0.3	5	-19.8±0.5	8.6±0.8	3	-20.0±0.4	10.1±0.7	-19.2±0.7	9.8±0.7
Chelon labrosus	2	-19.1±0.0	10.4±0.7	6	-19.0±0.4	9.8±0.2				3	-19.4±0.5	9.3±0.2	-19.1±0.4	9.8±0.5
Chelon ramada				11	-18.9±0.3	9.9±0.4	7	-19.8±0.4	8.4±0.7	9	-19.6±0.6	9.2±0.4	-19.3±0.6	9.3±0.8
Chelon saliens	5	-19.6±1.5	9.9±0.8	11	-19.3±2.2	9.0±0.7	8	-17.6±1.8	9.1±0.6	3	-20.2±0.5	9.9±0.6	-19.0±2.0	9.3±0.8
Pomatoschistus spp.	4	-18.4±1.2	10.7±0.4	13	-16.6±0.8	10.9±0.5	4	-17.6±1.0	10.1±0.2				-17.1±1.2	10.7±0.5
Salaria pavo				4	-17.8±1.1	10.3±0.3	2	-18.4±0.1	9.6±0.6				-18.0±0.9	10.0±0.5
Sparus aurata				11	-17.7±0.8	10.8±0.2							-17.7±0.8	10.8±0.2
Benthic invertebrates														
Carcinus aestuarii (C.aes)							3	-16.0±2.1	8.9±0.2				-16.0±2.1	8.9±0.2
Glycera tridactyla (G.tri)	4	-19.7±0.7	8.7±0.3										-19.7±0.7	8.7±0.3
Macrobrachium rosenbergii (M.ros)				4	-16.3±0.6	9.7±0.2	10	-16.6±0.8	9.5±0.4				-16.5±0.8	9.6±0.3
Molgula sp. (*M*.sp)	12	-24.1±0.8	7.5±0.5				3	-23.9±0.5	7.5±0.2				-24.1±0.8	7.5±0.4
Mytilaster marioni (M.mar)	5	-21.7±2.7	6.9±1.5	13	-23.2±1.9	6.4±1.0	3	-23.7±0.6	5.3±0.3	5	-24±1.2	5.8±0.4	-23.1±1.9	6.2±1.0
Platynereis dumerilii (P.dum)										3	-20.4±1.2	8.2±0.8	-20.4±1.2	8.2±0.8
*Serpula vermicularis (S.ver)**				4	-22.9±0.2	7.4±0.2				4	-24.1±0.9	7.1±0.2	-23.5±0.9	7.3±0.2
Tritia neritea (T.ner)				3	-15.9±0.9	9.7±0.5							-15.9±0.9	9.7±0.5
Tritia varicosa (T.var)	5	-18.4±3.7	8.7±2.4	5	-16.9±0.6	9.2±0.5				5	-16.8±0.4	9.9±0.2	-17.4±2.2	9.3±1.4
Pelagic invertebrates														
Mesozooplankton (ZPK)				3	-20.5±1.0	6.1±1.6				3	-19.9±0.4	8.6±1.7	-20.2±0.8	7.4±2.0
Food sources														
POM	2	-22.8±0.0	4.1±0.0	3	-22.9±0.1	3.5±0.1	3	-23.2±0.5	4.3±0.2	3	-22.8±0.2	3.3±0.1	-22.9±0.3	3.8±0.5
SOM	2	-22.1±0.5	4.0±0.3	3	-21.0±0.1	3.6±0.1	2	-20.5±0.3	4.2±0.5	3	-20.9±0.2	4.0±0.3	-21.2±0.6	4.0±0.3

compositions did not differ significantly among stations (Kruskall-Wallis, p > 0.05) (Table 3, Fig. 5). Benthic invertebrates had mean stable isotope compositions that range from -25.6‰ to -14.5‰ for $\delta^{13}C$ and 4.4-10.2‰ for $\delta^{15}N$ (Table 3, Fig. 4A). The suspension-feeding ascidian *Molgula* sp., polychaete *S. vermicularis,* and bivalve *M. marioni* had the lowest mean $\delta^{13}C$ (-24.1‰ to -23.1‰) and $\delta^{15}N$ (6.2-7.5‰), indicating an influence of freshwater from the rivers. In contrast, the gastropods *Tritia neritea* and *Tritia varicosa* and the crustaceans *Macrobrachium rosenbergii* and *Carcinus aestuarii* had the highest mean $\delta^{13}C$ (-17.4‰ to -15.9‰) and $\delta^{15}N$ (8.9-9.7‰) (Table 3, Fig. 3). Stable isotope compositions of benthic invertebrates followed the same trend among stations. Only $\delta^{13}C$ of the polychaete *S. vermicularis* and $\delta^{15}N$ of the bivalve *M. marioni* differed significantly among stations (Kruskall-Wallis, $p < 0.05$), but they were relatively small mean differences of 1.2‰ and 1.6‰, respectively (Table 3, Fig. 5).

Fish $\delta^{13}C$ and $\delta^{15}N$ compositions

Stable isotope compositions of the nine most abundant fish species were analysed: four migratory marine fish (*C. auratus*, *Chelon labrosus*, *C. saliens* and *S. aurata*), one diadromous fish (*C. ramada*) and four lagoon species (*A. fasciatus*, *A. boyeri*, *Pomatoschistus* spp. and *S. pavo*) (Table 3). In EML as a whole, mean $\delta^{13}C$ was highest for *A. fasciatus*, *Pomatoschistus* spp., and *S. aurata* (-17.7‰, -17.1‰ and -17.7‰, respectively) and lowest for Mugilidae species (-19.0‰ to -19.3‰) (Table 3, Fig. 4). Mean $\delta^{15}N$ of fish species followed the same pattern, exceeding 10‰ for most fish, except Mugilidae species (9.3-9.8‰).

The $\delta^{13}C$ and $\delta^{15}N$ compositions of fish differed significantly (PERMANOVA, p < 0.05) among stations only for *C. auratus*, *C. labrosus*, *C. ramada*, *C. saliens* and *Pomatoschistus* spp.. Mean $\delta^{13}C$ was lowest for *C. ramada* at station 3 (-19.8‰); *C. auratus*, *C. labrosus* and *C. saliens* at station 4 (-20.0‰, -19.4‰ and -20.2‰, respectively), and *Pomatoschistus* spp. at station 1 (-18.4‰), whereas it was highest for all of these species at station 2 (-19.0‰ to -18.8‰). Mean $\delta^{15}N$ was highest for *C. saliens, C. auratus,* and *C. labrosus* at station 1 (9.9‰, 10.2‰ and 10.4‰, respectively) and *C. ramada* and *Pomatoschistus* spp. at station 2 (9.9‰ and 10.9‰, respectively), whereas it was lowest for all of these species at station 3 (8.4-10.1‰), except for *C. labrosus* for which it was lowest at station 4 (9.3‰) (Table 3).

Fish food-web structure

The food web of EML was structured by POM and SOM as food sources, pelagic and benthic invertebrates as primary and secondary consumers, and fish as apex consumers (Fig. 4). The trophic positions of Mugilidae species were 3.0, while those of other fish species were higher, from 3.2 for *S. pavo* to 3.4 for *A. fasciatus* and *A. boyeri* (Fig. 6). The trophic positions of Mugilidae species differed among stations, being highest at station 4 (3.0-3.3) and lowest at station 1 (2.9-3.0) (Fig. 6). Benthic invertebrates had a trophic position from 2.0 for *M. marioni* to 3.2 for *M. rosenbergii* (Fig. 6). Only the trophic position of the gastropod *T. varicosa* varied among stations, being lowest at station 1 (2.5) and highest at stations 2 and 4 (2.8-3.2) (Fig. 6). Pelagic invertebrates had a mean trophic position of 2.3, which range from 1.7 at station 2 to 2.8 at station 4 (Fig. 6).

Isotopic niches (SEA_c) of the fish ranged from 0.4-1.7%, with 3.1% for *A. fasciatus* and 4.6% for *C. saliens* (Table 4). SEA_c also varied among stations, with the

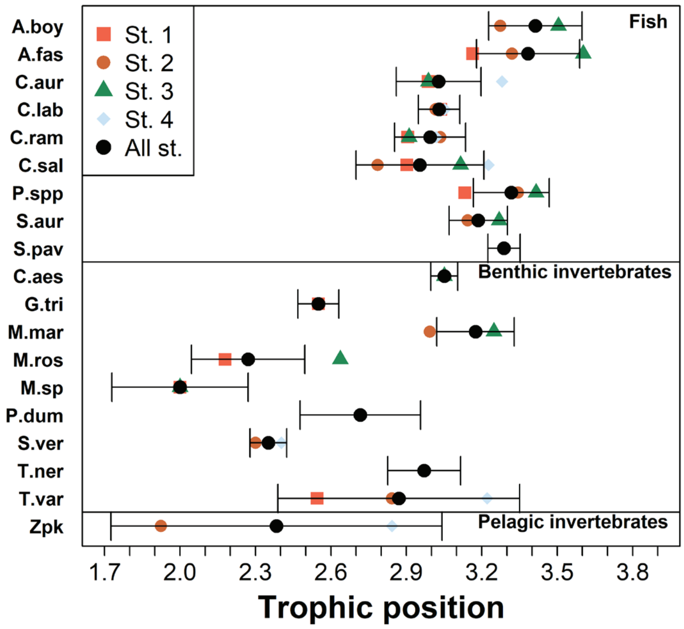


Fig. 6: Mean ± standard deviation of trophic position of fish and pelagic and benthic invertebrates in the four sampling stations in El Mellah Lagoon located in the southern Mediterranean during the spring 2019. See Tables 3 for abbreviations.

Table 4. Isotopic metrics with mean ± standard deviation of $\delta^{13}C$ and $\delta^{15}N$ (‰), carbon range (CR), nitrogen range (NR), total convex hull area (TA, %), standard ellipse areas (SEA, %) and corrected standard ellipse areas (SEA_c, %) of fish and pelagic and benthic invertebrates in the four sampling stations in El Mellah Lagoon located in the southern Mediterranean during the spring 2019.

Species	station 1					station 2					station 3					station 4					All stations				
	CR	NR	TA	SEA	SEAc	CR	NR	TA	SEA	SEAc	CR	NR	TA	SEA	SEAc	CR	NR	TA	SEA	SEAc	CR	NR	TA	SEA	SEAc
Fish																									
Aphanius fasciatus						5.4	2.1	6.3	4.2	4.9	4.9	1.6	4.6	1.9	2.1						6.4	2.5	9.2	3.0	3.1
Atherina boyeri	0.5	0.4	0.1	0.1	0.1	1.9	0.9	1.1	0.6	0.7	2.3	1.2	0.8	0.4	0.5						3.1	1.3	1.7	0.4	0.4
Chelon auratus	2.9	1.5	1.7	1.0	1.1	1.2	1.1	0.9	0.4	0.4	1.2	1.8	1.0	1.1	1.4	0.7	1.5	0.5	1.0	1.9	3.1	3.2	5.9	1.5	1.5
Chelon labrosus	0.0	0.9				0.9	0.6	0.3	0.2	0.3						1.0	0.4	0.2	0.3	0.6	1.2	1.7	1.2	0.5	0.6
Chelon ramada						1.2	1.2	0.7	0.4	0.4	1.1	2.2	1.0	0.7	0.9	1.7	1.0	1.1	0.7	0.8	2.3	3.0	3.4	1.1	1.2
Chelon saliens	3.8	1.8	3.2	3.0	4.0	8.2	2.0	9.4	5.1	5.7	4.7	1.8	4.1	2.4	2.8	1.0	1.1	0.2	0.4	0.8	8.2	2.4	11.5	4.5	4.6
Pomatoschistus spp.	2.5	0.9	1.0	1.4	2.0	2.5	1.8	2.1	1.0	1.0	2.1	0.4	0.3	0.4	0.5						4.0	1.9	4.4	1.6	1.7
Salaria pavo						2.7	0.6	0.8	0.9	1.3	0.1	0.8									2.7	1.3	1.7	1.3	1.6
Sparus aurata						2.2	0.7	0.8	0.4	0.5											2.2	0.7	0.8	0.4	0.5
Benthic invertebrates																									
Carcinus aestuarii											3.8	0.3	0.2	0.3	0.7						3.8	0.3	0.2	0.4	0.7
Glycera tridactyla	1.6	0.7	0.2	0.3	0.4																1.6	0.7	0.2	0.3	0.4
Macrobrachium rosenbergii						1.2	0.5	0.4	0.4	0.6	2.9	1.3	1.6	0.8	0.9						2.9	1.3	1.7	0.7	0.8
Molgula sp.	2.6	1.7	2.6	1.1	1.2						0.9	0.4	0.1	0.2	0.4						2.6	1.7	2.6	0.9	1.0
Mytilaster marioni	6.5	3.5	0.8	0.9	1.2	8.3	4.1	7.0	3.0	3.3	1.1	0.5	0.1	0.2	0.5	2.4	1.1	0.6	0.5	0.7	8.6	4.4	8.5	2.8	2.9
Platynereis dumerilii																2.2	1.5	0.5	0.8	1.7	2.2	1.5	0.5	0.8	1.7
Serpula vermicularis						0.5	0.4	0.1	0.1	0.2						1.9	0.3	0.3	0.4	0.6	2.7	0.7	0.7	0.4	0.5
Tritia neritea						1.7	1.0	0.5	0.9	1.7											1.7	1.0	0.5	0.9	1.7
Tritia varicosa	8.6	5.6	2.8	2.8	3.8	1.5	1.3	0.9	0.8	1.1						0.9	0.4	0.1	0.1	0.2	8.8	5.7	8.1	3.4	3.6
Pelagic invertebrates																									
Mesozooplankton						2.0	2.8	2.6	4.7	9.5						0.7	3.0	0.8	1.4	2.7	2.1	4.6	5.4	4.0	5.0

narrowest niches for Mugilidae species at station 2 (0.3-0.4%), except for *C. saliens* (5.7%) (Table 4). For other fish, SEA_c was widest at station 2 (0.5-5.7%). Isotopic niches of pelagic and benthic invertebrates followed the same pattern as those of fish, with narrower niches for all species (SEA_c of 0.4-1.7%) except *M. marioni*, *T. varicosa* and pelagic invertebrates (2.9%, 3.6%, and 5.0%, respectively) (Table 4).

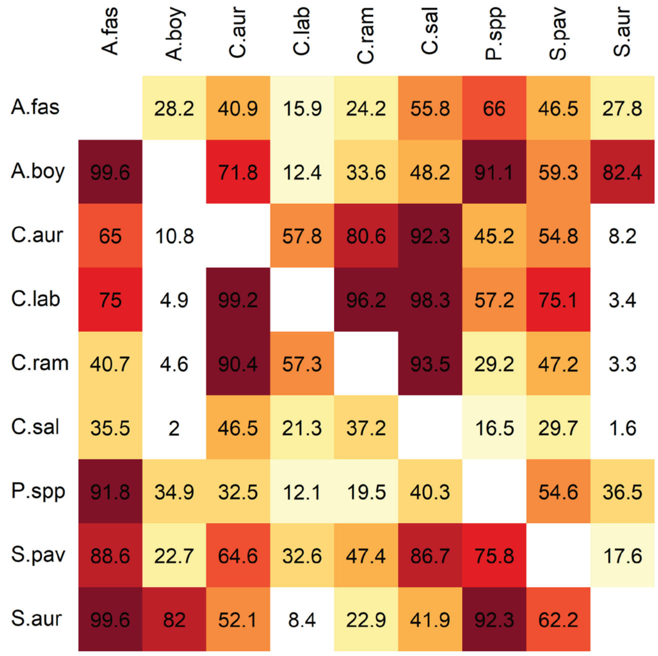
The probabilistic niche-region method indicated that the isotopic overlap was 81-99% between Mugilidae species and 63-84% between other fish species (Fig. 7). In contrast, that between Mugilidae and other fish species was less than 80%, suggesting that they occupied distinct isotopic niches (Fig. 4B). Other fish species had an isotopic niche overlap mainly with *A. fasciatus* (71.0-99.8%).

Discussion

Structure of fish communities and spatial variations

Total of 14 fish species were identified in EML in the spring, dominated mainly by species of families Atherinidae (mainly *A. boyeri*) and Mugilidae (mainly *C. ramada*), primarily juveniles with a mean length less than 7 cm and short adults such as *A. fasciatus* and *Pomatoschistus* spp.. The number of species caught in EML is similar to that of a previous study of EML during the same season (Embarek, 2019) and that of other southern Mediterranean lagoons (e.g., 15 species in Nador Lagoon, Morocco; Jaafour *et al.*, 2015) but is lower than that of in other Mediterranean lagoons. Pérez-Ruzafa *et al.* (2011, 2007) found that in 40 lagoons in the Atlantic Mediterranean, species richness ranged from 6-48 species, with a mean of ca. 23 species. EML had fewer fish species than most southern Mediterranean lagoons, including Ghar El Melh in Tunisia (26 species) and Lake Manzala in Egypt (17), (Bouchereau *et al.*, 2000; Jaafour *et al.*, 2015). This difference in fish species richness among lagoon environments could be related to characteristics of each lagoon (e.g., area, depth, connection to the sea), hydrological parameters (e.g., tidal range, temperature, salinity), the sampling period (e.g., season), and fishing effort, as well as the type of fishing gear used for sampling (Akin *et al.*, 2005; Franco *et al.*, 2008). Pérez-Ruzafa *et al.*, (2011) suggested that the main factor that influences the structure of lagoon communities is the degree of isolation from the sea. EML's confinement results from hydrological isolation (i.e., long and narrow channel) and being relatively deep (up to 6 m) in relation to its area (8 km²) (Guelorget *et al.*, 1989). This may explain EML's low species richness and dominance of opportunistic species, such as lagoon residents and migrating marine species, such as Mugilidae, which have a wide ecological tolerance (Whitfield *et al.*, 2012). In addition, EML behaves as a dilution basin (Draredja, 2007) due to the channel silting up and the decrease in salinity during flooding, which can lead to a loss of marine species. A beach seine is considered effective for sampling fish shorter than 10 cm in shallow waters such as lagoons, but it cannot catch longer fish (Franco *et al.*, 2012). In a previous study of EML, Chaoui *et al.* (2006) identified 38 fish species the maximum number recorded there, by using multiple types of fishing gear (i.e., fish traps, gillnets, and beach seines) at multiple depths over several seasons and years.

The spatial distribution indicated that migratory marine species tended to be caught closer to the sea, whereas lagoon-resident species tended to be caught closer to freshwater inputs from the rivers at the edge of EML.



	A.fas	A.boy	C.aur	C.lab	C.ram	C.sal	P.spp	S.pav	S.aur
A.fas		28.2	40.9	15.9	24.2	55.8	66	46.5	27.8
A.boy	99.6		71.8	12.4	33.6	48.2	91.1	59.3	82.4
C.aur	65	10.8		57.8	80.6	92.3	45.2	54.8	8.2
C.lab	75	4.9	99.2		96.2	98.3	57.2	75.1	3.4
C.ram	40.7	4.6	90.4	57.3		93.5	29.2	47.2	3.3
C.sal	35.5	2	46.5	21.3	37.2		16.5	29.7	1.6
P.spp	91.8	34.9	32.5	12.1	19.5	40.3		54.6	36.5
S.pav	88.6	22.7	64.6	32.6	47.4	86.7	75.8		17.6
S.aur	99.6	82	52.1	8.4	22.9	41.9	92.3	62.2	

Fig. 7: Mean estimates of fish isotopic niche region overlap (%) with 95% Bayesian credible intervals of fish (probability that fish shown in rows overlap with those shown in columns) at the four sampling stations in El Mellah Lagoon located in the southern Mediterranean during the spring 2019.

Based on the PCA and CA, the depth and distances from the channel and nearest rivers (i.e., proxy of salinity) appeared to structure the fish community of EML spatially. Salinity is one of the main factors that influence spatial variation in fish communities in coastal lagoons (Maci & Basset, 2009) as well as the functioning of lagoon ecosystems by influencing fish reproduction, growth, and migration (Embarek *et al.*, 2017). Salinity should be measured in future studies to confirm these results.

Lagoon-resident species in EML represented 43% of the total catch; dominate by species of families Atherinidae (mainly *A. boyeri*) and Cyprinodontidae (mainly *A. fasciatus*). The dominance of lagoon-resident species has been observed in other southern Mediterranean lagoons (e.g., Nador, in Morocco (Jaafour *et al.*, 2015); Ichkeul, in Tunisia (Sellami *et al.*, 2010)) and in some northern Mediterranean lagoons (Manzo *et al.*, 2016). Due to adaptive plasticity, *A. boyeri* is able to occupy a large ecological niche (Koutrakis *et al.*, 2005), which would explain its presence near the rivers. *A. boyeri* was found in shallow areas directly influenced by freshwater and in *Ruppia* seagrass beds, which covers much of the shallow areas of EML and provides a favourable habitat for fish to complete their life cycle and form large populations (Leonardos & Sinis, 1999). The greater complexity of this vegetated habitat supports more diverse fauna and provides greater food availability and refuge from predators (Franco *et al.*, 2006).

Migratory marine fish were caught mainly in the northern section of EML near the channel, under marine influence. Composed mainly of Mugilidae species, they represented up to 31% of the catches. Similar observations were made for EML in a previous study (Embarek, 2019) and for a similar closed lagoon, Bizerte Lagoon in Tunisia (Embarek *et al.*, 2017). These observations are similar to those of studies of 19 lagoons in the northern Mediterranean that described fish communities with a large proportion of migratory marine species (Franco *et al.*, 2008). EML would thus be a favourable habitat for juvenile migratory marine species in spring (Ezzat, 1965). These ubiquitous fish colonise lagoons where food is available and which can protect them, as predation is much lower in lagoons than in the sea (Bouchereau *et al.*, 2000).

Potential food sources for fish in El Mellah Lagoon

The mean POM δ^{13}C (-23.7‰ to -22.6‰) indicated that it originate primarily from marine sources, and increased relatively little from the rivers on the western edge of EML to the channel. These compositions are similar to those of previous studies of north-western Mediterranean lagoons, including Lapalme Lagoon (Carlier *et al.*, 2007; 2008), Salses-Leucate Lagoon (Carlier *et al.*, 2009), the Catalan Sea (Papiol *et al.*, 2013), and Sabaudia Lake (Sara *et al.*, 2002), but higher than those of Canet Lagoon (Carlier *et al.*, 2008) and Berre Lagoon (Marchessaux *et al.*, 2021). Lagoon POM generally comes from multiple sources; mainly phytoplankton, as well as microzooplankton, aquatic bacteria, detritus, and faecal pellets (Cresson *et al.*, 2012; Liénart *et al.*, 2017). The high POM δ^{13}C, which is characteristic of lagoons with a large opening to the sea (Carlier *et al.*, 2007; Vizzini & Mazzola, 2008), indicated that marine phytoplankton is one of the main primary producers and could thus be an important food source in EML, especially for pelagic and benthic invertebrates. Freshwater in EML comes directly from precipitation via the rivers, whereas marine water comes from the sea via the channel. This would explain the high δ^{13}C observed, which indicate an increase in salinity and a strong marine influence during the dry season (Embarek *et al.*, 2017; Draredja *et al.*, 2019). The POM δ^{13}C, which varies as a function of salinity (Vizzini *et al.*, 2005; Prado *et al.*, 2014), showed no significant spatial variability, confirming that EML has no salinity gradient (Draredja & Kara, 2004; Draredja, 2007; Embarek *et al.*, 2017), except during extreme events (e.g., heavy precipitation).

Mean SOM δ^{13}C (-22.4‰ to -20.3‰) were similar to those of POM, which suggest a common origin, and to those of north-western Mediterranean lagoons (Sara *et al.*, 2002; Vizzini *et al.*, 2005; Carlier *et al.*, 2007; 2008; Marchessaux *et al.*, 2021), except Canet Lagoon (Carlier *et al.*, 2008) and Salses-Leucate Lagoon (Carlier *et al.*, 2009), whose δ^{13}C were lower and higher, respectively. Lagoon SOM generally comes from multiple sources; sedimented POM, microphytobenthos and detritus (Carlier *et al.*, 2007; 2008; Cresson *et al.*, 2012). The δ^{13}C can also increase due to decomposition of macroalgae and seagrass (Cresson *et al.*, 2012). The influence of *Ruppia* seagrass the beds could partly explain the high SOM δ^{13}C in EML, even though the beds are not a major food source for primary consumers. Mean SOM δ^{15}N in EML were also similar to those of POM (3.8‰ and 4.0‰, respectively), and no well-defined spatial variation was identified. Although it is common for amounts of nitrogen to decrease as salinity increases from freshwater to marine water due to mixing (Baeta *et al.*, 2009; Connolly *et al.*, 2013), the δ^{15}N observed confirmed the absence of a salinity gradient in EML. The δ^{15}N is often used as a tracer to detect human sources of nitrogen, particularly in lagoon and estuarine environments (Vizzini & Mazzola, 2004; Vizzini *et al.*, 2005; Bouaziz *et al.*, 2021), As higher δ^{15}N can be considered to originate from human activities (Fry, 2002; Vizzini & Mazzola, 2004; Vizzini *et al.*, 2005). The δ^{15}N in EML highlights relatively low anthropogenic nitrogen input, which could be due to the absence of human activities (Draredja *et al.*, 2019).

To determine potential food sources for fish in EML, we analysed the food-web structure assuming that δ^{15}N and δ^{13}C increases by 3.4‰ and 1.0‰ from prey to consumers, respectively (i.e., sequential trophic positions) (DeNiro & Epstein, 1981; Minagawa & Wada, 1984). Benthic suspension feeders had lower δ^{13}C (-24.1‰ to -23.1‰) than POM (-22.9‰) or SOM (-21.2‰) did, indicating that they likely consumed a mixture of freshwater and marine phytoplankton. This may have been due to the location of suspension feeders near the rivers and the recent shift from the rainy to the dry season. Similar POM

$\delta^{13}C$ (-26.0‰ to -22.0‰) were observed at the mouth of the Rhône River in the Gulf of Lions in the north-western Mediterranean due to high river flows, which suggests lowing $\delta^{13}C$ in terrestrial organic matter (Darnaude *et al.*, 2004). Pelagic invertebrates and the benthic polychaetes *P. dumerilii* had $\delta^{13}C$ (-20.4‰ to -19.7‰) similar that of SOM, likely due to consuming marine phytoplankton. In contrast, the gastropods *T. neritea* and *T. varicosa* and the crustaceans *M. rosenbergii* and *C. aestuarii* had the highest mean $\delta^{13}C$ (-19.4‰ to -15.9‰, respectively), being influenced more by microphytobenthos. These $\delta^{13}C$ could correspond to those of microphytobenthos (-19.2‰ to -19.0‰) and detritus (detritivores) exclusively from autochthonous organic matter (Sokołowski *et al.*, 2012). The isotope composition of fish was consistent with the consumption of pelagic and benthic invertebrates, especially pelagic invertebrates, suspension feeders (e.g., *S. vermicularis*, *M. marioni*, *Molgula* sp.), and deposit feeders (e.g., *P. dumerilii*). In contrast, gastropods and crustaceans seemed to be a negligible food source for fish, as their relatively high trophic position (i.e., 2.9-3.2) was similar to that of fish species (e.g., Mugilidae). The higher $\delta^{13}C$ for gastropods and crustaceans invertebrates (-17.4‰ to -15.9‰) than for fish species (-19.3‰ to -17.1‰) suggest that they consume different food sources. Marine SOM and POM, as well as microphytobenthos, appear to be major food sources for pelagic and benthic invertebrates in EML. Thus, pelagic and benthic invertebrates can be considered primary and secondary consumers that represent an important link between POM/SOM and fish species (Little *et al.*, 2000; Mann & Wetzel, 2000).

Structure of the fish food-web

We identified two fish communities in EML, one near the channel under marine influence (migratory marine juveniles) and the other near the rivers (lagoon-resident species). Juveniles of migratory marine species of Mugilidae had the lowest $\delta^{13}C$ (-19.3‰ to -19.0‰), which was approximately 2‰ higher than that of SOM, indicating a contribution from microphytobenthos and detritus. The four Mugilidae species have a detritivorous diet based on the same types of prey composed mainly of benthic detritus (macrophytes and algae), as well as zoobenthos and gastropods (Shaiek *et al.*, 2015). The *Ruppia* seagrass which covers much of the shallow area (> 70%) of EML (Embarek *et al.*, 2017) can be considered a feeding area, as juvenile Mugilidae graze on seagrass or silt to obtain organic matter, including microphytobenthos. Isotopic niches of Mugilidae species were similar (63-89%) and narrow (SEA_c of 0.6-4.6%), except for the station near the *Ruppia* seagrass, likely due to consuming seagrass detritus. This hypothesis needs to be confirmed by measuring the stable isotope composition of the *Ruppia* seagrass to determine its contribution to the lagoon food-web.

In contrast, lagoon-resident fish species had $\delta^{13}C$ (-18.0‰ to -17.1‰) similar to those of pelagic and benthic invertebrates, revealing that microphytobenthos and SOM are be a major food source. *A. boyeri*, the dominant lagoon-resident fish, had higher $\delta^{13}C$ than Mugilidae species but lower $\delta^{13}C$ than other lagoon-resident fish, and an isotopic niche that overlapped that of *S. aurata* (84%); both species occupied a high trophic positions (3.3-3.4) and had narrow isotopic niches (SEA_c of 0.4% and 0.5%, respectively). *S. aurata* is a micro- and macro-benthivore that feeds mainly on crustaceans and polychaetes (Tancioni *et al.*, 2003), whereas *A. boyeri* is hyperbenthivorous/zooplanktivorous, as it consume prey of high trophic position such as *S. aurata,* gastropods, and crustaceans (i.e., amphipods and isopods) (Shaiek *et al.*, 2015).

A. fasciatus, *S. pavo* and *Pomatoschistus* sp. had overlapping isotope niches (62-77%), which suggests that they were trophically similar. The isotope compositions of *A. fasciatus* and *S. aurata* were similar, but *A. fasciatus* occupied a wider isotopic niche (SEA_c of 3.1%), indicating that it consummed a wider range of prey and may have competed for food with the other two lagoon-resident fish. *A. fasciastus* is an omnivore that feeds mainly on amphipods and isopods (Shaiek *et al.*, 2015). However*, S. pavo* and *Pomatoschistus* sp. generally follow an opportunistic feeding strategy determined by intra- and inter-specific competition (Post *et al.*, 1999; Brown *et al.*, 2012) and prey availability. The diet of *S. pavo* a generalist, includes a wide range of crustaceans (i.e., amphipods, isopods, decapods, copepods, cumaceans and ostracods), gastropods, and polychaetes (Compaire *et al.*, 2016). *Pomatoschistus* sp. feeds on zooplankton, zoobenthos, and amphipod/isopod crustaceans (Shaiek *et al.*, 2015).

Conclusion

The present study revealed that the food-web structure in EML in the spring (dry season) was based essentially on marine POM and SOM, which is common in northern Mediterranean lagoons. Our results reveal the contribution of microphytobenthos to the fish food-web, and the importance of *Ruppia* seagrass, which is a basic feeding area for juvenile migratory marine fish. The seagrass habitat supports more diverse fauna, such as benthic invertebrates, which are a food source for benthivores lagoon-resident fish. Our study revealed that freshwater inputs influence the functioning of the food web in EML little in the spring, and that juvenile marine fish may visit the lagoon for reasons other than feeding. Coastal lagoons provide ecological functions such as a nursery for many fish species, especially for juveniles (e.g., to avoid predation). We highlight the need to consider other trophic compartments (e.g., microphytobenthos) to describe the structure of the fish food-web better. We also recommend studying seasonal variations in its structure to assess the feeding-area fidelity of juvenile marine fish living in EML.

These results of the fish food-web in EML could be supplemented in future studies by considering all trophic compartments, such as *Ruppia* seagrass meadows in stable isotope analyses. In addition, stable isotope analyses should be extended to include all four seasons to consider seasonal variations in the structure of the fish food-web, as these variations are influenced by fluctuations in organic matter input from rivers and the sea, as well as variations in the composition of fish and invertebrate communities, depending on the period of migration and/or reproduction.

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