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Multi-biochemical tracers reveal the complexity of energy and matter pathways within a pelagic food web in the Mediterranean Sea (Bay of Marseille)- average food web structure from organic matter to planktivorous fishes

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Keywords

Small pelagic fish; plankton; carbon and nitrogen stable isotopes; biochemical composition; organic matter transfer; mixing model

Abstract

In the context of decline of planktivorous fishes in the North-Western Mediterranean Sea (NWMS), this study is the first, to analyze simultaneously stable isotope and biochemical contents in coastal particulate organic matter (POM) size classes (0.7-2.7 μm , 2.7-20 μm , 20-200 μm) including mainly phytoplankton groups, in zooplankton size classes (200-300 μm , 300-500 μm , 500-1000 μm , 1000-2000 μm , > 2000 μm) and taxonomic groups, and planktivorous fish species (*Engraulis encrasicolus*, *Sardina pilchardus*, *Sardinella aurita*, *Sprattus sprattus*, *Cepola macrophthalma*, *Chromis chromis*, *Boops boops*, *Spicara maena*). This study highlights how POM is transferred through these compartments (size classes and taxonomic groups) in the pelagic food web of the bay of Marseille. We demonstrated that: (1) isotopic composition differed on POM origins around the Bay of Marseille, according to its taxonomic and biochemical compositions; (2) an increase in $\delta^{15}\text{N}$ values between zooplankton size classes and groups highlighting different trophic level in this planktonic component; and (3) phytoplankton were lipid-rich (~ 55%), while zooplankton (~ 61%) and fish muscles (~ 66%) were protein-rich. Stable isotope mixing models highlighted that: (1) oceanic POM contributed the most to the bay POM (> 51%); (2) the bay POM was dominated by pico-POM (~ 43%); (3) nano-POM contributed the most (~ 84%) to the carbon and nitrogen of 200-1000 μm zooplankton, micro-POM contributed the most (~ 64%) to the 1000-2000 μm zooplankton, while pico-POM contributed the most (~ 86%) to the > 2000 μm zooplankton; (4) mesozooplankton (200-2000 μm) contributed the most (~ 42%) to the carbon and nitrogen sources of all the planktivorous fish species, while macrozooplankton organisms (> 2000 μm) were the main food resources (~ 43%) for *B. boops* and *S. sprattus*. This multi-tracers' study highlighted the trophic characteristics of the pelagic food web and the bottom-up transfer of the organic matter from the smallest phytoplankton size fractions up to planktivorous fishes.

1. Introduction

Particulate organic matter (POM) is considered as the pelagic food web basis and fuels the pelagic food webs (Harmelin-Vivien et al. 2008; Bănaru et al. 2014; Fey et al. 2020). Living and detrital particles from autochthonous (*in situ* pelagic and benthic primary producers) and allochthonous (continental) reservoirs constitute the POM mixture in coastal systems (Savoie et al. 2012). Thus, we refer to POM here as a potential source of organic matter for the pelagic food web.

Zooplankton plays a prominent role in marine pelagic food webs as it is very responsive to environmental changes, and it contributes to the transfer of organic matter from phytoplankton to planktivorous consumers (Banse 1995; Mitra et al. 2014). Small planktivorous fish also act as an essential trophic compartment in many ecosystems (Peck et al. 2020; Fey et al. 2021) as they feed on diverse plankton groups and are forage species for many predators (Palomera et al. 2007; Bănaru et al. 2013, 2019).

These three highly interconnected compartments: phytoplankton, zooplankton and planktivorous fish constitute the first major trophic levels of the pelagic food webs (Middelburg 2019).

Bottom-up changes in the plankton community, induced by both climate and anthropogenic pressures, have been hypothesized to be the cause of the decline of biomass, associated with decrease of individual body length and relative body condition, of several commercially important small pelagic fish stocks in the Mediterranean Sea, including the North-Western Mediterranean Sea (NWMS) (Saraux et al. 2019; Feuilloley et al. 2020). Given the importance of commercial fisheries in the Gulf of Lion (FAO 2020), there is a pressing need to provide an integrated global characterization of the pelagic food web. This may contribute to better understand the causes of the decline of biomass of planktivorous fish species toward future ecosystem-based management (Le Bourg et al. 2015; Chen et al. 2021, 2022).

To better apprehend the complex trophic interactions in pelagic food-webs, several studies compared diet of planktivorous fish (European sardine *Sardina pichardus*, anchovy *Engraulis encrasicolus*, sardinella *Sardinella aurita*) in the Gulf of Lion (Le Bourg et al. 2015; Albo-Puigserver et al. 2019; Bachiller et al. 2020, 2021; Chen et al. 2022). In the same area, the importance of the trophic role of plankton size classes and groups has also been considered increasingly in recent studies (Bănaru et al. 2014; Bachiller et al. 2021; Chen et al. 2021, 2022). However, most of these studies focus on

only two successive compartments (phytoplankton and zooplankton, or zooplankton and fish) (Bănaru et al. 2014; Costalago et al. 2014; Le Bourg et al. 2015; Chen et al. 2021). Such studies have been usually conducted for a short period of time (Cresson et al. 2014a; Le Bourg et al. 2015; Bachiller et al. 2021).

In the present study, we aimed at studying the three compartments simultaneously over an annual scale duration (Fig. 1 and Table 1). Phytoplankton and POM were collected in the bay of Marseille at Solemio site (below 'Bay POM') and sieved over three size classes (0.7-2.7 μm , 2.7-20 μm , 20-200 μm), whereas bulk POM samples were collected in different origins around the bay (oceanic, anthropogenic and riverine origins). Zooplankton was also collected at Solemio site and sieved over 5 size classes (200-300 μm , 300-500 μm , 500-1000 μm , 1000-2000 μm , > 2000 μm). Eight planktivorous fish species (*Engraulis encrasicolus*, *Sardina pilchardus*, *Sardinella aurita*, *Sprattus sprattus*, *Cepola macrophthalma*, *Chromis chromis*, *Boops boops*, *Spicara maena*) were also sampled in the Bay of Marseille (Gulf of Lion, NWMS).

Stable isotopes analyses (hereafter SIA), a powerful and widely applied tool to produce integrated over time diet estimations, were used to determine flows of organic matter (Bachiller et al. 2021). Stable isotopes of carbon ($\delta^{13}\text{C}$) is employed to identify the organic matter origins, while nitrogen stable isotope ratio ($\delta^{15}\text{N}$) indicates the relative trophic level (Post 2002). The combination of carbon and nitrogen SIA together with taxonomic and biochemical composition of POM, allows the characterization of the different POM origins to the Bay of Marseille. It also allows us to comprehend the trophic relationship between size classes and groups/species through trophic levels. These results may be compared with fish stomach content analyses reported in previous studies at the same area (Chen et al. 2022).

We also aimed at estimating how POM from different origins (oceanic, anthropogenic and riverine) gets transferred up in the planktonic food web from zooplankton of different sizes to planktivorous fish species. We thus used Bayesian mixing models, in which variability of source isotopic compositions and of trophic fractionation factors can be considered (Stock et al. 2018). Such models provide ranges of food source contributions to consumer's diet. We also determined biochemical composition (proteins, carbohydrates and lipids) and energy content of POM and of size classes and groups (Chen et al. 2019). The originality of this study lays in this multi trophic marker approach combined to biochemical analyses to infer food web functioning. Studies using these above cited methods altogether remains rare, while

they can help elucidate hidden processes or reveal unexpected importance of some taxa (Fey et al. 2021).

More specifically, we examined: (1) how different were isotopic compositions of POM size classes, zooplankton size classes and groups, (2) how estimates of trophic levels varied between these groups, and planktivorous fish species, (3) how biochemical composition and energy content varied between them, and (4) we discussed how trophic fractionation factors influenced the results of mixing models. Our data provide the first comparative analysis of the isotopic and biochemical composition of the three main compartments of the pelagic food web in the NW Mediterranean Sea. The results of this study may contribute to improve the representation of trophic interactions between phytoplankton and zooplankton size classes in biogeochemical models and in ecosystem models.

2. Material and methods

2.1. Study site

The Bay of Marseille is located in the eastern part of the Gulf of Lion (North-Western Mediterranean Sea, Fig. 1). It is influenced southwards by intrusions of the offshore Northern Current (Millot, 1987; Petrenko et al., 2005) and by the coastal Huveaune River on its eastern side, as well as by occasional intrusions of the Rhone river plume, depending on wind and rain events (Cresson et al. 2012; Fraysse et al. 2014). The bay is also subject to anthropogenic and terrestrial inputs from the Marseille sewage water treatment plant at Cortiou on its southeastern part (Ourgaud et al. 2015; Millet et al. 2018). The Huveaune River flow is deflected to Cortiou most of the time, but flows directly to the sea through its natural bed after heavy rain events (Bănaru et al. 2014). Thus, in this bay, phyto- and zooplankton communities benefit from multiple main potential sources of nutrients and POM (seawater, river runoff and sewage water particles) (Bănaru et al. 2014; Chen et al. 2019, 2022).

2.2. Sampling and sample processing

2.2.1. Particulate organic matter (POM)

Three pools of particulate organic matter (hereafter POM) were considered as potential food sources fueling the planktivorous food web within the bay (at Solemio site): oceanic phytoplankton (collected at Julio site), anthropogenic inputs from Cortiou sewage treatment plant, and terrestrial inputs from the Huveaune river (Fig. 1). The sampling of POM was done on board the R/V ANTEDON II from October 2016 to May

2018. Due to logistical constraints, samplings at the bay station (Solemio) took place twice a month and once a month at Cortiou and Julio stations. Huveaune river water samples (10 L of water) were collected after major rain events. For Solemio, Julio and Cortiou, 60 L of surface seawater was collected with a pump for each sample date.

The sampled bay POM water was filtered consecutively through 200 μm and 20 μm mesh size sieves, and vacuum-filtered through Whatman GF/D membranes (2.7 μm) and GF/F filters (0.7 μm) that were all precombusted (500°C, 6h) and rinsed with Mili-Q water. After filtration, filters were rinsed with Mili-Q water and oven-dried. We thus obtained three size classes of particles corresponding to the micro- (20-200 μm), the nano- (2.7-20 μm) and the pico- (0.7-2.7 μm) POM. For the rest of the sampling sites, water was filtered through the 200 μm mesh size sieve to remove large particles and size classes were not separated to obtain a bulk fraction (0.7-200 μm). The number of different categories of samples are given in Table 1.

2.2.1.1. Flow cytometry analysis (< 20 μm organisms)

For all the sampling stations, type and size of organisms < 20 μm were quantified on a flow cytometer (FACScalibur analyzer, BD Biosciences) (PRECYM flow cytometry platform <http://precy.mio.univ-amu.fr>). Standard protocols were used to enumerate phytoplankton as described in Bănaru et al. (2014). Based on particle scatters and fluorescences, picoplankton (< 3 μm) was discriminated from nanoplankton (> 3 μm), then different populations were determined: picoplankton cells (*Prochlorococcus*, *Synechococcus*, picoeukaryotes), nanoplankton cells (cryptophyceans, nanoeukaryotes, nano-cyanobacteria filaments and detritus).

Organisms from the cryptophycean group with a cell size from 3 to 10 μm were named as “crypto-like” since the molecular analyses were not done to confirm their identity. Larger cells (from 10-50 μm), identified under the microscope, were named cryptophyceans. Cryptophyceans thus overlap both the nano- and micro- size fractions. While smaller groups may be identified only with by flow cytometry and larger groups only by microscopic counts.

2.2.1.2. Light microscopy (10-100 μm organisms)

For bay POM (Solemio), diatoms and large phytoplankton cells (nano- and microphytoplankton of size ranging from 10 to 100 μm) were identified and enumerated by light microscopy at X200 and X400 magnification on a Nikon TE-2000 inverted microscope, in 100 mL Utermöhl sedimentation Chambers (Utermöhl 1931). The broad

taxonomic groups identified were diatoms, dinobionts, cryptophyceans, undetermined nanoflagellates.

2.2.2. Zooplankton

Zooplankton was collected twice a month from October 2016 to May 2018 at the bay site (Fig. 1, Solemio). Zooplankton was sampled by vertical tows with a 80 μm mesh-size WP2 net and the sample was sieved in five size classes (Table 1). Detailed taxonomic identification was done with bulk plankton samples following the website ‘Marine Planktonic Copepods’ (<https://copepodes.obs-banyuls.fr/en/loc.php?loc=14>) (Razouls et al. 2005) to obtain the relative numerical abundance of each group. Such information has been already published (Table 2 in Chen et al. (2019)).

2.2.3. Planktivorous fish species

In addition to results shown by Chen et al. (2022), we added the data blotched picarel *Spicara maena* (Linnaeus, 1758) (Sparidae) *Spicara maena*, which we found to be feeding essentially on copepods (Centropagidae and Corycaeidae) with stomach content analysis. In total, eight fish species were thus studied: European sardine *Sardina pilchardus* (Walbaum, 1792) (Clupeidae), round sardinella *Sardinella aurita* (Valenciennes, 1847) (Clupeidae), European sprat *Sprattus sprattus* (Linnaeus, 1758) (Clupeidae), red bandfish *Cepola macrophthalma* (Linnaeus, 1758) (Cepolidae), damselfish *Chromis chromis* (Linnaeus, 1758) (Pomacentridae), bogue *Boops boops* (Linnaeus, 1758) (Sparidae). Fish were sampled monthly by local fishermen (Fig. 1, Table 1) and dorsal white muscle was prepared for SIA as described by Chen et al. (2022).

2.3. Stable isotope and biochemical analyses

As both POM/phytoplankton and zooplankton may contain carbonates, their samples were acidified using 1% HCl added drop-by-drop (DeNiro and Epstein 1978) for measurements of $\delta^{13}\text{C}$ values in the particulate organic matter (POM). These samples were then rinsed with Milli-Q water, vacuum-filtered and oven-dried. Raw (i.e. non-acidified) samples were analyzed for measurement of $\delta^{15}\text{N}$ values. POM and zooplankton samples were collected by scraping the surface of acidified and nonacidified filters. Three replicates were analyzed for each zooplankton size class and group, and for each site. SIA of POM, zooplankton and planktivorous fishes were performed as described by Chen et al. (2022) (Table 1).

Carbohydrate, protein and lipid concentrations were assessed and the energy

content provided was estimated for POM, as described by Chen et al. (2019) for zooplankton size classes and groups.

We used data of muscle energy content in *S. pilchardus* available from the Catalan Sea (i.e. around $25.13 \pm 4.88 \text{ J mg}^{-1} \text{ DW}$) to make an estimate the energy transfer from POM and zooplankton size fractions to *S. pilchardus* (Albo-Puigserver et al. 2017). However, the concentrations of biochemical components such as total proteins, carbohydrates and lipids were not well documented in previous studies. According to Batista et al. (2009) and Markovic et al. (2015), carbohydrates seem to be absent in the proximate composition of the muscles of *S. pilchardus*, and proteins and lipids account for 66.4% and 33.6% of the ash free dry mass respectively. These data were used to discuss the differences of biochemical composition between POM, zooplankton and *S. pilchardus*.

2.4. Modeling and trophic level assessments

The contributions of the different food sources to the diet of different consumers was estimated using a Bayesian mixing model based on sources and consumers $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Parnell et al. 2013). This approach incorporates sources' variability and generates probability distributions of potential food source contributions. Trophic fractionation factors (TFF) are considered in Bayesian mixing models, which strongly influence the model outputs, as discussed in previous studies (Bond and Diamond 2011; Chen et al. 2018; Figueiredo et al. 2020). There is no well-established set of TFFs for different size classes and taxonomic groups. Moreover, zooplankton groups consumed by planktivorous fishes (Chen et al. 2021, 2022) present in each size class can belong to different diet trophic groups (Table S1). TFF values were thus estimated based on the results of this study and the mixing model outputs were compared with mixing model results run with TFF values issued from the literature (Table S2).

As the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values appeared similar between zooplankton of 200-300, 300-500 and 500-1000 μm size classes (later in the Results section), these size classes were grouped as the 200-1000 μm size fraction for mixing models. Three zooplankton size fractions were considered when running the Bayesian mixing models: 200-1000, 1000-2000 and $> 2000 \mu\text{m}$, to run the Bayesian mixing models. Three different levels of POM transfer were modeled (i.e. POM origins to POM mixture, POM size classes to zooplankton size fractions, and POM size classes and zooplankton size fractions to planktivorous fishes) (Table S2).

Models were run using mean and standard deviation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of sources and with a Markov Chain Monte Carlo run length set as 100,000 using the package MixSIAR (Stock et al. 2018) in R (R Core Team 2021).

Trophic levels (TL) of each zooplankton size class, group and fish species were calculated following Vander Zanden and Rasmussen (2001):

$$TL_{predator} = \lambda + (\delta^{15}\text{N}_{predator} - \delta^{15}\text{N}_{baseline}) \div TFF$$

where $\delta^{15}\text{N}_{predator}$ is the $\delta^{15}\text{N}$ value of the consumer, $\delta^{15}\text{N}_{baseline}$ is the mean $\delta^{15}\text{N}$ value of the pico-POM sampled at Solemio site, considered here as baseline (primary producers) with a trophic position $\lambda = 1$. TFF is the mean increase in $\delta^{15}\text{N}$ value from the source to the consumer. According to Harmelin-Vivien et al. (2008), the micro-POM of Gulf of Lion was dominated by autotrophic organisms (diatoms) whereas the nano-POM, was dominated by heterotrophic dinoflagellates. Since POM isotopic compositions measured in this study were similar to those published in Harmelin-Vivien et al. (2008), we assigned a TL of 1 to micro-POM along with pico-POM. We estimated the TLs of nano-POM and those of the zooplankton size classes, groups and fish species using the $\delta^{15}\text{N}$ value of pico-POM as a baseline. TL of POM of different origins was also assigned as 1.

Different values of TFF were used for mixing models (Table S2). Later in the Results and Discussion section, we discuss if the different model outputs were realistic with different TFF values.

2.5. Statistical analyses

Data from the whole sampling period were pooled to describe the average planktonic food web structure and flows of organic matter. Temporal/seasonal variations in the food web structure and organic matter flows are presented in Chen et al. (in prep).

Data normality and homogeneity were tested using Shapiro-Wilk and Levene tests. Analysis of variance (ANOVA) or its non-parametric equivalent Kruskal–Wallis test were used to examine differences in stable isotope compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), C:N ratios and estimated TLs between the POM from different origins, size classes, zooplankton size classes and groups, and the planktivorous fish species. ANOVA was also done to test the significance of differences of biochemical composition between POM origins. Post-hoc Tukey and Dunn's test were applied when needed after ANOVA or Kruskal-Wallis test, respectively. Classifications (based on Euclidean distance) were

performed on $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ values, and C:N ratios to study the similarities between zooplankton size classes and groups. A threshold of Euclidean distance as 2 was used to discuss the dissimilarities between zooplankton size classes, taxonomic groups and fish species. Statistical analyses were performed with R (R Core Team 2021).

3. Results

3.1. Taxonomic, stable isotope and biochemical composition of POM

3.1.1. Composition differences between POM origins

Pico- and nanoplankton taxonomic compositions from cytometry ($< 20 \mu\text{m}$) differed significantly between POM origins ($\chi^2 = 190.83$, $P < 0.001$, Fig. 2). *Synechococcus* spp. and *Prochlorococcus* spp. dominated in bay and oceanic POM, while nano-cyanobacteria filaments and detritus were the most abundant in anthropogenic and terrestrial POM (Fig. 3, Table S3). For bay POM, microscopic counts (cells $> 10 \mu\text{m}$) showed that nanoflagellates cryptophyceans dominated the nano- and microplankton, followed by diatoms and undetermined nanoflagellates (Table S3).

Mean values of isotopic compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and C:N ratios were significantly different between POM origins (Table 2). Anthropogenic and terrestrial POM had the lowest $\delta^{13}\text{C}$ values, while the bay and oceanic POM had highest ones (Fig. 3). Terrestrial POM had the highest mean $\delta^{15}\text{N}$ value and C:N ratio.

The concentration of biochemical components differed between all the POM origins ($P < 0.05$ for all, Table 3). Bay POM was mostly composed of proteins and lipids followed by carbohydrates, while POM from oceanic and anthropogenic origins had a higher lipid content, followed by protein and carbohydrate content. Terrestrial POM had the lowest energy content, related to the low content in proteins, carbohydrates and lipids.

3.1.2. POM size classes

The $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ values, and C:N ratios increased with size (Table 4 and Fig. 3). The TL values of nano-POM estimated with TFF values in the literature were the same and similar to those obtained with TFF estimated with data of this study. Concerning the biochemical content of the different size classes of bay POM (Table 3), nano-POM had the high carbohydrate and lipid content, but the values did not differ significantly from micro-POM.

3.2. Taxonomic and stable isotope compositions of zooplankton

3.2.1. Zooplankton size classes

Mean composition of zooplankton size classes, the dominant copepod groups in each size class are shown in Table S4. Copepods dominated the 200-1000 μm size classes, while the 1000-2000 and > 2000 μm size classes were more diversified with gelatinous organisms, larger crustaceans, pteropods and fish larvae.

Our data and literature sources on the feeding habits of zooplankton groups in Table S1 allowed to identify the main trophic guilds,: 1) omnivores-detritivores, comprising species which feed on POM, marine snow, phytodetritus, such as for Oncaeidae, *Microsetella/Macrosetella* spp., and Euterpinidae; 2) herbivores, bacterivores and virovores for appendicularians, pyrosomes, dolioids, and salps; 3) omnivores-herbivores for some of the species of Clausocalanidae/Paracalanidae, Acartiidae, Calanidae, and cypris larvae; 3) omnivores for Centropagidae, Oithonidae, ostracods, decapod, bivalve larvae and pteropods; 4) omnivores-carnivores for euphausiids, siphonophores, *Velevella velevella*; 5) carnivores for Corycaeidae., Candaciidae, Sapphirinidae, cladocerans and chaetognaths; 6) filter-feeders for salps and pyrosomes. The overall diet of each size class was summarized in Table S4, showing that as an example of the 200-300 μm size class, the diet was omnivore-detritivore for Oncaeidae, *Microsetella/Macrosetella* spp., and Euterpinidae, omnivore-herbivore for Clausocalanidae/Paracalanidae, omnivore for Oithonidae, and carnivore for Corycaeidae. Thus, the overall diet would be a mix of detritivores, herbivores, omnivores and with a increasing proportion of carnivores with size. The $\delta^{13}\text{C}$ values did not differ significantly between size classes. The $\delta^{15}\text{N}$ values and thus TL values increased with size between 200 and 2000 μm (Table 5 and Fig. 3). The C:N ratios were the highest in zooplankton > 2000 μm .

With a threshold of Euclidean distance of 2, clustering analysis highlighted similarities of isotopic compositions between the 200-300 μm , 300-500, and 500-1000 size classes, followed by the 1000-2000 μm size class, whereas the isotopic composition of the zooplankton > 2000 μm was the most dissimilar (Fig. S1). Thus, the 200-300, 300-500 and 500-1000 μm size classes were grouped as one size fraction in the mixing models.

3.2.2. Zooplankton taxonomic groups

Standard deviation of $\delta^{13}\text{C}$ values were different, but the $\delta^{13}\text{C}$ values did not differ significantly between groups (Fig. 3, Table 6). The $\delta^{15}\text{N}$ values and estimated TLs significantly differed between zooplankton groups (Table 6). Fish eggs, followed by

chaetognaths and euphausiids had the highest mean $\delta^{15}\text{N}$ values and therefore the estimated TLs, and amphipods had the lowest $\delta^{15}\text{N}$ value. Lower TL values were obtained when using literature TFF values compared to our own estimations (Table 6). However, along with $\delta^{15}\text{N}$ values, the order of organisms with the highest to the lowest TL estimated with different TFF values remained the same.

Even though the C:N ratios did not differ significantly between zooplankton groups, the C:N ratio values in siphonophores and salps were very high and sometimes > 10 .

Clustering analysis highlighted three different groups: One grouping stomatopods, euphausiids and chaetognaths, one grouping pyrosomes, decapod larvae and copepods and all other taxa, and a last one grouping teleost eggs by itself (Fig. S2).

3.3. SIA of planktivorous fish species

Mean values of isotopic compositions, C:N ratios and estimated TLs could significantly differ between fish species (Table 7). In addition to results shown by Chen et al. (2022), we added the data of *S. maena*, which is *S. sprattus* had the highest $\delta^{13}\text{C}$ values, while *B. boops*, *C. macrophthalma*, *S. pilchardus* and *C. chromis* had the lowest. Mean $\delta^{15}\text{N}$ and TL values were the highest for *B. boops*, *C. macrophthalma* and *C. chromis* and the lowest for *E. encrasicolus* and *S. sprattus* (Fig. 3). The C:N ratios were lower for *S. aurita*. Fish TL values were much lower when the TFF of 3.4‰ by Post (2002) and 2.75‰ by Caut et al. (2009) were used than with estimated TFF of 2.34‰ of this study (Table 7).

Clustering analysis highlighted two groups: One grouping *Boops boops* and *C. macrophthalma* and the other grouping the rest of the species (Fig. S3), with highest similarities between *S. maena*, *C. chromis*, followed by *S. aurita* and *S. pilchardus*. *Engraulis encrasicolus* and *S. sprattus* were similar between each other.

3.4. Food web structure

The mixing model displayed that oceanic POM contributed the most to bay POM ($51.5 \pm 41.2\%$), followed by terrestrial ($33.7 \pm 38.7\%$) and anthropogenic ($14.8 \pm 28.9\%$) POM, which contributed the least (Fig. S4).

The mixing model displayed that pico-POM contributed the most to the bay POM ($42.9 \pm 43.5\%$), followed by nano-POM ($38.3 \pm 43.0\%$), but the credibility intervals of pico- and nano-POM were very similar. Micro-POM contributed the least ($18.8 \pm 33.4\%$) (Fig. S5).

Considering estimated TFF values (Table S2), the mixing model highlighted that

pico-POM contributed the most to the carbon and nitrogen sources of the 200-1000 μm ($72.5 \pm 40.4\%$) and $> 2000 \mu\text{m}$ zooplankton ($53.3 \pm 45.9\%$), while nano-POM contributed the most to the those of the 1000-2000 μm zooplankton ($80.4 \pm 35.7\%$) (Fig. S6A and B). Strong differences in results were observed when using TFF values from the literature (see Table S2 and Fig. S6C and D).

With the TFF from Caut et al. (2009) for the invertebrates, the 1000-2000 μm zooplankton contributed the most to the carbon and nitrogen sources of *E. encrasicolus* and *S. maena* ($35.5 \pm 43.6\%$ and $35.5 \pm 43.0\%$, respectively), while the 200-1000 μm zooplankton contributed the most to the those of *S. pilchardus*, *S. aurita*, *C. macrophthalma* and *C. chromis* ($40.7 \pm 44.8\%$, $39.2 \pm 44.4\%$, $35.8 \pm 43.7\%$ and $40.1 \pm 44.8\%$, respectively) and the $> 2000 \mu\text{m}$ zooplankton contributed the most to those of *S. sprattus* ($45.1 \pm 45.2\%$) and *B. boops* ($58.4 \pm 44.8\%$) (Fig. S7A & B).

With TFF values from Post (2002), $> 2000 \mu\text{m}$ zooplankton contributed the most to the carbon and nitrogen sources of all the planktivorous species (mean $> 32\%$), followed by the micro-POM for *E. encrasicolus*, *S. pilchardus*, *S. sprattus* and *C. macrophthalma* ($23.0 \pm 33.2\%$, $22.3 \pm 33.2\%$, $22.3 \pm 33.1\%$ and $18.9 \pm 30.2\%$, respectively). The 200-1000 μm zooplankton contributed second most for *S. aurita* ($22.8 \pm 33.3\%$), while 1000-2000 μm zooplankton contributed the second most for *C. chromis* ($19.4 \pm 30.7\%$) and *B. boops* ($22.8 \pm 33.4\%$) (Fig. S7C & D).

With a conceptual diagram of energy transfer in the planktonic food web with energy content ($\text{J mg}^{-1} \text{DW}$) provided by proteins, carbohydrates and lipids (Fig. 4), we resume that (I) from POM size classes (average of 0.7 to 200 μm) to zooplankton (average of 200 to 2000 μm), an increase of 1.07 times in energy content was observed. POM size classes were lipid-rich, while zooplankton size classes were protein-rich; (II) an increase of 2.30 times in energy content was observed from zooplankton size classes to fish muscles with an increase in protein and lipid contents; (III) an increase of 2.46 times in energy content from POM to the muscle tissue of *S. pilchardus* was observed.

4. Discussion

The originality of this study consists in the combination of stable isotope and biochemical analyses of three compartments: POM/phytoplankton, zooplankton and planktivorous fish species, to elucidate the structure of a coastal pelagic food web and related organic matter channeling.

4.1. POM/phytoplankton characterization in the Bay of Marseille

In terms of phytoplankton community of bay POM at the Solemio station, the fact that picoplankton and nanoflagellates outnumbered diatoms and that pico-POM contributed the most to the total POM mass may explain that the similarities (Fig. 3) between the stable isotope composition of bulk bay POM and those of pico- and nano-POM, which was also highlighted by the mixing model.

We assumed that micro-POM was dominated by autotrophic diatoms and nano-POM was dominated by heterotrophic dinoflagellates, and designed trophic level as 1 for pico- and micro-POM. However, our results showed that $\delta^{13}\text{C}$, and C:N ratios, $\delta^{15}\text{N}$ as an index of the trophic level increased with POM size, and higher lipid and energy content were observed for the nano-POM. This may be explained by the fact that the bulk micro-POM samples might include microzooplankton covering the same size range as the microphytoplankton (Azam et al. 1983), which we could not separate from the collected samples. Higher uptake of ammonium (preferred by nanoflagellates), which is more ^{15}N -depleted than nitrate (preferred by diatoms) and with higher constant accompanying isotopic fractionation may also explain the lower $\delta^{15}\text{N}$ values for nano-POM than micro-POM (Chen et al. 2018). This highlights the importance of including stable isotope along with taxonomic analyses of microzooplankton in further studies of POM size classes, and consequently to better estimate their trophic level (Giering et al. 2019).

The ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured for the POM correspond to those observed previously in the Bay of Marseille (Cresson et al. 2012; Bănaru et al. 2014). Our results highlight that isotopic compositions significantly differed depending on POM origin in the Bay of Marseille. POM from the two terrigenous origins (Cortiou sewage and Huveaune river) had relatively low $\delta^{13}\text{C}$ values ($< -25\text{‰}$), while marine POM (Julio) had higher $\delta^{13}\text{C}$ values ($> -24\text{‰}$), as terrestrial C_3 -plant detritus exhibit much lower $\delta^{13}\text{C}$ values than marine phytoplankton (Carlier et al. 2007; Harmelin-Vivien et al. 2008; Bănaru et al. 2014; Briand et al. 2015).

These differences of isotopic compositions between pools of POM may also be related to their taxonomic composition. Those were more similar between bay (Solemio) and the oceanic POM with higher proportions of picoplankton than with terrigenous origins with higher proportions of nano-cyanobacteria filaments and detritus. Terrigenous POM had also significantly higher C:N ratios related to terrestrial refractory material (Hedges et al. 1986). The lower energy content of Huveaune POM

is consistent with the high C:N ratios, indicating that this POM may be a food resource with low quality for zooplankton.

The results of the mixing model highlighted the dominant contribution of oceanic POM in the Bay of Marseille, consistent to previous observation (Cresson et al. 2012; Liénart et al. 2017).

4.2. Zooplankton size and groups and fish species

Generally, zooplankton size classes had similar $\delta^{13}\text{C}$ values, as previously observed in the Bay of Marseille within the same value ranges (Bănaru et al. 2014; Millet et al. 2018) and in the Gulf of Lion (Espinasse et al. 2014). This may be related to the reliance of both these groups on the same POM sources.

Compared to $\delta^{13}\text{C}$ values, $\delta^{15}\text{N}$ values and estimated TLs significantly increased with size of zooplankton from 200 to 2000 μm (dominated by copepods). Such a pattern has been well-described, and is related to the different diet between size classes (Rolff 2000; Bănaru et al. 2014; Harmelin-Vivien et al. 2019; Figueiredo et al. 2020) and also the feeding strategy changes related to ontogeny (Im et al. 2015). The differences in $\delta^{15}\text{N}$ values between size classes and groups may also be related to the $\delta^{15}\text{N}$ values of their food. The overall diet of each size class in the Bay of Marseille is shown with Table S4, the low $\delta^{15}\text{N}$ values of zooplankton from the 200-300 μm size class compared to other size classes is likely linked to the dominance of detritivorous and herbivorous copepods (both copepodites and adult forms)(Feliú et al. 2020). The dominance of carnivorous copepods and other organisms increased with size class.

The $\delta^{15}\text{N}$ values of the large mesozooplankton groups in the Bay of Marseille were similar to previous observation by and Bănaru et al. (2014). Large filter-feeders like salps dominating the $> 2000 \mu\text{m}$ size class, had much lower $\delta^{15}\text{N}$ values than predators (chaetognaths and large crustaceans), which were more abundant in the 1000-2000 μm size class (Figueiredo et al. 2020). This can explain the decrease of $\delta^{15}\text{N}$ values and estimated TL in the $> 2000 \mu\text{m}$ zooplankton.

Our results that siphonophores and *Velella velella* (which were known to be also predators of copepods) presented lower $\delta^{15}\text{N}$ values than chaetognaths and euphausiids and the classification also showed that siphonophores and *Velella velella* were not classified in the same groups with chaetognaths and euphausiids. This is consistent with previous observations made by Tilves et al. (2018) in the Catalan Sea, NW Mediterranean Sea. The C:N ratios of siphonophores and salps also seemed higher than

those of chaetognaths even though the differences were not significant. This may be related to their biochemical compositions (Ikeda 2014). Salps and siphonophores contain less protein but higher proportions of carbohydrates (Chen et al. 2019), a high percentage of water and their ash content increase with body dry mass (Ikeda 2014), while chaetognaths contain higher protein and energy content (Chen et al. 2019).

Lower $\delta^{15}\text{N}$ values and higher C:N ratios in siphonophores and *Verella verella* may also be related to a wider range of prey types (including the consumption of other gelatinous plankton such as salps) as observed by Damian-Serrano et al. (2021, 2022). In line with our results, this suggests that gelatinous zooplankton have diverse functional roles in the food web (Hetherington et al. 2022).

The highest $\delta^{15}\text{N}$ values and TLs were observed in teleost eggs. These values were even higher than those of teleost larvae, probably because the isotopic compositions of eggs may be close to those of spawning females (González-Ortegón et al. 2018; Pizarro et al. 2019). Fish larvae usually feed on microzooplankton prey, such as copepod eggs, nauplii, copepodites, protozoans, and bivalve veligers (Purcell and Grover 1990; Conway et al. 1994), which are smaller than the prey of spawning females with lower $\delta^{15}\text{N}$ values and TLs.

The relationships between the stable isotope and diet compositions of planktivorous fish species in the Bay of Marseille have already been discussed (Chen et al. 2022), but here our results highlighted that the stable isotope composition reflects the similarities of diet between species as *S. maena*, *C. chromis*, *S. pilchardus*, *S. aurita*, *E. encrasicolus* and *S. sprattus* feed on copepods essentially, while *C. macrophthalma* and *B. boops* feed on larger and more diversified prey, showing higher $\delta^{15}\text{N}$ and thus TL values. The higher TLs of *B. boops* and *C. macrophthalma* may be related to their benthic-pelagic feeding behavior, and the capability of these species to consume a large diversity of prey, ranging from polychaetes, macroalgae to gelatinous zooplankton (Milisenda et al. 2014; El-Maremie and El-Mor 2015; Sever and İlhan 2016; Chen et al. 2022).

4.3. TFF choice and their influences on mixing models

Defining the right value for the TL baseline and the TFF is challenging when studying planktonic food webs. TLs estimated with the TFF values proposed by Post (2002) (TFF = 3.4) and Caut et al. (2009) (TFF = 2.75) for zooplankton size classes and taxonomic groups were both lower than those obtained with the estimated TFF of this study (TFF = 2.34). Figueiredo et al. (2020) also highlighted that the choice of TFF

values has a considerable effect on the estimates of the size and mass ratio between predator and prey.

The mixing models run with the TFF values proposed by Caut et al. (2009) demonstrated that nano-POM contributed the most to the carbon and nitrogen sources of 200-1000 μm zooplankton and that micro-POM to those of 1000-2000 μm zooplankton. These results differed from those obtained mixing models run on estimated TFF (i.e. showing that the pico-POM contributed the most to the carbon and nitrogen of 200-1000 μm and > 2000 μm zooplankton). However, both models indicated an increase of prey size with predator size, which is consistent with the enrichment in ^{15}N with zooplankton size for the 200 to 2000 μm size classes, as previously observed (Hunt et al. 2017; Giering et al. 2019).

The fact that the > 2000 μm zooplankton depended also the most on pico-POM may be explained by the high proportion of filter-feeders among this group, such as salps and pyrosomes (Table S4) (Conley et al. 2018). The high protein and energy content of nano-POM at Solemio may indicate the higher quality of the POM as a food resource for zooplankton compared to micro- and pico-POM.

Microzooplankton (ciliates) in the oligotrophic area of the Yello Sea had a strong grazing pressure on picoplankton, such as *Synechococcus* spp. (Zhao et al. 2022) and free bacteria are controlled by heterotrophic flagellates, which are ubiquitous in the marine water column, covering the same size range as the phytoplankton (Azam et al. 1983). The flagellates in turn are preyed upon by microzooplankton, thus provide an additional source of energy from the microbial loop to the planktonic food chain via copepods (Mitra et al. 2014; Jo et al. 2017). Thus, instead of pico-POM being directly consumed by meso- and macrozooplankton, we believe that the contribution of pico-POM to the carbon and nitrogen sources of meso- and macrozooplankton via microzooplankton would be more plausible as the predator:prey size ratio would be in line with the observations of previous studies (Hansen et al. 1994; Calbet et al. 2007; Gonçalves et al. 2014). However, we could not separate microzooplankton from the bulk micro-POM samples that we collected. The relationship between microzooplankton and pico-, nano-, and micro-POM should be further analyzed in order to obtain a more integrated view of planktonic food web in the Bay of Marseille.

Estimated TL were much higher than those calculated with the TFF proposed by Caut et al. (2009) and by Post (2002) and seemed too high to be realistic for small pelagic fish, such as *B. boops* and *C. macrophthalma*. With the theoretical TFF

proposed by Post (2002), > 2000 μm zooplankton contributed the most to the carbon and nitrogen sources of fish species than those ranging from 200 to 2000 μm , which was not consistent with the results of the stomach content analyses (Chen et al. 2022). We thus considered that TLs calculated with TFF proposed by Caut et al. (2009) gave the most coherent results, highlighting that the 200-2000 μm mesozooplankton contributed the most to the carbon and nitrogen sources of most planktivorous species in the Bay of Marseille. These results are consistent with stomach content observations (Chen et al. 2022). However, the high contribution of macrozooplankton in the stomach contents of *C. chromis* and *C. macrophthalma* was not revealed by SIA. This may be explained by the different aspects of diet revealed by these two methods, with stomach content analysis revealing a snapshot of the diet and stable isotope analyses providing information on the assimilated food resources over a longer time period (i.e. one to two months). The ingestion of large prey may have been punctual during the sampling period of these species. Firstly, these results suggest that theoretical values from the literature may not always fit, and that the estimation of TFF values from field data should be done when possible to find adaptable values for different systems. Secondly, it would be interesting to further investigate the diet and stable isotope composition of these species on a longer term for better comparisons.

4.4. Planktonic food web and implications for the management of small pelagic fish

In the Bay of Marseille, the average energy content of Solemio POM (0.7-200 μm size class dominated by phytoplankton) provided a high proportion of lipids (~55% of total biochemical composition). Between phytoplankton and zooplankton, the increase in protein content (~61% of total biochemical composition) and thus of energy content may be related to the transfer efficiencies and the assimilation of POM and in zooplankton. The lipid content of phytoplankton can have significantly positive relationships with the protein content in mesozooplankton (Yun et al. 2015) and precisely with a month of time lag for assimilation (Jo et al. 2017). Proteins are shown to have higher transfer efficiency than lipids and carbohydrates since they are mainly used for respiration (Scott 1980). Compared to the Kerguelen waters, Harmelin-Vivien et al. (2019) reported a lower energy content of phytoplankton (around 2 J mg^{-1} DW for the 80-200 μm size class) and estimated that OM energy density was multiplied by 4.2 times from phytoplankton (80-200 μm size class) to zooplankton (> 500 μm size class). This may suggest the capacity of a more efficient transfer and integration of OM by

zooplankton in this colder region than in the Mediterranean Sea.

An increase of energy content (~2.3 times) corresponded to an increase in protein and lipid content from zooplankton (200-2000 μm size classes) and the absence of carbohydrates in fish muscle (*S. pilchardus*) also suggest the transformation and assimilation of POM to their body tissue by *S. pilchardus*.

In the sub-polar Kerguelen waters (southwest Indian Ocean), the energy content of myctophids (fish) ranges from 23.2 to 34.3 J mg^{-1} DW (Lea et al. 2002). Compared to the results of Harmelin-Vivien et al. (2019) (only 1.3 times from euphausiids to myctophids), we found a larger qualitative leap in energy content in the Bay of Marseille, probably related to the differences of the capacity to transfer and assimilate POM by different species (Sargent et al. 1979).

Food availability has been shown to affect growth, but also the biochemical composition of fish larval tissue. A poor nutritional condition can have a direct effect on protein synthesis and tissue accretion rates of fish larvae, which also reduces their swimming capacity and thus leave them prone to predators (Purcell and Grover 1990). The lower transfer efficiency may also be related to lower food availability. It may be interesting for further studies to analyze the effects of food availability on the transfer efficiency of POM by planktivorous fishes.

In the context of a hypothesized bottom-up control on the populations of small pelagic fish in the NWMS related to potential changes in the plankton assemblages and diet of small pelagic fish (Saraux et al. 2019), the assessment of the functioning of the planktonic food web becomes essential. So far, interactions between POM, zooplankton and fish in the Gulf of Lion were mostly assessed between only two out of these three compartments at a time. For instance, studies based on stomach content highlighted the prey selectivity of some fish species (Costalago et al. 2014; Le Bourg et al. 2015; Chen et al. 2021) or relationships between POM and zooplankton (Bănară et al. 2014; Espinasse et al. 2014; Hunt et al. 2017). Studies presenting the interactions between the three compartments (i.e. POM, zooplankton and fish) at the same site are rare due to the difficulty to obtain such complete and consistent data sets in similar time and space frame (Cresson et al. 2014b; Chen et al. 2021).

The use of stable isotope analyses, mixing models and biochemical analyses allowed to build conceptual diagrams, which provide the first integrated views of the trophic relationships in the Bay of Marseille, and thus allow further understanding of the planktonic food-web, from POM to fish. We can summarize the food-web as follows

(Fig. 5): POM of oceanic origin contributes the most to the carbon and nitrogen sources of Solemio bay POM (> 51%). Pico-POM contributed the most (~ 43%) to Solemio POM. Nano-POM, which was more protein- and energy-rich, contributed the most (~ 84%) to the carbon and nitrogen sources of 200-1000 μm , micro-POM contributed the most to the 1000-2000 μm zooplankton (~ 64%), while pico-POM contributed the most to the carbon and nitrogen sources of > 2000 μm zooplankton (~ 86%). The 200-2000 μm mesozooplankton contributed the most (~ 42%) to the carbon and nitrogen sources of planktivorous species while > 2000 μm macrozooplankton appeared to be important (~ 43%) to some species.

Our results may serve as a reference baseline to apprehend food web changes of the pelagic ecosystem related to food web sources or community changes. Analyses of temporal variations of POM composition and micro-, together with meso- and macro-zooplankton community, combined with diet and relative body condition of planktivorous fish species data, may help to reinforce our understandings of trophic relationship variations between these compartments. Moreover, temporal variations in phyto- and zooplankton communities should be related to changing environmental forcing factors in the Gulf of Lion, which may indirectly impact fish species (Feuilleley et al. 2020).

5. Conclusion

The present study is the first in the NWMS to combine stable isotope and biochemical compositions of POM considering its size and origin, zooplankton size and groups, and planktivorous fish species. We demonstrated how POM is transferred through these compartments in the planktonic food web. We observed: (1) that isotopic and biochemical composition differed between terrigenous and marine POM, zooplankton size classes and groups; (2) that $\delta^{15}\text{N}$ and trophic levels increase with zooplankton size; (3) that planktivorous fish species have relatively similar isotopic compositions generally in line with their diet; (4) that mixing models can provide completely different results when run with different TFF, highlighting the importance of estimating specific TFF for each food web. Further estimations of TFF based on experiments focusing on different size classes and biochemical composition of phyto- and zooplankton may be useful to validate or improve our results about pelagic food web structure and organic matter flows. We provide an overview of POM transfer and the pelagic food web structure. However, primary producers' isotopic signatures are

known to fluctuate over time and also the importance of microzooplankton in the POM transfer. Understanding the dynamics of first trophic levels of the pelagic food webs can provide insight into how species interact and how they are likely to be affected by climate change. This knowledge can then be used to inform management decisions, such as the implementation of conservation measures or the development of strategies to mitigate the impacts of climate change. Therefore, temporal variability of POM transfer and the improvement of knowledge on microzooplankton remain necessary for the effective management of coastal areas in the context of climate change.

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Declarations

Conflict of interest

The authors declare that they have no conflicts of interest.

Ethical approval

All applicable national and/or institutional guidelines for sampling, care, and experimental use of organisms for the study were followed.

References

1. Albo-Puigserver M, Borme D, Coll M, et al (2019) Trophic ecology of range-expanding round sardinella and resident sympatric species in the NW Mediterranean. *Mar Ecol Prog Ser* 620:139–154. <https://doi.org/10.3354/meps12962>
2. Albo-Puigserver M, Muñoz A, Navarro J, et al (2017) Ecological energetics of forage fish from the Mediterranean Sea: Seasonal dynamics and interspecific differences. *Deep-Sea Research Part II: Topical Studies in Oceanography*. <https://doi.org/10.1016/j.dsr2.2017.03.002>
3. Azam F, Fenchel T, Field J, et al (1983) The Ecological Role of Water-Column Microbes in the Sea. *Mar Ecol Prog Ser* 10:257–263. <https://doi.org/10.3354/meps010257>
4. Bachiller E, Albo-Puigserver M, Giménez J, et al (2020) A trophic latitudinal gradient revealed in anchovy and sardine from the Western Mediterranean Sea using a multi-proxy approach. *Sci Rep* 10:17598. <https://doi.org/10.1038/s41598-020-74602-y>
5. Bachiller E, Giménez J, Albo-Puigserver M, et al (2021) Trophic niche overlap between round sardinella (*Sardinella aurita*) and sympatric pelagic fish species in the Western Mediterranean. *Ecology and Evolution* 11:16126–16142. <https://doi.org/10.1002/ece3.8293>
6. Bănaru D, Carlotti F, Barani A, et al (2014) Seasonal variation of stable isotope ratios of size-fractionated zooplankton in the Bay of Marseille (NW Mediterranean Sea). *J Plankton Res* 36:145–156. <https://doi.org/10.1093/plankt/fbt083>
7. Bănaru D, Diaz F, Verley P, et al (2019) Implementation of an end-to-end model of the Gulf of Lions ecosystem (NW Mediterranean Sea). I. Parameterization, calibration and evaluation. *Ecol Modell* 401:1–19. <https://doi.org/10.1016/j.ecolmodel.2019.03.005>
8. Bănaru D, Mellon-Duval C, Roos D, et al (2013) Trophic structure in the Gulf of Lions marine ecosystem (north-western Mediterranean Sea) and fishing impacts. *J Mar Syst* 111–112:45–68. <https://doi.org/10.1016/j.jmarsys.2012.09.010>
9. Banse K (1995) Zooplankton: Pivotal role in the control of ocean production: I. Biomass and production. *ICES J Mar Sci* 52:265–277. [https://doi.org/10.1016/1054-3139\(95\)80043-3](https://doi.org/10.1016/1054-3139(95)80043-3)
10. Batista I, Ramos C, Mendonça R, Nunes ML (2009) Enzymatic Hydrolysis of Sardine (*Sardina pilchardus*) By-products and Lipid Recovery. *Journal of Aquatic Food Product Technology* 18:120–134. <https://doi.org/10.1080/10498850802581823>
11. Bond AL, Diamond AW (2011) Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. *Ecol Appl* 21:1017–1023. <https://doi.org/10.1890/09-2409.1>

12. Briand MJ, Bonnet X, Goiran C, et al (2015) Major Sources of Organic Matter in a Complex Coral Reef Lagoon: Identification from Isotopic Signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). PLOS ONE 10:e0131555. <https://doi.org/10.1371/journal.pone.0131555>
13. Calbet A, Carlotti F, Gaudy R (2007) The feeding ecology of the copepod *Centropages typicus* (Kröyer). Progress in Oceanography 72:137–150. <https://doi.org/10.1016/j.pocean.2007.01.003>
14. Carlier A, Riera P, Amouroux J-M, et al (2007) Benthic trophic network in the Bay of Banyuls-sur-Mer (northwest Mediterranean, France): An assessment based on stable carbon and nitrogen isotopes analysis. Estuarine, Coastal and Shelf Science 72:1–15. <https://doi.org/10.1016/j.ecss.2006.10.001>
15. Caut S, Angulo E, Courchamp F (2009) Variation in discrimination factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. J Appl Ecol 46:443–453. <https://doi.org/10.1111/j.1365-2664.2009.01620.x>
16. Chen C-T, Bănaru D, Carlotti F, et al (2019) Seasonal variation in biochemical and energy content of size-fractionated zooplankton in the Bay of Marseille (North-Western Mediterranean Sea). J Mar Syst 199:103223. <https://doi.org/10.1016/j.jmarsys.2019.103223>
17. Chen C-T, Carlotti F, Harmelin-Vivien M, et al (2021) Temporal variation in prey selection by adult European sardine (*Sardina pilchardus*) in the NW Mediterranean Sea. Prog Oceanogr 196:102617. <https://doi.org/10.1016/j.pocean.2021.102617>
18. Chen C-T, Carlotti F, Harmelin-Vivien M, et al (2022) Diet and trophic interactions of Mediterranean planktivorous fishes. Mar Biol 169:119. <https://doi.org/10.1007/s00227-022-04103-1>
19. Chen M, Kim D, Liu H, Kang C-K (2018) Variability in copepod trophic levels and feeding selectivity based on stable isotope analysis in Gwangyang Bay of the southern coast of the Korean Peninsula. Biogeosciences 15:2055–2073. <https://doi.org/10.5194/bg-15-2055-2018>
20. Conley KR, Lombard F, Sutherland KR (2018) Mammoth grazers on the ocean's minuteness: a review of selective feeding using mucous meshes. Proceedings of the Royal Society B: Biological Sciences 285:20180056. <https://doi.org/10.1098/rspb.2018.0056>
21. Conway D, Coombs S, Puellas M, Tranter P (1994) Feeding of larval sardine *Sardina pilchardus* (Walbaum) off the north coast of Spain. Oceanographic Literature Review 10:165–175
22. Costalago D, Palomera I, Tirelli V (2014) Seasonal comparison of the diets of juvenile European anchovy *Engraulis encrasicolus* and sardine *Sardina pilchardus* in the Gulf of Lions. J Sea Res 89:64–72. <https://doi.org/10.1016/j.seares.2014.02.008>
23. Cresson P, Ruitton S, Fontaine M-F, Harmelin-Vivien M (2012) Spatio-temporal variation of suspended and sedimentary organic matter quality in the Bay of Marseilles (NW Mediterranean) assessed by biochemical and isotopic analyses.

Mar Poll Bull 64:1112–1121. <https://doi.org/10.1016/j.marpolbul.2012.04.003>

24. Cresson P, Ruitton S, Harmelin-Vivien M (2014a) Artificial reefs do increase secondary biomass production: mechanisms evidenced by stable isotopes. *Mar Ecol Prog Ser* 509:15–26. <https://doi.org/10.3354/meps10866>
25. Cresson P, Ruitton S, Ourgaud M, Harmelin-Vivien M (2014b) Contrasting perception of fish trophic level from stomach content and stable isotope analyses: A Mediterranean artificial reef experience. *J Exp Mar Biol Ecol* 452:54–62. <https://doi.org/10.1016/j.jembe.2013.11.014>
26. Damian-Serrano A, Haddock SHD, Dunn CW (2021) The evolution of siphonophore tentilla for specialized prey capture in the open ocean. *Proceedings of the National Academy of Sciences* 118:e2005063118. <https://doi.org/10.1073/pnas.2005063118>
27. Damian-Serrano A, Hetherington ED, Choy CA, et al (2022) Characterizing the secret diets of siphonophores (Cnidaria: Hydrozoa) using DNA metabarcoding. *PLOS ONE* 17:e0267761. <https://doi.org/10.1371/journal.pone.0267761>
28. DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42:495–506. [https://doi.org/10.1016/0016-7037\(78\)90199-0](https://doi.org/10.1016/0016-7037(78)90199-0)
29. El-Maremie H, El-Mor M (2015) Feeding habits of the Bogue, *Boops boops* (Linnaeus, 1758) (Teleostei: Sparidae) in Benghazi Coast, Eastern Libya. *JLS* 10:189–196. <https://doi.org/10.17265/1934-7391/2015.05.001>
30. Espinasse B, Carlotti F, Zhou M, Devenon JL (2014) Defining zooplankton habitats in the Gulf of Lion (NW Mediterranean Sea) using size structure and environmental conditions. *Mar Ecol Prog Ser* 506:31–46. <https://doi.org/10.3354/meps10803>
31. FAO (2020) *The State of Mediterranean and Black Sea Fisheries* (FAO, Rome, 2020). FAO
32. Feliú G, Pagano M, Hidalgo P, Carlotti F (2020) Structure and function of epipelagic mesozooplankton and their response to dust deposition events during the spring PEACETIME cruise in the Mediterranean Sea. *Biogeosciences* 17:5417–5441. <https://doi.org/10.5194/bg-17-5417-2020>
33. Feuilleley G, Fromentin J-M, Stemmann L, et al (2020) Concomitant changes in the environment and small pelagic fish community of the Gulf of Lions. *Prog Oceanogr* 186:102375. <https://doi.org/10.1016/j.pocean.2020.102375>
34. Fey P, Parravicini V, Bănaru D, et al (2021) Multi-trophic markers illuminate the understanding of the functioning of a remote, low coral cover Marquesan coral reef food web. *Sci Rep* 11:20950. <https://doi.org/10.1038/s41598-021-00348-w>
35. Fey P, Parravicini V, Lebreton B, et al (2020) Sources of organic matter in an atypical phytoplankton rich coral ecosystem, Marquesas Islands: composition and properties. *Mar Biol* 167:92. <https://doi.org/10.1007/s00227-020-03703-z>

36. Figueiredo GGAA de, Schwamborn R, Bertrand A, et al (2020) Body size and stable isotope composition of zooplankton in the western tropical Atlantic. *Journal of Marine Systems* 212:103449. <https://doi.org/10.1016/j.jmarsys.2020.103449>
37. Fraysse M, Pairaud I, Ross ON, et al (2014) Intrusion of Rhone River diluted water into the Bay of Marseille: Generation processes and impacts on ecosystem functioning. *J Geophys Res* 119:6535–6556. <https://doi.org/10.1002/2014JC010022>
38. Giering SLC, Wells SR, Mayers KMJ, et al (2019) Seasonal variation of zooplankton community structure and trophic position in the Celtic Sea: A stable isotope and biovolume spectrum approach. *Progress in Oceanography* 177:101943. <https://doi.org/10.1016/j.pocean.2018.03.012>
39. Gonçalves RJ, Gréve H van S, Couespel D, Kiørboe T (2014) Mechanisms of prey size selection in a suspension-feeding copepod, *Temora longicornis*. *Marine Ecology Progress Series* 517:61–74. <https://doi.org/10.3354/meps11039>
40. González-Ortegón E, Vay LL, Walton MEM, Giménez L (2018) Maternal trophic status and offspring phenotype in a marine invertebrate. *Sci Rep* 8:9618. <https://doi.org/10.1038/s41598-018-27709-2>
41. Hansen B, Bjornsen PK, Hansen PJ (1994) The size ratio between planktonic predators and their prey. *Limnology and Oceanography* 39:395–403. <https://doi.org/10.4319/lo.1994.39.2.0395>
42. Harmelin-Vivien M, Bănaru D, Dromard CR, et al (2019) Biochemical composition and energy content of size-fractionated zooplankton east of the Kerguelen Islands. *Polar Biol* 42:603–617. <https://doi.org/10.1007/s00300-019-02458-8>
43. Harmelin-Vivien M, Loizeau V, Mellon C, et al (2008) Comparison of C and N stable isotope ratios between surface particulate organic matter and microphytoplankton in the Gulf of Lions (NW Mediterranean). *Cont Shelf Res* 28:1911–1919. <https://doi.org/10.1016/j.csr.2008.03.002>
44. Hedges JI, Clark WA, Quay PD, et al (1986) Compositions and fluxes of particulate organic material in the Amazon River I: Amazon River particulate material. *Limnol Oceanogr* 31:717–738. <https://doi.org/10.4319/lo.1986.31.4.0717>
45. Hetherington ED, Damian-Serrano A, Haddock SHD, et al (2022) Integrating siphonophores into marine food-web ecology. *Limnology and Oceanography Letters* 7:81–95. <https://doi.org/10.1002/lo12.10235>
46. Hunt BPV, Carlotti F, Donoso K, et al (2017) Trophic pathways of phytoplankton size classes through the zooplankton food web over the spring transition period in the north-west Mediterranean Sea. *J Geophys Res Oceans* 122:6309–6324. <https://doi.org/10.1002/2016JC012658>
47. Ikeda T (2014) Synthesis toward a global model of metabolism and chemical composition of medusae and ctenophores. *Journal of Experimental Marine Biology and Ecology* 456:50–64. <https://doi.org/10.1016/j.jembe.2014.03.006>

48. Im D-H, Wi JH, Suh H-L (2015) Evidence for ontogenetic feeding strategies in four calanoid copepods in the East Sea (Japan Sea) in summer, revealed by stable isotope analysis. *Ocean Sci J* 50:481–490. <https://doi.org/10.1007/s12601-015-0044-y>
49. Jo N, Kang JJ, Park WG, et al (2017) Seasonal variation in the biochemical compositions of phytoplankton and zooplankton communities in the southwestern East/Japan Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 143:82–90. <https://doi.org/10.1016/j.dsr2.2016.12.001>
50. Le Bourg B, Bănaru D, Saraux C, et al (2015) Trophic niche overlap of sprat and commercial small pelagic teleosts in the Gulf of Lions (NW Mediterranean Sea). *J Sea Res* 103:138–146. <https://doi.org/10.1016/j.seares.2015.06.011>
51. Lea M-A, Nichols PD, Wilson G (2002) Fatty acid composition of lipid-rich myctophids and mackerel icefish (*Champsocephalus gunnari*) – Southern Ocean food-web implications. *Polar Biol* 25:843–854. <https://doi.org/10.1007/s00300-002-0428-1>
52. Liénart C, Savoye N, Bozec Y, et al (2017) Dynamics of particulate organic matter composition in coastal systems: A spatio-temporal study at multi-systems scale. *Prog Oceanogr* 156:221–239. <https://doi.org/10.1016/j.pocean.2017.03.001>
53. Markovic G, Mladenovic J, Cvijovic M, Miljkovic J (2015) Total protein and lipid contents of canned fish on the Serbian market. *Act Agr Serb* 20:67–74. <https://doi.org/10.5937/AASer1539067M>
54. Middelburg JJ (2019) The Return from Organic to Inorganic Carbon. In: Middelburg JJ (ed) *Marine Carbon Biogeochemistry : A Primer for Earth System Scientists*. Springer International Publishing, Cham, pp 37–56
55. Milisenda G, Rosa S, Fuentes VL, et al (2014) Jellyfish as prey: frequency of predation and selective foraging of *Boops boops* (Vertebrata, Actinopterygii) on the Mauve Stinger *Pelagia noctiluca* (Cnidaria, Scyphozoa). *PLoS One* 9:e94600. <https://doi.org/10.1371/journal.pone.0094600>
56. Millet B, Pinazo C, Bănaru D, et al (2018) Unexpected spatial impact of treatment plant discharges induced by episodic hydrodynamic events: Modelling Lagrangian transport of fine particles by Northern Current intrusions in the bays of Marseille (France). *PLoS One* 13:e0195257. <https://doi.org/10.1371/journal.pone.0195257>
57. Millot C (1987) Circulation in the hydrodynamics general circulation Mediterranean Sea mesoscale phenomena. *Oceanol Acta* 10:143–149
58. Mitra A, Castellani C, Gentleman WC, et al (2014) Bridging the gap between marine biogeochemical and fisheries sciences; configuring the zooplankton link. *Progress in Oceanography* 129:176–199. <https://doi.org/10.1016/j.pocean.2014.04.025>
59. Ourgaud M, Ruitton S, Bell JD, et al (2015) Response of a seagrass fish assemblage to improved wastewater treatment. *Mar Poll Bull* 90:25–32. <https://doi.org/10.1016/j.marpolbul.2014.11.038>

60. Palomera I, Olivar MP, Salat J, et al (2007) Small pelagic fish in the NW Mediterranean Sea: An ecological review. *Prog Oceanogr* 74:377–396. <https://doi.org/10.1016/j.pocean.2007.04.012>
61. Parnell AC, Phillips DL, Bearhop S, et al (2013) Bayesian stable isotope mixing models. *Environmetrics* 24:387–399. <https://doi.org/10.1002/env.2221>
62. Peck MA, Alheit J, Bertrand A, et al (2020) Small pelagic fish in the new millennium: A bottom-up view of global research effort. *Prog Oceanogr* 191:102494. <https://doi.org/10.1016/j.pocean.2020.102494>
63. Petrenko A, Leredde Y, Marsaleix P (2005) Circulation in a stratified and wind-forced Gulf of Lions, NW Mediterranean Sea: in situ and modeling data. *Cont Shelf Res* 25:7–27. <https://doi.org/10.1016/j.csr.2004.09.004>
64. Pizarro J, Docmac F, Harrod C (2019) Clarifying a trophic black box: stable isotope analysis reveals unexpected dietary variation in the Peruvian anchovy *Engraulis ringens*. *PeerJ* 7:e6968. <https://doi.org/10.7717/peerj.6968>
65. Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:16. <https://doi.org/10.2307/3071875>
66. Purcell J, Grover J (1990) Predation and food limitation as causes of mortality in larval herring at a spawning ground in British Columbia. *Mar Ecol Prog Ser* 59:55–61. <https://doi.org/10.3354/meps059055>
67. R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
68. Razouls C, Bovée F, Kouwenberg J, Desreumaux D (2005) Biodiversity of marine planktonic copepods (morphology, geographic distribution and biological data). Sorbonne University, CNRS. In: *Marine Planktonic Copepods*. Available at <https://copepodes.obs-banyuls.fr/en> [Accessed February 10, 2023]
69. Rolff C (2000) Seasonal variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of size-fractionated plankton at a coastal station in the northern Baltic proper. *Mar Ecol Prog Ser* 203:47–65
70. Saraux C, Van Beveren E, Brosset P, et al (2019) Small pelagic fish dynamics: A review of mechanisms in the Gulf of Lions. *Deep-Sea Res Pt II* 159:52–61. <https://doi.org/10.1016/j.dsr2.2018.02.010>
71. Sargent JR, McIntosh R, Bauermeister A, Blaxter JHS (1979) Assimilation of the wax esters of marine zooplankton by herring (*Clupea harengus*) and rainbow trout (*Salmo gairdnerii*). *Mar Biol* 51:203–207. <https://doi.org/10.1007/BF00386799>
72. Savoye N, David V, Morisseau F, et al (2012) Origin and composition of particulate organic matter in a macrotidal turbid estuary: The Gironde Estuary, France. *Estuarine, Coastal and Shelf Science* 108:16–28. <https://doi.org/10.1016/j.ecss.2011.12.005>
73. Scott JM (1980) Effect of growth rate of the food alga on the growth/ingestion efficiency of a marine herbivore. *Journal of the Marine Biological Association of*

the United Kingdom 60:681–702. <https://doi.org/10.1017/S0025315400040376>

74. Sever TM, İlhan D (2016) Diet composition of red bandfish, *Cepola macrophthalma* (Actinopterygii: Perciformes: Cepolidae), from the Aegean Sea of Turkey. *Acta Ichthyol Piscat* 46:211–224. <https://doi.org/10.3750/AIP2016.46.3.05>
75. Stock BC, Jackson AL, Ward EJ, et al (2018) Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ* 6:e5096. <https://doi.org/10.7717/peerj.5096>
76. Tilves U, Fuentes VL, Milisenda G, et al (2018) Trophic interactions of the jellyfish *Pelagia noctiluca* in the NW Mediterranean: evidence from stable isotope signatures and fatty acid composition. *Marine Ecology Progress Series* 591:101–116
77. Utermöhl H (1931) Neue Wege in der quantitativen Erfassung des Plankton. (Mit besonderer Berücksichtigung des Ultraplanktons.). *SIL Proceedings, 1922-2010* 5:567–596. <https://doi.org/10.1080/03680770.1931.11898492>
78. Vander Zanden MJ, Rasmussen JB (2001) Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: Implications for aquatic food web studies. *Limnol Oceanogr* 46:2061–2066. <https://doi.org/10.4319/lo.2001.46.8.2061>
79. Yun MS, Lee DB, Kim BK, et al (2015) Comparison of phytoplankton macromolecular compositions and zooplankton proximate compositions in the northern Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 120:82–90. <https://doi.org/10.1016/j.dsr2.2014.05.018>
80. Zhao Y, Yang T, Shan X, et al (2022) Stable Isotope Analysis of Food Web Structure and the Contribution of Carbon Sources in the Sea Adjacent to the Miaodao Archipelago (China). *Fishes* 7:32. <https://doi.org/10.3390/fishes7010032>

Table 1. Sampling periods and number of samples of particulate organic matter (POM)/phytoplankton, zooplankton size classes and planktivorous fish species. POM was only separated in size classes (pico = 0.7-2.7 μm , nano = 2.7-20 μm and micro = 20-200 μm) for bay POM collected at station Solemio since May 2017 (see text).

| POM | | |
|--------------------------------|--|---------|
| Sources | Sampling period | Samples |
| Bay (Solemio) | | |
| - Bulk material | Oct 2016 – May 2018 | 38 |
| - Size-classes | May 2017– May 2018 | 21 |
| Oceanic (Julio) | Oct 2016 – May 2018 | 19 |
| Anthropogenic (Cortiou) | Oct 2016 – Dec 2017 | 15 |
| Riverine (Huveaune) | Oct, Nov 2016 & 2017, Mar 2017, Feb 2018 | 6 |
| Zooplankton | | |
| Size classes (μm) | Sampling period | Samples |
| 200-300 | Oct 2016 – May 2018 | 40 |
| 300-500 | Oct 2016 – May 2018 | 38 |
| 500-1000 | Oct 2016 – May 2018 | 36 |
| 1000-2000 | Oct 2016 – May 2018 | 32 |
| > 2000 | Oct 2016 – May 2018 | 28 |
| Teleost | | |
| Species | Sampling period | Samples |
| <i>Engraulis encrasicolus</i> | Mar, May, Jul, Oct 2017, May 2018 | 33 |
| <i>Sardina pilchardus</i> | Oct 2016 – May 2018 | 175 |
| <i>Sardinella aurita</i> | Oct 2016 – Oct 2017 | 71 |
| <i>Sprattus sprattus</i> | Jan, May, Sep, Oct 2017 | 24 |
| <i>Cepola macrophthalma</i> | Dec 2016, June 2017 | 18 |
| <i>Chromis chromis</i> | May 2017 – August 2017 | 24 |
| <i>Boops boops</i> | March 2017 | 11 |
| <i>Spicara maena</i> | May 2017 | 15 |

Table 2. Mean (\pm SD, standard deviation) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (in ‰) and C:N ratio of bulk particulate organic matter (0.7-200 μm) sampled at different stations in the Bay of Marseille. n = sample size. F = ANOVA F statistics and H = Kruskal-Wallis χ^2 statistics and P = their associated p-value. Superscript letters represent post-hoc groups. Values with similar post-hoc letters are not significantly different ($P > 0.05$). Data from the whole study period (October 2016 to May 2018) are pooled.

| POM source | n | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | C:N |
|-------------------------|----|-----------------------------|--------------------------|---------------------------|
| Bay (Solemio) | 38 | $-23.0 \pm 1.1^{\text{ab}}$ | $2.4 \pm 1.6^{\text{a}}$ | $5.4 \pm 0.9^{\text{a}}$ |
| Oceanic (Julio) | 19 | $-23.6 \pm 0.1^{\text{a}}$ | $0.1 \pm 0.6^{\text{a}}$ | $5.7 \pm 0.1^{\text{ab}}$ |
| Anthropogenic (Cortiou) | 15 | $-25.2 \pm 0.6^{\text{b}}$ | $2.6 \pm 1.6^{\text{a}}$ | $4.9 \pm 0.7^{\text{a}}$ |
| Riverine (Huveaune) | 6 | $-25.9 \pm 1.5^{\text{b}}$ | $5.6 \pm 1.1^{\text{b}}$ | $10.5 \pm 3.5^{\text{b}}$ |
| Analysis of variance | | H = 62.65 P < 0.001 | F = 63.57 P < 0.001 | H = 50.78 P < 0.001 |

Table 3. Biochemical composition (proteins, carbohydrates, lipids, and ash in $\mu\text{g mg}^{-1}$ DW), energy content (in J mg^{-1} DW) and mass of the particulate organic matter (POM) by size class for bay, oceanic, anthropogenic and riverine POM sampled between October 2016 and May 2018 in the Bay of Marseille, NW Mediterranean Sea. Abbreviations of size classes: Bulk = bulk POM (0.7-200 μm), Pico = pico-POM (0.7-2.7 μm), Nano = nano-POM (2.7-20 μm), Micro = micro-POM (20-200 μm). n = sample size. H = Kruskal-Wallis χ^2 statistics and P = their associated p-value. Superscript letters represent post-hoc groups. Values with similar post-hoc letters are not significantly different ($P > 0.05$). Data from the whole study period (October 2016 to May 2018) were pooled.

| Site | Size class | n | Mass (mg L^{-1}) | Mass % of POM | Proteins ($\mu\text{g mg}^{-1}$ DW) | Carbohydrates ($\mu\text{g mg}^{-1}$ DW) | Lipids ($\mu\text{g mg}^{-1}$ DW) | Ash ($\mu\text{g mg}^{-1}$ DW) | Energy (J mg^{-1} DW) |
|-------------------------|------------|----|--------------------------------|------------------|---|--|---------------------------------------|------------------------------------|------------------------------------|
| Bay (Solemio) | Bulk | 38 | 0.22 | | 114.58 ± 87.40^c | 48.30 ± 25.22^b | 113.64 ± 65.95^b | 723.47 ± 156.73^a | 7.33 ± 3.85^c |
| Oceanic (Julio) | Bulk | 19 | 0.13 | | 153.43 ± 53.63^{ac} | 46.69 ± 32.85^b | 224.09 ± 161.55^a | 580.95 ± 244.56^a | 12.06 ± 7.52^a |
| Anthropogenic (Cortiou) | Bulk | 15 | 1.95 | | 167.74 ± 43.09^a | 120.92 ± 23.45^a | 213.30 ± 181.86^a | 518.20 ± 265.17^a | 13.26 ± 8.62^a |
| Riverine (Huveaune) | Bulk | 6 | 114.80 | | 37.05 ± 11.82^b | 59.37 ± 14.93^b | 90.23 ± 21.26^c | 813.35 ± 127.95^b | 5.03 ± 3.70^b |
| Analyses of variance | | | | | H = 40.02 P < 0.001 | H = 37.65 P < 0.001 | H = 30.22 P < 0.001 | H = 49.24 P < 0.001 | H = 45.21 P = < 0.001 |
| Bay (Solemio) | Pico | 26 | 0.12 | 41 | 80.80 ± 56.84^a | 49.50 ± 38.36^b | 125.19 ± 142.86^b | 747.31 ± 186.16^a | 6.98 ± 5.91^b |
| | Nano | 26 | 0.06 | 21 | 88.49 ± 56.87^a | 78.22 ± 27.63^a | 208.18 ± 110.37^a | 614.58 ± 310.53^a | 11.08 ± 9.74^{ab} |
| | Micro | 26 | 0.11 | 38 | 66.88 ± 37.10^b | 67.48 ± 42.16^{ab} | 189.92 ± 63.13^{ab} | 580.11 ± 189.56^a | 12.50 ± 6.71^a |
| Analyses of variance | | | | | H = 1.26 P = 0.033 | H = 0.37 P = 0.031 | H = 1.70 P = 0.027 | H = 6.05 P = 0.049 | H = 5.36 P = 0.038 |

Table 4. Mean (\pm SD, standard deviation) stable isotope compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, in ‰) and C:N ratio and trophic levels (TL) for the different size classes of particulate organic matter (POM) sampled at the Solemio station in the Bay of Marseille. n = sample size. H = Kruskal-Wallis χ^2 statistics and P = their associated p-value. Superscript letters represent post-hoc groups. Values with similar post-hoc letters are not significantly different ($P > 0.05$).

| Size class | n | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | C:N | TL _{Caut} | TL _{Post} | TL _{Estimated} |
|----------------------------------|----|-----------------------|-----------------------|-----------------------|--------------------|--------------------|-------------------------|
| Pico (0.7–2.7 μm) | 21 | -23.0 ± 0.2^a | 1.7 ± 0.2^a | 5.4 ± 0.3^a | 1.0 | 1.0 | 1.0 |
| Nano (2.7–20 μm) | 21 | -22.5 ± 0.4^{ab} | 2.9 ± 0.6^{ab} | 6.3 ± 0.3^{ab} | 1.4 ± 0.2 | 1.4 ± 0.2 | 1.5 ± 0.3 |
| Micro (20–200 μm) | 21 | -21.2 ± 0.1^b | 4.5 ± 0.2^b | 6.6 ± 0.1^b | 1.0 | 1.0 | 1.0 |
| Analysis of variance | | H = 5.57 P = 0.032 | H = 6.41 P = 0.040 | H = 7.63 P = 0.046 | | | |

Table 5. Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (in ‰), C:N ratios and trophic levels (TL) of zooplankton size classes sampled at the Solemio station in the Bay of Marseille. n = sample size. H = Kruskal-Wallis χ^2 statistics and P = their associated p-value. Superscript letters represent post-hoc groups. Values with similar post-hoc letters are not significantly different ($P > 0.05$). Data from the whole study period (October 2016 to May 2018) were pooled.

| Size class (μm) | n | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | C:N | TL _{Caut} | TL _{Post} | TL _{estimated} |
|------------------------------|----|-----------------------|------------------------|------------------------|-------------------------|-------------------------|-------------------------|
| 200-300 | 40 | -22.1 ± 0.7^a | 3.4 ± 1.3^c | 4.6 ± 1.6^{bc} | 1.6 ± 0.5^b | 1.5 ± 0.4^b | 1.8 ± 0.5^b |
| 300-500 | 38 | -22.0 ± 0.8^a | 4.0 ± 1.4^{acd} | 4.3 ± 1.4^{bc} | 1.8 ± 0.5^{bc} | 1.7 ± 0.4^{bc} | 2.0 ± 0.6^{bc} |
| 500-1000 | 36 | -21.9 ± 0.6^a | 4.4 ± 1.3^{ad} | 3.9 ± 1.7^c | 2.0 ± 0.5^c | 1.8 ± 0.4^c | 2.2 ± 0.6^c |
| 1000-2000 | 30 | -21.6 ± 1.1^a | 5.9 ± 1.9^b | 3.3 ± 2.1^c | 2.6 ± 0.7^d | 2.3 ± 0.6^d | 2.8 ± 0.8^d |
| > 2000 | 28 | -22.9 ± 3.2^a | 5.0 ± 2.4^{ab} | 7.0 ± 7.0^{ab} | 2.2 ± 0.9^{cd} | 2.0 ± 0.7^{cd} | 2.4 ± 1.0^{cd} |
| Analysis of variance | | H = 5.30 P = 0.258 | H = 44.29 P < 0.001 | H = 34.86 P < 0.001 | H = 133.20 P < 0.001 | H = 133.18 P < 0.001 | H = 133.20 P < 0.001 |

Table 6. Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (in ‰), C:N ratios and trophic levels (TL) of large zooplankton groups ($> 1000 \mu\text{m}$) sampled at the Solemio station in the Bay of Marseille. n = sample size. H = Kruskal-Wallis χ^2 statistics and P = their associated p-value. Superscript letters represent post-hoc groups. Values with similar post-hoc letters are not significantly different ($P > 0.05$). Data from the whole study period (October 2016 to May 2018) were pooled.

| Zooplankton groups | n | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | C:N | TL _{Caut} | TL _{Post} | TL _{estimated} |
|----------------------|----|------------------------|------------------------|------------------------|------------------------|------------------------|-------------------------|
| Copepods | 14 | -21.8 ± 0.9^a | 4.4 ± 1.5^{abd} | 3.5 ± 0.9^a | 2.0 ± 0.5^{abd} | 1.8 ± 0.4^{abd} | 2.1 ± 0.6^{ab} |
| Decapods | 14 | -21.0 ± 0.9^a | 4.6 ± 1.0^{bcd} | 3.9 ± 1.5^a | 2.1 ± 0.4^{bcd} | 1.9 ± 0.3^{bcd} | 2.3 ± 0.4^{b} |
| Euphausiids | 6 | -21.4 ± 0.6^a | 5.8 ± 2.1^{bc} | 3.7 ± 3.3^a | 2.5 ± 0.8^{bc} | 2.2 ± 0.6^{bc} | 2.7 ± 0.8^{b} |
| Stomatopods | 2 | -21.1 ± 0.0^a | 5.8 ± 0.1^{bcd} | 4.8 ± 0.0^a | 2.5 ± 0.0^{bcd} | 2.2 ± 0.0^{bcd} | 2.7 ± 0.0^{b} |
| Amphipods | 4 | -21.2 ± 1.6^a | 3.1 ± 0.2^a | 3.3 ± 2.6^a | 1.5 ± 0.1^a | 1.4 ± 0.1^a | 1.6 ± 0.1^a |
| Chaetognaths | 12 | -20.6 ± 0.8^a | 6.7 ± 2.2^{bc} | 3.5 ± 2.7^a | 2.9 ± 0.8^{bc} | 2.5 ± 0.6^{bc} | 3.1 ± 1.1^{b} |
| Siphonophores | 8 | -20.2 ± 0.4^a | 4.1 ± 0.5^{abcd} | 9.6 ± 6.1^a | 1.9 ± 0.2^{abcd} | 1.7 ± 0.2^{abcd} | 2.0 ± 0.3^{ab} |
| <i>Veleva veleva</i> | 4 | -20.9 ± 0.6^a | 3.9 ± 0.5^{abcd} | 5.0 ± 0.7^a | 1.8 ± 0.2^{abcd} | 1.7 ± 0.2^{abcd} | 1.9 ± 0.2^{ab} |
| Salps | 10 | -21.8 ± 1.8^a | 3.4 ± 1.0^{ad} | 10.3 ± 10.0^a | 1.6 ± 0.4^{ad} | 1.5 ± 0.3^{ad} | 1.8 ± 0.5^{a} |
| Pyrosomes | 2 | -21.2 ± 0.0^a | 5.1 ± 0.0^{bcd} | 4.5 ± 0.6^a | 2.2 ± 0.0^{bcd} | 2.0 ± 0.0^{bcd} | 2.5 ± 0.0^{b} |
| Teleost eggs | 6 | -21.6 ± 1.2^a | 8.4 ± 2.4^c | 3.6 ± 2.7^a | 3.5 ± 0.9^c | 3.0 ± 0.7^c | 3.9 ± 1.5^c |
| Teleost larvae | 2 | -21.2 ± 0.1^a | 3.8 ± 0.1^{abcd} | 3.7 | 1.8 ± 0.0^{abcd} | 1.6 ± 0.0^{abcd} | 1.9 ± 0.0^{ab} |
| Analysis of variance | | H = 19.26 P = 0.057 | H = 44.90 P < 0.001 | H = 15.60 P = 0.157 | H = 44.90 P < 0.001 | H = 44.90 P < 0.001 | H = 44.90 P < 0.001 |

Table 7. Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (in ‰), C:N ratios and trophic levels (TL) of planktivorous species sampled at the Solemio station in the Bay of Marseille. n = sample size. H = Kruskal-Wallis χ^2 statistics and P = their associated p-value. Superscript letters represent post-hoc groups. Values with similar post-hoc letters are not significantly different ($P > 0.05$). Data from the whole study period (October 2016 to May 2018) were pooled.

| Planktivorous species | n | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | C:N | TL _{Caut} | TL _{Post} | TL _{Estimated} |
|-------------------------------|-----|-----------------------------|---------------------------|--------------------------|---------------------------|---------------------------|---------------------------|
| <i>Engraulis encrasicolus</i> | 33 | $-19.8 \pm 0.2^{\text{ab}}$ | $7.1 \pm 0.5^{\text{c}}$ | $3.3 \pm 0.1^{\text{a}}$ | $3.0 \pm 0.2^{\text{c}}$ | $2.6 \pm 0.1^{\text{c}}$ | $3.3 \pm 0.2^{\text{c}}$ |
| <i>Sardina pilchardus</i> | 175 | $-19.9 \pm 0.4^{\text{a}}$ | $8.2 \pm 0.7^{\text{bd}}$ | $3.4 \pm 0.2^{\text{a}}$ | $3.4 \pm 0.3^{\text{bd}}$ | $2.9 \pm 0.2^{\text{bd}}$ | $3.8 \pm 0.3^{\text{bd}}$ |
| <i>Sardinella aurita</i> | 77 | $-19.6 \pm 0.3^{\text{b}}$ | $8.0 \pm 0.7^{\text{d}}$ | $3.2 \pm 0.0^{\text{b}}$ | $3.3 \pm 0.2^{\text{d}}$ | $2.9 \pm 0.2^{\text{d}}$ | $3.7 \pm 0.3^{\text{d}}$ |
| <i>Sprattus sprattus</i> | 15 | $-19.4 \pm 0.4^{\text{c}}$ | $7.1 \pm 1.0^{\text{cd}}$ | $3.6 \pm 0.6^{\text{a}}$ | $3.0 \pm 0.4^{\text{cd}}$ | $2.6 \pm 0.3^{\text{cd}}$ | $3.3 \pm 0.4^{\text{cd}}$ |
| <i>Cepola macrophthalma</i> | 18 | $-20.5 \pm 0.8^{\text{ab}}$ | $8.8 \pm 0.6^{\text{a}}$ | $3.3 \pm 0.0^{\text{a}}$ | $3.6 \pm 0.2^{\text{a}}$ | $3.1 \pm 0.2^{\text{a}}$ | $4.1 \pm 0.3^{\text{a}}$ |
| <i>Chromis chromis</i> | 17 | $-19.7 \pm 0.1^{\text{ab}}$ | $8.3 \pm 0.2^{\text{ab}}$ | $3.3 \pm 0.1^{\text{a}}$ | $3.4 \pm 0.1^{\text{ab}}$ | $3.0 \pm 0.1^{\text{ab}}$ | $3.9 \pm 0.1^{\text{ab}}$ |
| <i>Boop. boops</i> | 11 | $-20.2 \pm 0.4^{\text{a}}$ | $10.6 \pm 3.9^{\text{a}}$ | $3.4 \pm 0.2^{\text{a}}$ | $4.2 \pm 1.6^{\text{a}}$ | $3.6 \pm 3.9^{\text{a}}$ | $4.8 \pm 1.9^{\text{a}}$ |
| <i>Spicara maena</i> | 15 | $-19.5 \pm 0.4^{\text{bc}}$ | $8.3 \pm 1.2^{\text{bd}}$ | $3.4 \pm 0.1^{\text{a}}$ | $3.4 \pm 0.5^{\text{bd}}$ | $2.9 \pm 1.2^{\text{bd}}$ | $3.8 \pm 1.7^{\text{bd}}$ |
| Analysis of variance | | H = 43.66 P < 0.001 | H = 60.97 P < 0.001 | H = 90.86 P < 0.001 | H = 60.99 P < 0.001 | H = 61.14 P < 0.001 | H = 60.96 P < 0.001 |

Fig. 1. Map of the Bay of Marseille, located in the eastern part of the Gulf of Lion (NW Mediterranean Sea), and of sampling locations. Particulate organic matter (POM) was sampled at Solemio (red cross), in the Huveaune river (black diamond) and at the Cortiou sewage treatment plant (black triangle). POM was also sampled at station Julio (black square). Zooplankton was sampled only at station Solemio. Fish sampling sites are represented by black dots.

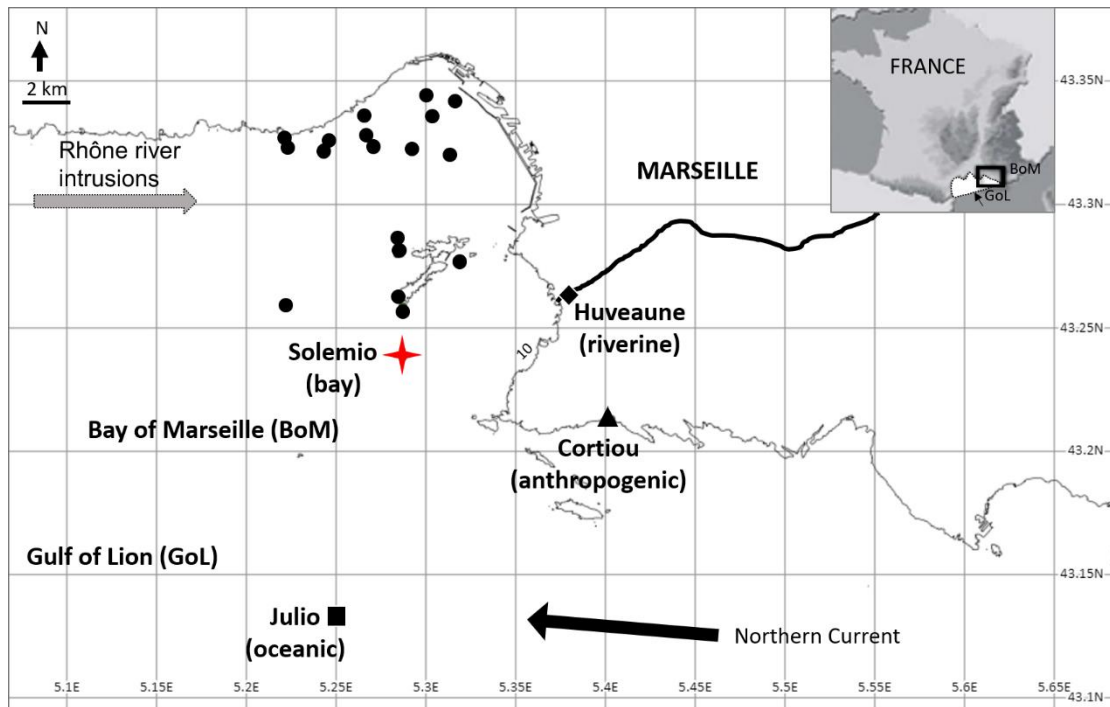


Fig. 2. Taxonomic compositions of pico- and nanoplankton groups (< 20 μm) of POM at (A) Solemio, (B) Julio, (C) Cortiou and (D) Huveaune in the Bay of Marseille. Data from October 2016 to May 2018 are pooled. Group abbreviations: Pico Euk. = picoeukaryotes, Nano Euk. = nanoeukaryotes, Nano-Cyano. = nano-cyanophycean filaments and detritus.

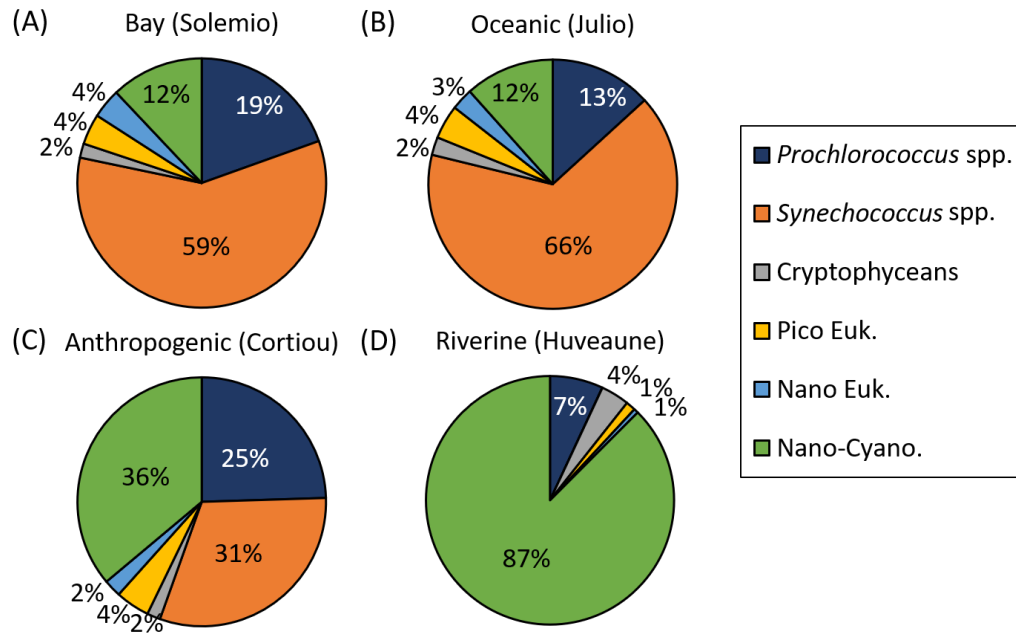


Fig. 3. Mean (\pm standard deviation) isotope compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) of particulate organic matter (POM) origins (diamonds), zooplankton size classes (triangles) and groups (circles), and fishes (rectangles) sampled in the Bay of Marseille from October 2016 to May 2018. The blue area represents the influence of Solemio POM on food webs. POM abbreviations: So = Solemio POM, Julio = Julio POM sampled in April 2019. Pico = 0.7-2.7 μm , Nano = 2.7-20 μm , Micro = 20-200 μm . Zooplankton size class abbreviations: x20 = 20-80 μm , x80 = 80-200 μm , x300 = 300-500 μm , x500 = 500-1000 μm , x1000 = 1000-2000 μm , x2000 = > 2000 μm . Zooplankton group abbreviations: cop = copepods, dec = decapods, eup = euphausiids, stom = stomatopods, amp = amphipods, cha = chaetognaths, pte = pteropods, sal = salps, sip = siphonophores, py = pyrosome, vel = *Veleva veleva*, tel = fish eggs, fl = fish larvae. Fish species abbreviations: EE = *Engraulis encrasicolus*, SP = *Sardina pilchardus*, SA = *Sardinella aurita*, SPSP = *Sprattus sprattus*, CMA = *Cepola macrophthalma*, CC = *Chromis chromis*, BB = *Boops boops*, SPM = *Spicara maena*.

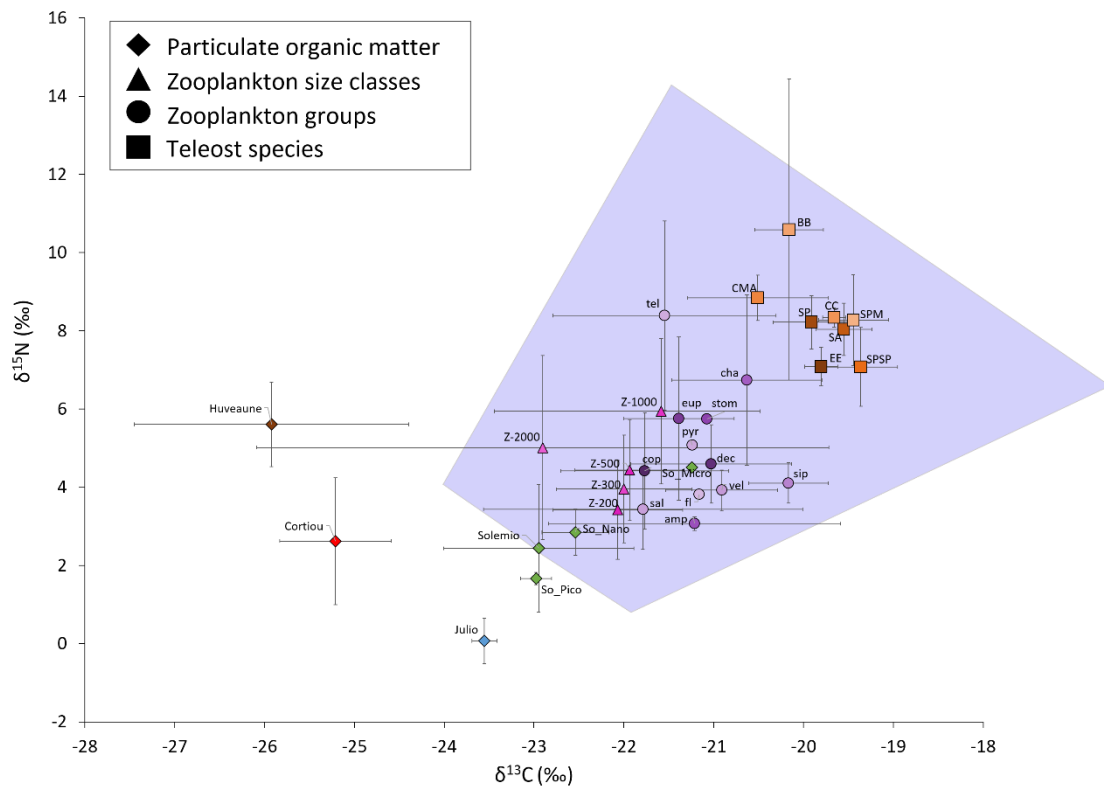


Fig. 4. Conceptual diagram of energy transfer in the planktonic food web with energy content ($J\ mg^{-1}\ DW$) provided by proteins, carbohydrates and lipids (I) from POM size classes (average of 0.7 to 200 μm) to zooplankton (average of 200 to 2000 μm), an increase of 1.07 times in energy content was observed. POM size classes were lipid-rich, while zooplankton size classes were protein-rich. (II) We observed an increase of 2.30 times in energy content from zooplankton size classes to fish muscles related to increase in protein and lipid contents. (III) Finally, we observed an increase of 2.46 times in energy content from POM to fish muscles. Biochemical data of muscle tissues of *S. pilchardus* are from Albo-Puigserver et al. (2017), obtained in the Ebro River Delta, Western Mediterranean Sea.

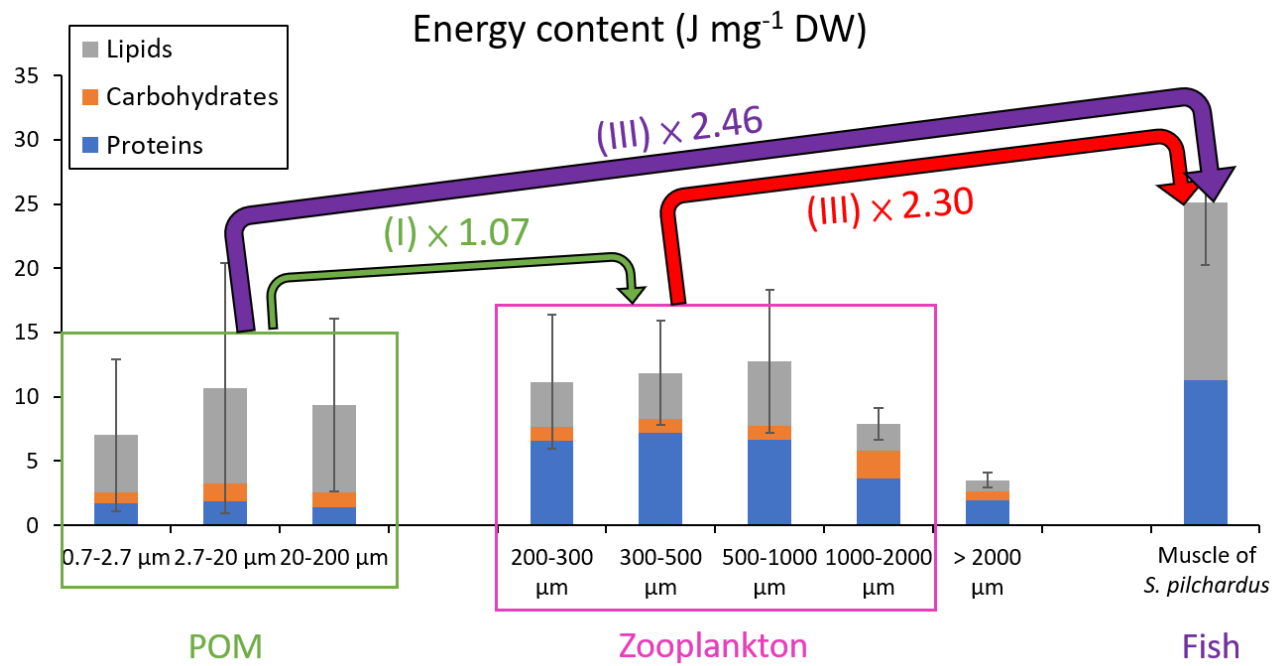


Fig. 5. Conceptual diagram of relative contributions of POM sources (Julio, Cortiou, Huveaune stations) to bay POM, (I), of POM/phytoplankton size classes (pico-, nano-, micro-) to bay POM composition (II), and of prey for different predators: POM size classes to zooplankton size fractions (200-1000, 1000-2000, > 2000 μm) (III) and micro-POM and zooplankton size fractions to the diet of fishes (IV) based on isotope mixing model outputs (see the “Results” section). Colored arrows indicate the transfer of material from the sources to the mixture and their thickness as well as the size of numbers are proportional to relative contributions. Zooplankton size fractions: Zoo 200 = 200-1000 μm , Zoo 1000 = 1000-2000 μm , Zoo 2000 = > 2000 μm . For the abbreviations of fish species, see the legend of Fig. 3. For POM origins and micro- and pico-POM, the trophic level is designated to 1.

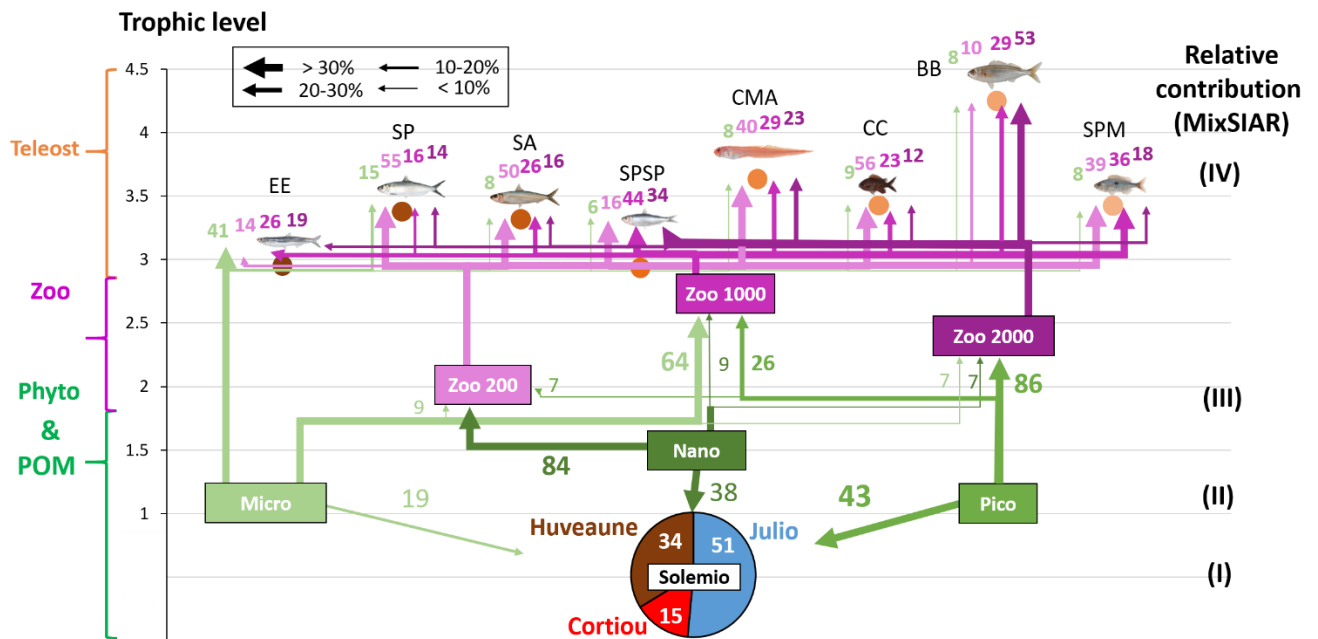


Table S1. Trophic group and observed size range of zooplankton groups collected in the field and/or in stomach contents of the studied fish species in the Bay of Marseille (Chen et al. 2021, 2022).

| | Zooplankton group | Size (µm) | Trophic group | Reference |
|--------------------|---|----------------------------|------------------------|---|
| Crustacea | | | | |
| Copepoda | Calanoida | | | |
| | Acartidae | 600 – 2700 | Omnivores-herbivores | Kouwenberg 1994; Swandling et al. 2011 |
| | Calanidae | 1900 – 3500 | Omnivores-herbivores | Kouwenberg 1994; Mauchline 1998 |
| | Candaciidae | 2400 – 3900 | Carnivores | Kouwenberg 1994; Mauchline 1998 |
| | Centropagidae | 900 – 2300 | Omnivores | Kouwenberg 1994; Swandling et al. 2011 |
| | Clausocalanidae/ Paracalanidae group | 700 – 2000 | Omnivores-herbivores | Kouwenberg 1994; Razouls et al. 2005; Swandling et al. 2011 |
| | <i>Isias clavipes</i> | 1200 – 1700 1000 – 2500 | Omnivores | Ohtsuka and Onbé 1991 Mauchline 1998; Yamaguchi et al. 2002; |
| | Lucicutidae | 1500 – 4500 | Omnivores-herbivores | Razouls et al. 2005 Wickstead 1962; Kouwenberg 1994; Mauchline 1998; |
| | <i>Pleuromamma</i> spp. | 1100 – 2500 | Omnivores | Razouls et al. 2005 Arcos and Fleminger |
| | <i>Nannocalanus minor</i> | 1000 – 2000 | Omnivores-herbivores | 1986; Kouwenberg 1994 |
| | Temoridae | 1000 – 2000 | Omnivores-herbivores | Kouwenberg 1994 |
| | Cyclopoida | 400 – 1600 | | Allredge 1972; Turner 1986; Ohtsuka et al. 1993; Steinberg et al. 1994 |
| | Oncaeidae | 700 – 2600 | Omnivores-detritivores | Turner et al. 1984; Kouwenberg 1994; |
| | Corycaeidae | 400 – 1600 | Carnivores | Swandling et al. 2011 Turner 1986; González and Smetacek 1994 |
| | Oithonidae | 1000 – 4900 | Omnivores | Takahashi et al. 2013 |
| | Sapphirinidae | 1000 – 4900 | Carnivores | Takahashi et al. 2013 |
| | Harpacticoida | 300 – 800 | | Allredge 1972; Ohtsuka et al. 1993; Steinberg et al. 1994; Maar et al. 2006 |
| | <i>Microsetella</i> spp. | | Omnivores-detritivores | 2006 |
| | <i>Macrosetella gracilis</i> | 800 – 1800 300 – 900 | Omnivores-herbivores | Kouwenberg 1994 Kouwenberg 1994; Broglio et al. 2004; |
| | <i>Euterpina acutifrons</i> | | Omnivores-herbivores | Swandling et al. 2011 |
| Diplostraca | <i>Evadne</i> spp. | 300 – 1000 | Herbivores | |
| | <i>Podon</i> spp. | 300 – 1200 | Herbivores | Katechakis and Stibor 2004 |
| | <i>Penilia</i> spp. | 600 – 1100 | Herbivores | |
| Ostracoda | Ostracoda | 400 – 5000 | Omnivores | Cohen and Oakley 2017 |
| Hyperidea | <i>Phronima</i> spp. | 1500 – 20000 | Carnivores | Diebel 1988 |
| | <i>Hyperia</i> spp. | 2000 – 4000 | Carnivores | Bowman 1973 |
| | <i>Primno</i> spp. | 10000 – 12000 | Carnivores | Bowman 1978 |
| Larvae | | | | |

| | | | | |
|--------------------------|----------------------------------|---------------|--------------------------------------|---|
| Crustaceans | | 80 – 700 | | |
| (others) | Nauplii of copepoda | | Omnivores-bacterivores | Turner 2004 |
| | Cirripede cypris larvae | 400 – 1600 | Omnivores-herbivores | Gaonkar and Anil 2010 |
| | Zoea of Decapoda | 1100 – 3000 | Omnivores | Anger 2001 |
| | Euphausiacea | 2000 – 4800 | Omnivores-carnivores | Sogawa et al. 2017 |
| Molluscs | Pteropoda | 5000 – 10000 | Omnivores | Howes et al. 2014; Conley et al. 2018 |
| | Bivalvia | 300 – 3500 | Omnivores | Arapov et al. 2010 |
| Cnidaria | Calycophorae of Siphonophorae | 5000 – 10000 | Omnivores-carnivores | Purcell 1981 |
| | <i>Velella velella</i> | 40000 – 60000 | Omnivores-carnivores | Décima et al. 2019 |
| Pyrosoma | | 3000 – 5000 | Herbivores | Décima et al. 2019 |
| Doliolida | | 3000 – 3500 | Herbivores | Conley et al. 2018 |
| Salpida | | 3000 – 3500 | Herbivores | Pakhomov et al. 2019 |
| Chaetognatha | Chaetognatha | 5000 – 15000 | Carnivores | Kehayias 1996 |
| Appendicularia | | 6000 – 8000 | Herbivores, bacterivore, virovore | Conley et al. 2018; Décima et al. 2019 |
| Eggs of Teleostei | Anchovy eggs | 600 – 1000 | | This study |
| Decapod eggs | | 300 – 500 | | This study |

Table S2. Values (mean \pm standard deviation) of the trophic fractionation factors (TFF, $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$, in ‰) used for computation of trophic levels (TL, with $\delta^{15}\text{N}$ values) and for each of the Bayesian mixing model in this study. “Mean (Zoo “200 – > 2000 μm ” - bulk bay)” indicates how the mean TFF was calculated, i.e. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bulk bay POM (Solemio POM) subtracted to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of zooplankton from 200 to > 2000 μm , respectively.

| TL | | | | | |
|--------------|-----------------------------|----------------------------|-----------------------------|-----------------------------|---|
| | Baseline | Consumer | $\Delta\delta^{15}\text{N}$ | Reference | Estimation |
| | | Nano-POM | 2.75 | Caut et al. 2009 | |
| | | Nano-POM | 3.40 | Post 2002 | |
| | | Nano-POM | 2.34 | This study | Mean (Zoo “200 – > 2000 μm ” - bulk bay) |
| | | Zooplankton size classes | 2.75 | Caut et al. 2009 | |
| | | Zooplankton size classes | 3.40 | Post 2002 | |
| | | Zooplankton size classes | 2.34 | This study | Mean (Zoo “200 – > 2000 μm ” - bulk bay) |
| | Pico-POM | Zooplankton groups | 2.75 | Caut et al. 2009 | |
| | | Zooplankton groups | 3.40 | Post 2002 | |
| | | Zooplankton groups | 2.34 | This study | Mean (Zoo “200 – > 2000 μm ” - bulk bay) |
| | | Fish species | 2.75 | Caut et al. 2009 | |
| | | Fish species | 3.40 | Post 2002 | |
| | | Fish species | 2.34 | This study | Mean (Zoo “200 – > 2000 μm ” - bulk bay) |
| Mixing model | | | | | |
| | Source | Mixture | $\Delta\delta^{13}\text{C}$ | $\Delta\delta^{15}\text{N}$ | Reference or estimation |
| 1 | POM origins | Bay POM | 0.00 \pm 0.00 | 0.00 \pm 0.00 | |
| 2 | POM size classes | Bay POM | 0.00 \pm 0.00 | 0.00 \pm 0.00 | |
| 3 | Pico-POM | Zooplankton size fractions | 0.68 \pm 0.02 | 3.55 \pm 0.05 | TFF estimation formula for invertebrates by Caut et al. 2009 applied to each POM size class |
| | Nano-POM | (200-1000, 1000-2000, > | 0.63 \pm 0.04 | 3.18 \pm 0.19 | |
| | Micro-POM | 2000 μm) | 0.48 \pm 0.00 | 2.66 \pm 0.01 | |
| 4 | Pico-POM | Zooplankton size fractions | 1.11 \pm 1.56 | 2.41 \pm 1.80 | Mean (Zoo “200 – > 2000 μm ” - bulk bay) |
| | Nano-POM | (200-1000, 1000-2000, > | 1.11 \pm 1.56 | 2.41 \pm 1.80 | |
| | Micro-POM | 2000 μm) | 1.11 \pm 1.56 | 2.41 \pm 1.80 | |
| 5 | Micro-POM | Fishes | 0.48 \pm 0.00 | 2.66 \pm 0.01 | TFF estimation formula for fish by Caut et al. 2009 applied to each zooplankton size group |
| | Zoo 200-1000 μm | | 2.26 \pm 0.57 | 4.23 \pm 1.47 | |
| | Zoo 1000-2000 μm | | 1.84 \pm 0.57 | 2.23 \pm 1.47 | |
| | Zoo > 2000 μm | | 3.16 \pm 0.57 | 3.16 \pm 1.47 | |
| 6 | Micro-POM | Fishes | 0.39 \pm 1.30 | 3.40 \pm 1.00 | Post 2002 |
| | Zoo 200-1000 μm | | 0.39 \pm 1.30 | 3.40 \pm 1.00 | |
| | Zoo 1000-2000 μm | | 0.39 \pm 1.30 | 3.40 \pm 1.00 | |

Zoo > 2000 μm

0.39 ± 1.30 3.40 ± 1.00

Table S3. Cytometry counts of pico- and nanoplankton (< 20 µm) of POM from different sources and microscopic counts of nano- and microplankton (20 – 100 µm) of POM from Solemio station sampled in the Bay of Marseille, NW Mediterranean Sea. Data from the whole study period (October 2016 to May 2018) are pooled. Picoplankton group abbreviation: Pico Euk. = picoeukaryotes. Nanoplankton group abbreviations: Nano Euk. = nanoeukaryotes, Nano-cyano. = nano-cyanophycean filaments and detritus. Microplankton group abbreviations: Dinoflag. = dinobionts (dinoflagellates), Nanofl. Cry. = nanoflagellates cryptophyceans spp., Und. nanoflag. = undetermined nanoflagellates, Other microphy. = other microphytoplankton groups. H = Kruskal-Wallis χ^2 statistics, and P = their associated p-value. Superscript letters represent post-hoc groups.

| Cytometry counts (100 cells mL ⁻¹) | | | | | | | | |
|--|------------------------------|-----------------------------------|-----------------------------|------------------------------|------------------------------------|----------------------------|--------------------------------|--------------------------------|
| Source | Picoplankton | | | | Nanoplankton | | | |
| | <i>Prochlorococcus</i> | <i>Synechococcus</i> | Pico Euk. | Total pico. | Cryptophyceans | Nano Euk. | Nano-Cyano. | Total nano. |
| Bay | 46.30 ± 61.46 ^a | 139.22 ± 83.76^c | 9.44 ± 15.24 ^a | 194.96 ± 118.68 ^a | 4.36 ± 4.72 ^{ab} | 9.12 ± 7.34 ^{ab} | 28.58 ± 63.00 ^a | 39.05 ± 66.84 ^a |
| Oceanic | 27.91 ± 40.97 ^a | 138.31 ± 119.36 ^{bc} | 9.31 ± 15.59 ^a | 175.54 ± 123.29 ^a | 4.90 ± 9.95 ^{ab} | 5.98 ± 5.36 ^{ab} | 24.52 ± 49.77 ^a | 30.50 ± 50.43 ^a |
| Anthropogenic | 50.86 ± 88.17 ^a | 64.26 ± 49.07 ^{ab} | 9.23 ± 23.33 ^a | 124.35 ± 144.84 ^a | 3.60 ± 8.40^a | 4.71 ± 11.00 ^a | 74.90 ± 146.91 ^a | 83.20 ± 163.48 ^a |
| River | 378.76 ± 606.15 ^a | 1.27 ± 1.17^a | 68.58 ± 112.39 ^a | 448.61 ± 717.63 ^a | 203.01 ± 351.50^b | 31.83 ± 54.59 ^b | 4784.56 ± 8286.55 ^a | 5019.40 ± 8692.64 ^a |
| Analysis of variance | H = 3.93 P = 0.27 | H = 14.69 P = 0.002 | H = 4.89 P = 0.18 | H = 5.19 P = 0.16 | H = 11.76 P = 0.008 | H = 12.71 P = 0.005 | H = 1.32 P = 0.724 | H = 7.08 P = 0.070 |
| Microscopic counts (100 cells mL ⁻¹) | | | | | | | | |
| Source | Diatoms | Dinoflag. | Nanofl. Cry. | Und. nanoflag. | Other microphy. | Total counts | Analysis of variance | |
| Bay | 6.03 ± 7.82 ^b | 0.48 ± 0.71 ^c | 48.74 ± 53.96 ^a | 6.09 ± 9.81 ^b | 0.02 ± 0.02 ^d | 61.41 ± 63.33 | H = 149.06, P < 0.001 | |

Table S4. Mean composition of zooplankton size classes and overall diet within each size class sampled with vertical nets at the Solemio station. Dominant groups are indicated in **bold** characters by decreasing order of importance. Dominant copepods are not organized in decreasing order since the dominant groups changed between seasonally during the study period.

| Size class (µm) | Main groups | Main copepod groups | Overall diet |
|-----------------|--|--|--|
| 200-300 | Copepods (60-90%), cladocerans, larvae (gastropods, bivalves, annelids, brachyuran) | Oncaeidae, <i>Microsetella/Macrosetella</i> spp., Clausocalanidae/Paracalanidae, Corycaeidae, Euterpinidae, Oithonidae | Omnivores-detrivore, Omnivores-herbivore, Carnivore |
| 300-500 | Copepods (50-80%), cladocerans, larvae (gastropods, bivalves, annelids, brachyuran), appendicularians, ostracods | Clauso/Paracalanidae, Oithonidae, Oncaeidae, <i>Microsetella/Macrosetella</i> spp., Corycaeidae, Centropagidae, Euterpinidae, Acartiidae, Temoridae, Peltidiidae | Omnivores-detrivore, Bacterivore, Virovore, Omnivores-herbivore, Carnivore |
| 500-1000 | Copepods (40-60%), decapod larvae (brachyuran, macrurids) (10-20%), eggs of teleosts and crustaceans , euphausiids, appendicularians, chaetognaths, pteropods, ostracods | Clausocalanidae/Paracalanidae, Corycaeidae, Candaciidae, Metritinidae, Centropagidae, Temoridae, Acartiidae, Lucicutiidae, Calanidae | Omnivores-herbivore, Omnivores-carnivore, Carnivore, Filter-feeders |
| 1000-2000 | Siphonophores (30-40%), salps (20-30%), chaetognaths (10-20%), eggs of teleosts and crustaceans , copepods, pteropods, macrurid larvae, brachyuran larvae | Clauso/Paracalanidae, Candaciidae, Metritinidae, Centropagidae, Temoridae, Acartiidae, Calanidae, Pontellidae, Phaennidae | Filter-feeders, Omnivores, Carnivore |
| > 2000 | Salps (40-50%), siphonophores (30-40%), chaetognaths, doliolids, pteropods , macrurid larvae, brachyuran larvae, teleost larvae, euphausiids, copepods | Candaciidae, Calanidae, Pontellidae, Phaennidae, Euchaetidae, Sapphirinidae | Filter-feeders, Omnivores, Carnivore |

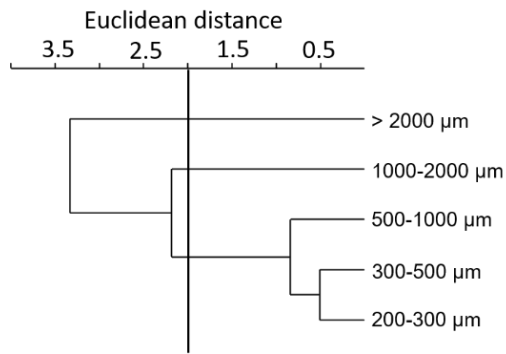


Fig. S1. Cluster analysis of isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, in ‰) and elemental composition (C:N ratios) dissimilarities based on Euclidean distance of the different size classes (μm) of zooplankton sampled at the Solemio site in the Bay of Marseille from October 2016 to May 2018. The vertical line (Euclidean distance = 2) separates the clusters.

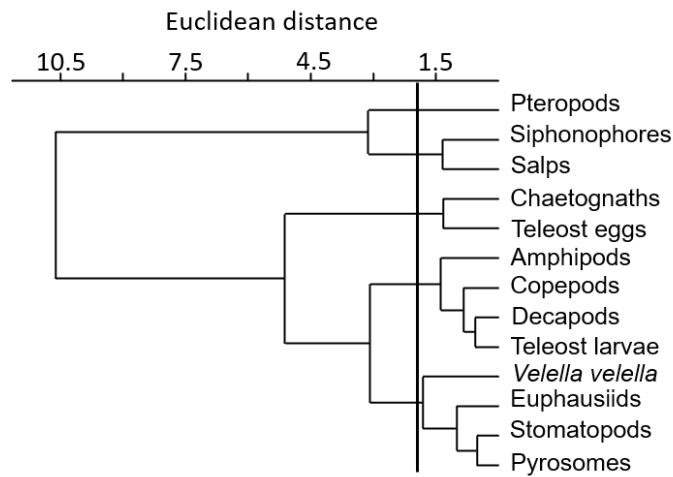


Fig. S2. Cluster analysis of isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, in ‰) and elemental composition (C:N ratios) dissimilarities based on Euclidean distance of the different taxonomic groups of zooplankton sampled at the Solemio site in the Bay of Marseille from October 2016 to May 2018. The vertical line (Euclidean distance = 2) separates the clusters.

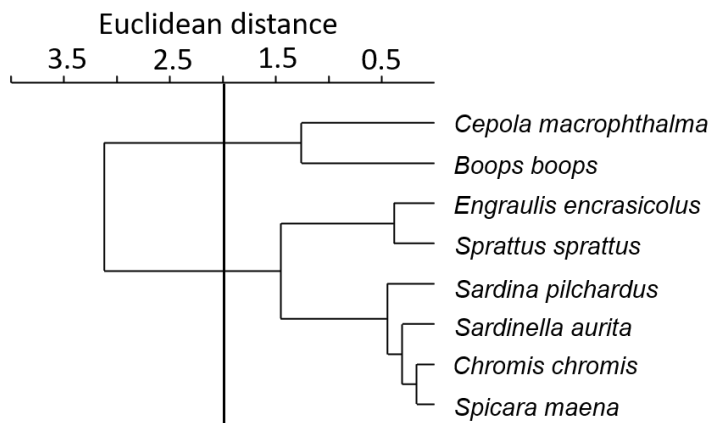


Fig. S3. Cluster analysis of isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, in ‰) and elemental composition (C:N ratios) dissimilarities based on Euclidean distance of the different species of planktivorous fish sampled in the Bay of Marseille from October 2016 to May 2018. The vertical line (Euclidean distance = 2) separates the clusters.

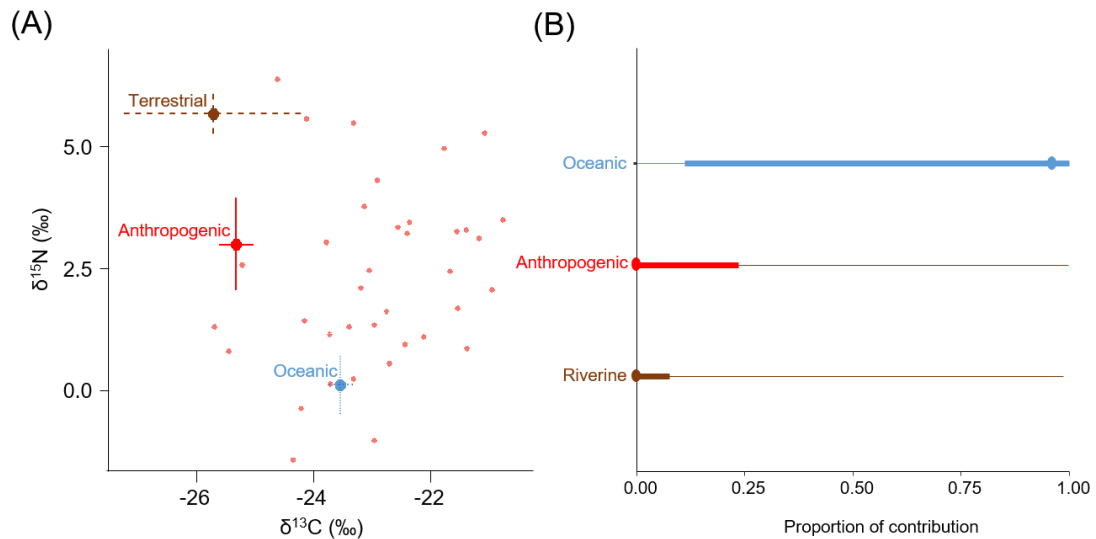


Fig. S4. Results of the mixing model: (A) Isospace plot of mixture points (pink) and mean and standard deviations of sources, and (B) Proportion estimates from three POM origins to bay POM (Solemio site) mixture model: posterior medians (points), 50% credible intervals (thick lines), and 90% credible intervals (thin lines). Data from October to May 2018 were used. TFF was set to null as no consumption process was involved and only the mixing of several potential sources of OM was considered.

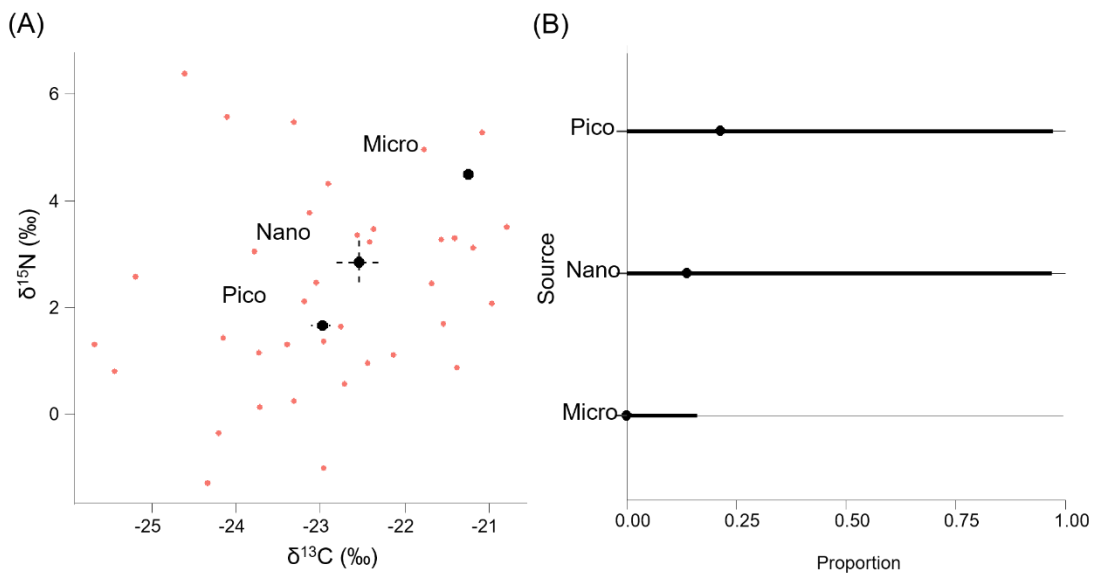


Fig. S5. Results of the mixing model: (A) Isospace plot of mixture points (pink) and mean and standard deviations of sources, and (B) Proportion estimates from three POM origins to bay POM (Solemio site) mixture model: posterior medians (points), 50% credible intervals (thick lines), and 90% credible intervals (thin lines). Data from October to May 2018 were used. TFF was set to null as no consumption process was involved and only the mixing of several potential sources of OM was considered.

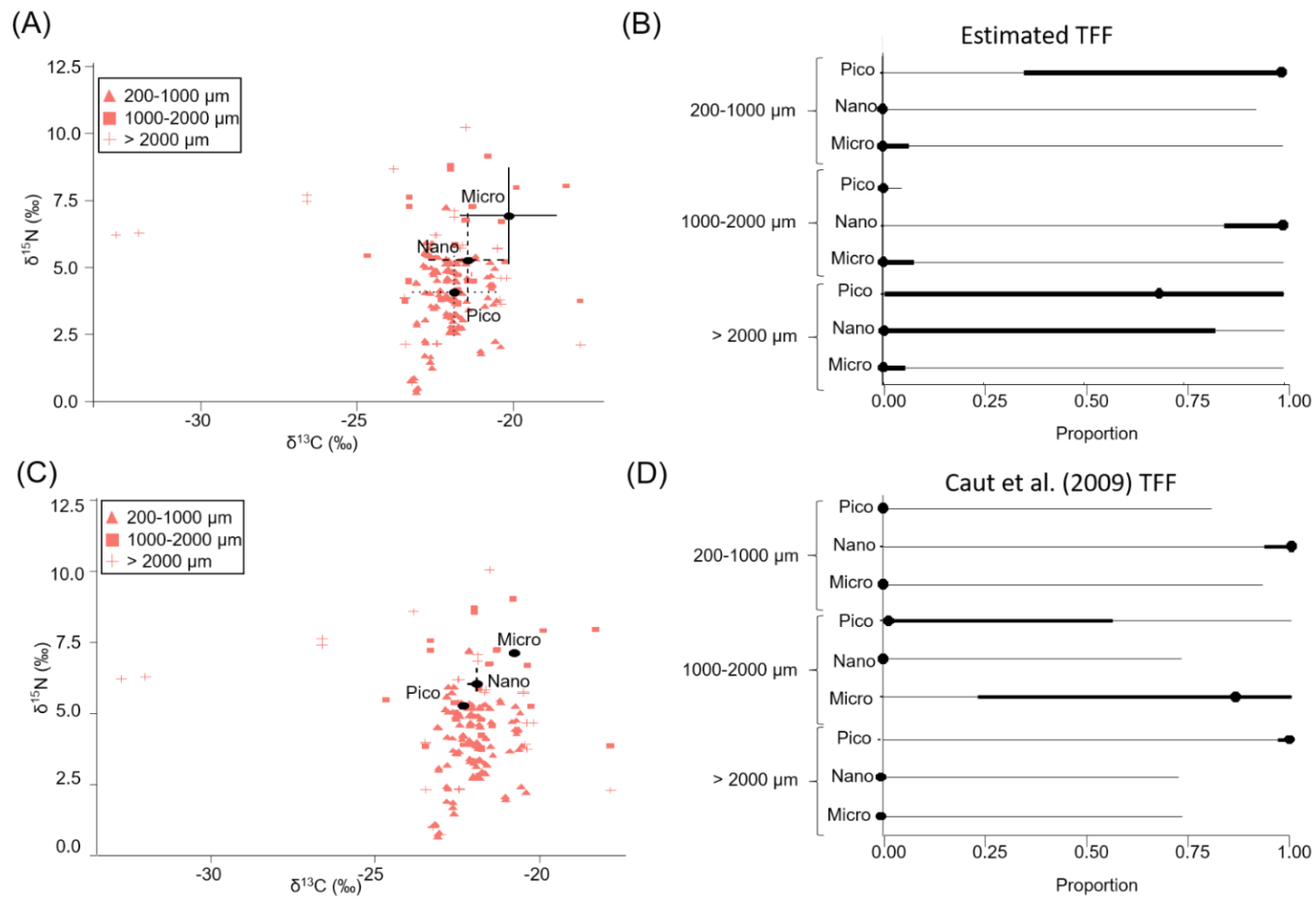


Fig. S6. Results of the mixing model: (A) & (C) Isospace plot of mixture points (pink) and mean and standard deviations of sources, and (B) & (D) Proportion estimates from three POM size class to zooplankton size fractions mixture model: posterior medians (points), 50% credible intervals (thick lines), and 90% credible intervals (thin lines). Data from October to May 2018 were used. TFFs values calculated in the present study (A and B, model 4 in Table S2) and TFFs estimated by the method of Caut et al. (2009) (C and D, model 3 in Table S2) were also used.

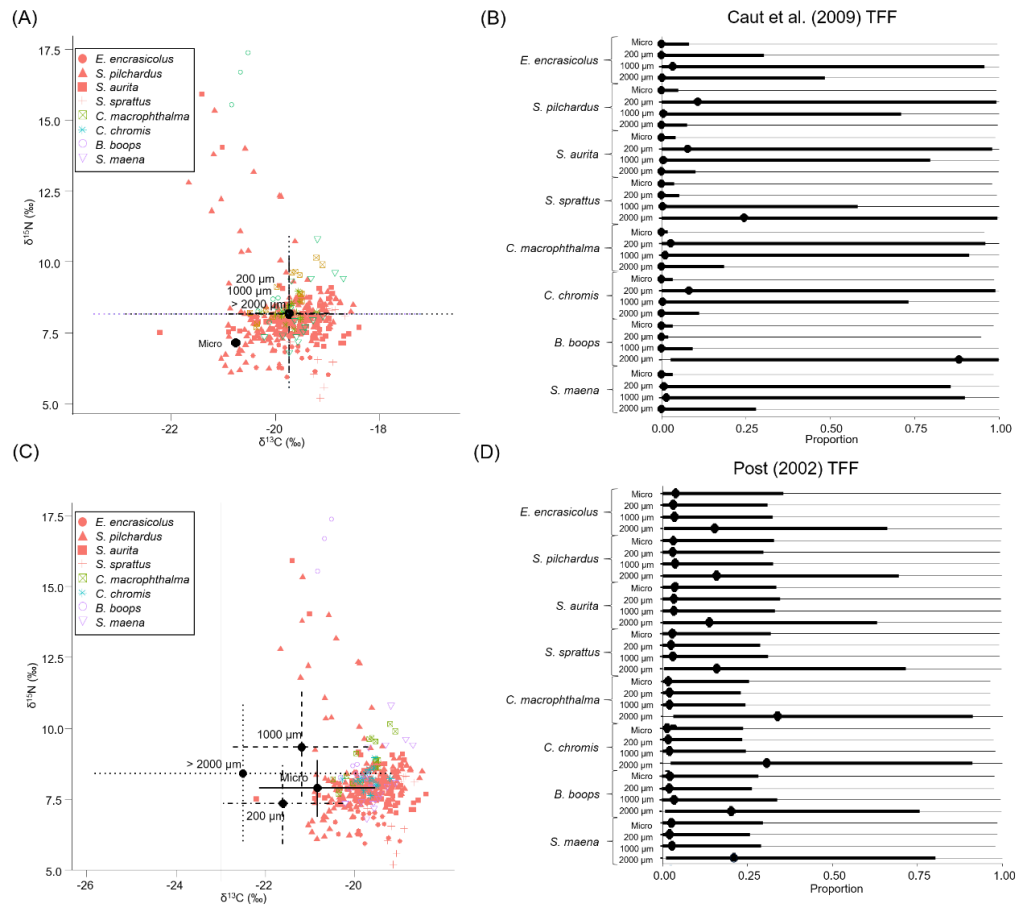


Fig. S7. Results of the mixing model: (A) & (C) Isospace plot of mixture points (pink) and mean and standard deviations of sources, and (B) & (D) Proportion estimates from micro-POM and three zooplankton size fractions to the diet of planktivorous fish species mixture model: posterior medians (points), 50% credible intervals (thick lines), and

90% credible intervals (thin lines). Data from October to May 2018 were used. TFFs used were estimated by the method of Caut et al. (2009) (A and B, model 5 in Table S2) and values from Post et al. (2002) (C and D, model 6 in Table S2) were also used.

References

- Allredge AL (1972) Abandoned Larvacean Houses: A Unique Food Source in the Pelagic Environment. *Science* 177:885–887
- Anger K (2001) *The biology of decapod Crustacean larvae*, 1st edn. A.A. Balkema, Lisse, The Netherlands
- Arapov J, Ezgeta D, Peharda M (2010) Bivalve feeding — how and what they eat? *Ribarstvo* 68:105–116
- Arcos F, Fleminger A (1986) Distribution of filter-feeding calanoid copepods in the Eastern Equatorial Pacific.
- Bowman TE (1978) Revision of the pelagic amphipod genus *Primno* (Hyperiiidea: Phrosinidae). In: *Smithsonian Contributions to Zoology*. pp 1–23
- Bowman TE (1973) Pelagic amphipods of the genus *Hyperia* and closely related genera (Hyperiiidea: Hyperiidae). *Smithson Contrib Zool* 1–76. <https://doi.org/doi.org/10.5479/si.00810282.136>
- Broglio E, Saiz E, Calbet A, et al (2004) Trophic impact and prey selection by crustacean zooplankton on the microbial communities of an oligotrophic coastal area (NW Mediterranean Sea). *Aquatic Microbial Ecology* 35:65–78. <https://doi.org/10.3354/ame035065>
- Caut S, Angulo E, Courchamp F (2009) Variation in discrimination factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. *J Appl Ecol* 46:443–453. <https://doi.org/10.1111/j.1365-2664.2009.01620.x>
- Chen C-T, Carlotti F, Harmelin-Vivien M, et al (2021) Temporal variation in prey selection by adult European sardine (*Sardina pilchardus*) in the NW Mediterranean Sea. *Prog Oceanogr* 196:102617. <https://doi.org/10.1016/j.pocean.2021.102617>
- Chen C-T, Carlotti F, Harmelin-Vivien M, et al (2022) Diet and trophic interactions of Mediterranean planktivorous fishes. *Mar Biol* 169:119. <https://doi.org/10.1007/s00227-022-04103-1>
- Cohen AC, Oakley TH (2017) Collecting and processing marine ostracods. *Journal of Crustacean Biology* 37:347–352. <https://doi.org/10.1093/jcobiol/rux027>
- Conley KR, Lombard F, Sutherland KR (2018) Mammoth grazers on the ocean's minuteness: a review of selective feeding using mucous meshes. *Proceedings of the Royal Society B: Biological Sciences* 285:20180056. <https://doi.org/10.1098/rspb.2018.0056>
- Décima M, Stukel MR, López-López L, Landry MR (2019) The unique ecological role of pyrosomes in the Eastern Tropical Pacific. *Limnology and Oceanography* 64:728–743. <https://doi.org/10.1002/lno.11071>

- Diebel CE (1988) Observations on the Anatomy and Behavior of *Phronima sedentaria* (Forskål) (Amphipoda: Hyperiidea). *J Crustacean Biol* 8:79–90. <https://doi.org/10.2307/1548433>
- Gaonkar CA, Anil AC (2010) What do barnacle larvae feed on? Implications in biofouling ecology. *J Mar Biol Ass* 90:1241–1247. <https://doi.org/10.1017/S0025315409991238>
- González HE, Smetacek V (1994) The possible role of the cyclopoid copepod *Oithona* in retarding vertical flux of zooplankton faecal material. *Mar Ecol Prog Ser* 113:233–246. <https://doi.org/10.3354/meps113233>
- Howes EL, Bednaršek N, Büdenbender J, et al (2014) Sink and swim: a status review of thecosome pteropod culture techniques. *Journal of Plankton Research* 36:299–315. <https://doi.org/10.1093/plankt/fbu002>
- Katechakis A, Stibor H (2004) Feeding selectivities of the marine cladocerans *Penilia avirostris*, *Podon intermedius* and *Evadne nordmanni*. *Marine Biology* 145:529–539. <https://doi.org/10.1007/s00227-004-1347-1>
- Kehayias G (1996) The diets of the chaetognaths *Sagitta enflata*, *S. serratodentata atlantica* and *S. bipunctata* at different seasons in Eastern Mediterranean coastal waters. *ICES J Mar Sci* 53:837–846. <https://doi.org/10.1006/jmsc.1996.0105>
- Kouwenberg JHM (1994) Copepod distribution in relation to seasonal hydrographics and spatial structure in the North-western Mediterranean (Golfe du Lion). *Estuarine, Coastal and Shelf Science* 38:69–90. <https://doi.org/10.1006/ecss.1994.1005>
- Maar M, Visser A, Nielsen T, et al (2006) Turbulence and feeding behaviour affect the vertical distributions of *Oithona similis* and *Microsetella norvegica*. <https://doi.org/10.3354/MEPS313157>
- Mauchline J (1998) The biology of calanoid copepods. In: Blaxter JHS, Southward AJ, Tyler PA (eds) *Advances in Marine Biology*. Academic Press, San Diego, USA, pp 245–292
- Ohtsuka S, Kubo N, Okada M, Gushima K (1993) Attachment and feeding of pelagic copepods on larvacean houses. *J Oceanogr* 49:115–120. <https://doi.org/10.1007/BF02234012>
- Ohtsuka S, Onbé T (1991) Relationship between mouthpart structures and in situ feeding habits of species of the family Pontellidae (Copepoda: Calanoida). *Mar Biol* 111:213–225. <https://doi.org/10.1007/BF01319703>
- Pakhomov EA, Henschke N, Hunt BPV, et al (2019) Utility of salps as a baseline proxy for food web studies. *Journal of Plankton Research* 41:3–11. <https://doi.org/10.1093/plankt/fby051>
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:16. <https://doi.org/10.2307/3071875>

- Purcell JE (1981) Dietary composition and diel feeding patterns of epipelagic siphonophores. *Mar Biol* 65:83–90. <https://doi.org/10.1007/BF00397071>
- Razouls C, Bovée F, Kouwenberg J, Desreumaux D (2005) Biodiversity of marine planktonic copepods (morphology, geographic distribution and biological data). Sorbonne University, CNRS. In: *Marine Planktonic Copepods*. Available at <https://copepodes.obs-banyuls.fr/en> [Accessed February 10, 2023]
- Sogawa S, Sugisaki H, Tadokoro K, et al (2017) Feeding habits of six species of euphausiids (Decapoda: Euphausiacea) in the northwestern Pacific Ocean determined by carbon and nitrogen stable isotope ratios. *Journal of Crustacean Biology* 37:29–36. <https://doi.org/10.1093/jcbiol/ruw014>
- Steinberg DK, Silver MW, Pilskaln CH, et al (1994) Midwater zooplankton communities on pelagic detritus (giant larvacean houses) in Monterey Bay, California. *Limnology and Oceanography* 39:1606–1620. <https://doi.org/10.4319/lo.1994.39.7.1606>
- Swandling K, Richardson A, Slotwinski A, et al (2011) *Australian Marine Zooplankton: a taxonomic guide and atlas*. <https://www.imas.utas.edu.au/zooplankton>. Accessed 30 Jun 2021
- Takahashi K, Ichikawa T, Saito H, et al (2013) Sapphirinid copepods as predators of doliolids: Their role in doliolid mortality and sinking flux. *Limnol Oceanogr* 58:1972–1984. <https://doi.org/10.4319/lo.2013.58.6.1972>
- Turner JT (1986) Zooplankton feeding ecology: contents of fecal pellets of the cyclopoid copepods *Oncaea venusta*, *Corycaeus amazonicus*, *Oithona plumifera*, and *O. simplex* from the Northern Gulf of Mexico. *Mar Biol* 7:289–302. <https://doi.org/10.1111/j.1439-0485.1986.tb00165.x>
- Turner JT (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zool Stud* 43:255–266. <https://doi.org/10.1.1.510.1028>
- Turner JT, Tester PA, Conley WJ (1984) Zooplankton feeding ecology: Predation by the marine cyclopoid copepod *Corycaeus amazonicus* F. Dahl upon natural prey. *J Exp Mar Biol Ecol* 84:191–202. [https://doi.org/10.1016/0022-0981\(84\)90212-0](https://doi.org/10.1016/0022-0981(84)90212-0)
- Wickstead JH (1962) Food and feeding in pelagic copepods. *Proc Zool Soc Lond* 139:545–555. <https://doi.org/10.1111/j.1469-7998.1962.tb01593.x>
- Yamaguchi A, Watanabe Y, Ishida H, et al (2002) Community and trophic structures of pelagic copepods down to greater depths in the western subarctic Pacific (WEST-COSMIC). *Deep-Sea Res Pt I* 49:1007–1025. [https://doi.org/10.1016/S0967-0637\(02\)00008-0](https://doi.org/10.1016/S0967-0637(02)00008-0)