



**HAL**  
open science

## Spatial variations of biochemical content and stable isotope ratios of size-fractionated plankton in the Mediterranean Sea (MERITE-HIPPOCAMPE campaign)

Javier Angel Tesán-Onrubia, Marc Tedetti, François Carlotti, Melissa Tenaille, Loic Guilloux, Marc Pagano, Benoit Lebreton, Gaël Guillou, Pamela Fierro-González, Catherine Guigue, et al.

### ► To cite this version:

Javier Angel Tesán-Onrubia, Marc Tedetti, François Carlotti, Melissa Tenaille, Loic Guilloux, et al.. Spatial variations of biochemical content and stable isotope ratios of size-fractionated plankton in the Mediterranean Sea (MERITE-HIPPOCAMPE campaign). *Marine Pollution Bulletin*, 2023, 189, pp.114787. 10.1016/j.marpolbul.2023.114787 . hal-04016417

**HAL Id: hal-04016417**

**<https://hal.science/hal-04016417v1>**

Submitted on 6 Mar 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 **Spatial variations of biochemical content and stable isotope ratios of size-fractionated**  
2 **plankton in the Mediterranean Sea (MERITE-HIPPOCAMPE campaign)**

3

4 Javier Angel Tesán-Onrubia<sup>a\*</sup>, Marc Tedetti<sup>a</sup>, François Carlotti<sup>a</sup>, Melissa Tenaille<sup>a</sup>, Loïc  
5 Guilloux<sup>a</sup>, Marc Pagano<sup>a</sup>, Benoit Lebreton<sup>b</sup>, Gaël Guillou<sup>b</sup>, Pamela Fierro-González<sup>a</sup>,  
6 Catherine Guigue<sup>a</sup>, Sandrine Chifflet<sup>a</sup>, Théo Garcia<sup>a</sup>, Ismail Boudriga<sup>c</sup>, Malika Belhassen<sup>c</sup>,  
7 Amel Bellaaj Zouari<sup>c</sup>, Daniela Bănar<sup>a\*</sup>

8

9 <sup>a</sup> Aix Marseille Univ., Université de Toulon, CNRS, IRD, MIO UM 110, 13288, Marseille,  
10 France

11 <sup>b</sup> UMR 7266 Littoral Environnement et Sociétés (CNRS - La Rochelle Université), La  
12 Rochelle, France

13 <sup>c</sup> Institut National des Sciences et Technologies de la Mer (INSTM), 28, rue 2 mars 1934,  
14 24 Salammbô 2025, Tunisia

15

16 \* Correspondence:

17 Javier Angel Tesán-Onrubia; [javier.tesan@mio.osupytheas.fr](mailto:javier.tesan@mio.osupytheas.fr)

18 Daniela Bănar; [daniela.banaru@mio.osupytheas.fr](mailto:daniela.banaru@mio.osupytheas.fr)

19

20 Revised version for submission to Marine Pollution Bulletin – Special issue “Plankton and  
21 Contaminants in the Mediterranean Sea: Biological pump and interactions from regional to  
22 global approaches”

23

24 **Abstract**

25 Plankton represents the main source of carbon in marine ecosystems and is consequently an  
26 important gateway for contaminants into the marine food webs. During the MERITE–  
27 HIPPOCAMPE campaign in the Mediterranean Sea (April-May 2019), plankton was sampled  
28 from pumping and net tows at 10 stations from the French coast to the Gulf of Gabès  
29 (Tunisia) to obtain different size fractions in contrasted regions. This study combines various  
30 approaches, including biochemical analyses, analyses of stable isotope ratios ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ),  
31 cytometry analyses and mixing models (MixSiar) on size-fractions of phyto- and zooplankton  
32 from 0.7 to  $> 2000 \mu\text{m}$ . Pico- and nanoplankton represented a large energetic resource at the  
33 base of pelagic food webs. Proteins, lipids, and stable isotope ratios increased with size in  
34 zooplankton and were higher than phytoplankton. Stable isotope ratios suggest different  
35 sources of carbon and nutrients at the base of the planktonic food webs depending on the  
36 coast and the offshore area. In addition, a link between productivity and trophic pathways was  
37 shown, with high trophic levels and low zooplankton biomass recorded in the offshore area.  
38 The results of our study highlight spatial variations of the trophic structure within the  
39 plankton size-fractions and will contribute to assess the role of the plankton as a biological  
40 pump of contaminants.

41

42 **Keywords:** Phytoplankton, zooplankton,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , plankton trophic structure, contaminants

43

## 44 1. Introduction

45

46 Phyto- and zooplankton play a central role in the functioning of marine ecosystems by  
47 producing, transforming and transferring the organic matter up to planktivorous species  
48 (Bănaru et al., 2019; Chen et al., 2022). Plankton thus represents the main source of carbon  
49 fueling the marine food webs (Bănaru et al., 2013; Cresson et al., 2020). Phyto- and  
50 zooplankton are composed of a myriad of organisms of great diversity in terms of size,  
51 metabolism, physiology, and diet that are governed by different trophic pathways, and  
52 complex ecological interactions. As taxonomic composition strongly differs between  
53 planktonic size-fractions, a size-based approach has become widely used to study the  
54 structure and functioning of the planktonic compartment (Rau et al., 1990; Rolff, 2000;  
55 Carlotti et al., 2008; Hunt et al., 2017). In pelagic food webs, body size determines rates of  
56 production (Banse and Mosher, 1980), energy requirements (Brown et al., 2004), mortality  
57 rates (Hirst and Kiørboe, 2002) and predator-prey interactions (Cohen et al., 1993;  
58 Ljungström et al., 2020). The biochemical composition of the different plankton size-fractions  
59 provides information on their energetic content, which may influence prey selection (Carlotti  
60 et al., 2008, Harmelin-Vivien et al., 2019; Chen et al., 2019, 2021, 2022), while the carbon  
61 and nitrogen isotopic ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values) of the plankton size-fractions provide  
62 information on the fluxes of organic matter within the planktonic food webs (Peterson et al.,  
63 1985; Cabana and Rasmussen, 1994; Vander Zanden and Rasmussen, 2001).

64 Besides its central role in the functioning of marine ecosystems, plankton is now recognized  
65 as a key gateway of inorganic and organic contaminants into the marine food web (Tao et al.,  
66 2018; Chauvelon et al., 2019; Tedetti et al., 2023). Phytoplankton is exposed to contaminants  
67 *via* water. Bioconcentration of contaminants in phytoplankton is driven mainly by partition  
68 equilibrium processes between the cells and the surrounding water (Frouin et al., 2013). For a  
69 given species or cell size of phytoplankton, and a given physico-chemical habitat  
70 (temperature, organic carbon content, etc.), the bioconcentration factors of organic  
71 contaminants may be directly correlated with their octanol-water partitioning coefficients ( $\log$   
72  $K_{ow}$ ), i.e., their degree of lipophilicity/hydrophobicity (Frouin et al., 2013). Correspondingly,  
73 the bioconcentration of a given contaminant has been shown to increase with decreasing size  
74 of phytoplankton (Fan and Reinfelder, 2003). Bioaccumulation processes in zooplankton are  
75 highly complex due to the entry of contaminants by both the water aqueous phase  
76 (bioconcentration) and diet, the trophic interactions and/or transfers between phytoplankton  
77 and various zooplankton, and the contaminant removal processes used by these organisms

78 (Tiano et al., 2014; Alekseenko et al., 2018; Tao et al., 2018). Biomagnification may also  
79 occur between the low and high trophic level organisms in the marine food webs (Chouvelon  
80 et al., 2019).

81 Therefore, the uptake, accumulation, and transfer of contaminants within the planktonic food  
82 webs may be strongly influenced by its characteristics such as the size-fraction distribution,  
83 the biochemical/energetic content (Hennig, 1986; Mason et al., 1995; Wu and Wang, 2011),  
84 the trophic interactions and the fluxes of organic matter (Peterson et al., 1985; Cabana and  
85 Rasmussen, 1994; Vander Zanden and Rasmussen, 2001). Characterizing the content of  
86 phyto-, and zooplankton in terms of size-fraction, biochemical/energetic content and stable  
87 isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) may thus provide key information on the structure, functioning,  
88 and trophic interactions of this planktonic food webs, but also on the capacity of accumulation  
89 and transfer of organic and inorganic contaminants within this planktonic network and  
90 potentially their transfer to higher trophic levels.

91 The Mediterranean Sea has a high diversity of planktonic and exploited resources, and  
92 contrasted biogeographical regions impacted by climate change and human activities (Durrieu  
93 de Madron et al., 2011; Mayot et al., 2017). As the Mediterranean Sea is mainly oligotrophic,  
94 its autotrophic biomass is dominated by small-size pico- and nanophytoplankton groups  
95 (Leblanc et al., 2018; Boudriga et al., 2022). These groups play a key role in the biomass and  
96 energy transfer to zooplankton (Bănaru et al., 2014; Hunt et al., 2017; Leblanc et al., 2018).  
97 However, coastal areas impacted by riverine and urban inputs may locally be more enriched  
98 and sometimes can even be characterized by higher phytoplankton biomass dominated by  
99 larger cells such as dinobionts and diatoms (Harmelin-Vivien et al., 2008). Champalbert  
100 (1996) highlighted spatial differences in the zooplankton diversity and biomass, with a lower  
101 diversity and a higher biomass in coastal waters relative to offshore areas. The Mediterranean  
102 Sea is also strongly exposed to chemical contamination due to the intensive human activities  
103 in the bordering countries, its semi-closed status that limits the dilution of contaminants, and  
104 the relatively short ventilation and residence times its waters (Durrieu de Madron et al., 2011;  
105 Tedetti et al., 2023).

106 In this context, the aims of this work, carried out in the frame of the MERITE-HIPPOCAMPE  
107 campaign, were: 1) to investigate the structure and functioning (in terms of trophic  
108 interactions and organic matter fluxes) of the planktonic food webs of the Mediterranean Sea  
109 through the characterization of the biomass, biochemical/energetic content and  $\delta^{13}\text{C}/\delta^{15}\text{N}$   
110 ratios of several size-fractions of phyto- and zooplankton ranging from 0.7 to  $> 2000 \mu\text{m}$ , 2)  
111 to explore variations in size-spectra and spatial variations of these characteristics

112 (biochemical/energetic content and  $\delta^{13}\text{C}/\delta^{15}\text{N}$  ratios), and relate these variations to their  
113 composition (*via* cytometry and imagery analyses) and also to the specificities of the studied  
114 areas, and 3) to discuss the implications of these findings regarding the accumulation and  
115 transfer of contaminants in the planktonic food webs.

116 To our knowledge, this work represents the first study to use a wide variety of approaches,  
117 and methodologies, such as biochemical analyses (proteins, carbohydrates, lipids and energy),  
118 analyses of isotopic ratios ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ), cytometry analyses and mixing models (MixSiar) on  
119 fine size-fractions of phyto- and zooplankton ranging from 0.7 to > 2000  $\mu\text{m}$  for the purpose  
120 of studying plankton food webs. The use of innovative sampling techniques, such as the  
121 deployment of *in situ* pumps equipped with a sequential filtration system, or the towing of a  
122 MultiNet device in chlorophyll maximum layer (CML), enabled us to obtain large amounts of  
123 size fractionated phyto- and zooplankton, material rarely acquired together.

124

## 125 **2. Material and methods**

126

### 127 **2.1. Study area and sampling**

128 The MERITE-HIPPOCAMPE cruise was conducted in the Mediterranean Sea in spring 2019,  
129 from April 13 to May 14, onboard the R/V *Antea* (Tedetti and Tronczynski, 2019; Tedetti et  
130 al., 2023). Ten stations were sampled from the French coast (La Seyne-sur-Mer, Northwestern  
131 Mediterranean) to the Gulf of Gabès in Tunisia (Southeastern Mediterranean) in coastal and  
132 offshore locations, including the Gulf of Lion, the Ligurian and Algerian consensus regions,  
133 the North Balearic Front and Sicilian Channel areas, and the gulfs of Hammamet and Gabès,  
134 which presented different hydrological, biogeochemical and bloom conditions, and different  
135 levels of anthropogenic pressures (Fig. 1, Table S1). Phytoplankton and zooplankton were  
136 sampled at each station at the CML, during spring bloom (April to May), when maximum  
137 primary and secondary production occurs (Liénart et al., 2018; Tedetti et al., 2023).

138 Suspended particulate matter (SPM) was collected and filtered using McLane Large Volume  
139 Water Transfer System Samplers (WTS6-142LV, 4–8 L  $\text{min}^{-1}$ ), hereinafter referred to as  
140 McLane *in situ* pumps. One pump was mounted with a regular 142-mm filter-holder holding  
141 one 142-mm-diameter filter. This pump was equipped with a  $\sim 0.7\text{-}\mu\text{m}$ -pore-size pre-  
142 combusted pre-weighed GF/F filter (Whatman) and covered with a  $60\text{-}\mu\text{m}$ -pore-size  
143 homemade sock-type pre-filter so that the filtered particle size-fraction was 0.7–60  $\mu\text{m}$ . A  
144 second McLane *in situ* pump was mounted with a mini-Multiple Unit Large Volume *in situ*  
145 Filtration System (MULVFS) filter holder composed of baffle tubes on the top followed by

146 successive baffle and filter support plates, for sequential filtration with three different filters  
147 (142-mm diameter) (Bishop et al., 2012). The filter series used were one ~ 0.7- $\mu\text{m}$ -pore-size  
148 pre-combusted (450 °C, 6 h), pre-weighed GF/F filter, one 2.7- $\mu\text{m}$ -pore-size pre-combusted,  
149 pre-weighed GF/D filter (Whatman), and one 20- $\mu\text{m}$ -pore-size pre-cleaned (HCl 0.05% v/v)  
150 pre-weighed home-made Nylon filter so that the filtered particle size fractions were 0.7–2.7,  
151 2.7–20, and > 20  $\mu\text{m}$  (hereafter labeled 20–60  $\mu\text{m}$ ). The pumps were deployed in the CML  
152 between 40 and 60 min. The volumes of filtered seawater ranged between 169 and 300 L  
153 depending on the stations. After pump deployment, filters were 'dried' by connecting the filter  
154 holder to a vacuum pump, stored in pre-combusted (450 °C, 6 h) aluminum sheets, and  
155 conserved at –20 °C and then freeze-dried. Then, punches with a known surface area were  
156 made into filters to obtain subsamples for the different analyses.

157 Zooplankton was sampled using a Multinet Plankton Sampler (Midi type with 0.25-m<sup>2</sup>  
158 aperture, Hydro-Bios), referred to hereafter as 'MultiNet', towed horizontally in the CML. The  
159 MultiNet position was maintained stable at the defined layer by means of a V-fin deflector  
160 and controlled vessel speed (2.5 knots), and real-time control of its position from the onboard  
161 desk-unit. The MultiNet was mounted with five individual (exchangeable) 2.5-m-long nylon  
162 nets with a mesh size of 60- $\mu\text{m}$  and cod ends of the same mesh size. The MultiNet frame was  
163 equipped with various sensors: two Hydro-Bios flowmeters (one at the mouth and the other  
164 on the side) to assess the volume of water filtered by the nets, a CTD sensor and a total  
165 chlorophyll *a* (TChl*a*) fluorometer. Connected to the onboard desk unit *via* the electro-  
166 mechanical cable, these captors inform on *in situ* depth, TChl*a* concentration, filtered volume  
167 and flow rate, allowing the operator to decide to open and close the nets. Nets were closed  
168 when the flow rate reached a threshold value to limit clogging. Filtered volumes for each net  
169 reached up to 185 m<sup>3</sup>. Once the five nets were filled, the MultiNet was hauled back on board,  
170 and the five cod ends linked by a helicoidal bucket connector were carefully recovered. The  
171 fifth net remained open until the end of the operation, filtering the layer between the CML  
172 and the surface. The cod ends were rinsed out with local seawater, and their content  
173 transferred to pre-cleaned 10-L PFA bottles. The MultiNet was then returned to the water.

174 This operation was repeated several times to get sufficient amounts of plankton for all  
175 possible further contaminant content analyses (Tedetti et al., 2023). In the clean onboard  
176 container lab, plankton collected in PFA bottles was then size-fractionated through a column  
177 of five stainless steel sieves (60, 200, 500, 1000 and 2000  $\mu\text{m}$  mesh-size) by wet-sieving with  
178 seawater previously filtered onto GF/F filters and stored in stainless steel jerrycans to obtain  
179 the following size-fractions: 60–200, 200–500, 500–1000, 1000–2000 and > 2000  $\mu\text{m}$ .

180 Samples were stored in pre-combusted (450 °C, 6 h) Pyrex bottles, conserved at –20 °C and  
181 freeze-dried. Large fractions (> 2000 µm) were most likely under-sampled compared to  
182 smaller fractions. These fractions should be carefully treated because they represent a  
183 relatively low – and difficult to estimate – biomass, form colonies, and may actively evade  
184 capture by swimming. The detailed methods to determine zooplankton group composition  
185 analysis presented in this paper and related to our results are detailed in Fierro-González et al.  
186 (2023).

187

## 188 **2.2. Analyses**

189

### 190 **2.2.1. Particulate organic carbon and nitrogen**

191 Samples (i.e., 22-mm diameter filter or 1 mg dry weight DW zooplankton) were leached with  
192 100 µL of sulfuric acid (H<sub>2</sub>SO<sub>4</sub> 0.5 mol L<sup>-1</sup>) to remove any inorganic carbon. Samples were  
193 then stored in 25 mL Schott® glass bottles for subsequent analyses. Filter blanks were  
194 conditioned with 1 mL of ethanol and with 600 mL of 0.2-µm filtered seawater.  
195 Determination of particulate organic carbon (POC) and nitrogen (PON) concentrations were  
196 carried out simultaneously on the same sample using the persulfate wet-oxidation procedure  
197 according to Raimbault et al. (1999).

198

### 199 **2.2.2. Suspended particulate matter and plankton dry weight**

200 Suspended particulate matter dry weight (SPM<sub>DW</sub>) was measured in the 0.7–60 and 20–60-µm  
201 filters gravimetrically by weighing the tare, wet and dry filters with a precision balance (d =  
202 0.01 mg). Briefly, we subtracted from the dry filter the tare and the salts associated with the  
203 evaporated water, considering a salinity of 38. Tests conducted with filtered seawater  
204 evidenced a higher mass after drying than the salt present in water, and most likely related to  
205 the highly hygroscopic characteristics of salts. A ratio of 1.2 between the observed mass and  
206 the theoretical mass associated with salt was applied to correct the water bonded to salt. When  
207 biomasses were low, as for 0.7–2.7 and 2.7–20-µm filters, high uncertainty in weighing  
208 increased the margin of error. SPM<sub>DW</sub> in the 0.7–2.7 and 2.7–20-µm filters were thus  
209 estimated by multiplying their relative fraction of POC by the biomass measured  
210 gravimetrically in the 0.7–60-µm size-fraction. POC can be employed as a proxy of SPM<sub>DW</sub>,  
211 based on the correlations assessed by Trimble and Baskaran (2005). SPM<sub>DW</sub> at the CML is  
212 mainly composed of POC (around 50%) but also contains biogenic silica, calcium carbonate  
213 and lithogenic matter (Bishop et al., 1977; Krasakopoulou and Karageorgis, 2005). On the



214 basis of these observations, relative POC was used to assess the contribution of the different  
215 size-fractions to the total biomass. Plankton dry weight (Plankton<sub>DW</sub>) of size fractions 60–  
216 200, 200–500, 500–1000, 1000–2000, and > 2000 µm were determined after drying samples  
217 on pre-weighed GF/F filters (60 °C, 24 h) and then re-weighed with a microbalance, taking  
218 into consideration the volumes of water filtered by the MultiNet (Fierro-González et al.,  
219 2023).

220

### 221 **2.2.3. Biochemical and energy content**

222 Biochemical compounds (proteins, carbohydrates, and lipids) were extracted in triplicate from  
223 freeze-dried filters and zooplankton samples and expressed in µg mg<sup>-1</sup> DW. Absorbance of  
224 the extracts was then measured at different wavelengths using a spectrophotometer  
225 (Shimadzu, UV-1280). Briefly, proteins were extracted using a Folin phenol reagent  
226 following the Lowry et al. (1951) method and measured at 700 nm. Carbohydrates were  
227 extracted using the phenol-sulfuric acid reaction described in Dubois et al. (1956) and  
228 measured at 490 nm. Finally, lipids were extracted with a monophasic methanol-  
229 dichloromethane solution (Bligh and Dyer, 1959) and measured at 360 nm. Ashes and  
230 residual organic compounds not recovered by these standard biochemical assays (chitin for  
231 example) may be estimated by subtracting the weight of the biochemical compounds from the  
232 total dry weight, but were not presented in this study. The energy content ( $E_i$ ) was estimated  
233 by summing the three biochemical compounds after converting them into energetic units  
234 (21.4 kJ g<sup>-1</sup> for proteins, 17.2 kJ g<sup>-1</sup> for carbohydrates and 35.6 kJ g<sup>-1</sup> for lipids) (Postel et al.,  
235 2000). The plankton energy amount ( $E_T$ ) provided by plankton per cubic meter per station at  
236 CML (kJ m<sup>-3</sup>) was calculated for all the plankton size-fractions by multiplying the SPM<sub>DW</sub> or  
237 the biomass ( $B_i$  in mg DW m<sup>-3</sup>) of each size-fraction at a given station by its energy content  
238 ( $E_i$  in kJ mg<sup>-1</sup> DW) and the sum of  $E_T$  of all size-fractions represents the plankton total energy  
239 amount,  $E_{TS}$ :  $E_T = B_i \times E_i$ .

240

### 241 **2.2.4. Stable isotope analyses ( $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ )**

242 The SPM<sub>DW</sub> collected on filters was scraped off with a scalpel. Zooplankton samples were  
243 ground to a fine powder with an agate mortar and pestle. Presence of carbonates on samples  
244 can bias the measurement of  $\delta^{13}\text{C}$  values as they are enriched in <sup>13</sup>C compared to organic  
245 matter (Pinnegar and Polunin, 1999). Therefore, samples were acidified prior to the  
246 measurement of  $\delta^{13}\text{C}$  values of the particulate organic matter (POM). Samples were acidified  
247 using HCl 1% and immediately rinsed with MilliQ-water. Measurements of  $\delta^{15}\text{N}$  values of the

248 POM were carried out on raw samples. For zooplankton, approximately 0.5 mg of powder  
249 was weighed into a tin cup (8 × 5 mm) using a precision balance (d = 0.01 mg). Carbon and  
250 nitrogen stable isotope analyses were performed using a continuous-flow isotope-ratio mass  
251 spectrometer (Delta V Plus, Thermo Scientific) with a ConFlo IV interface coupled to an  
252 elemental analyzer (EA Isolink, Thermo Scientific). Analyses were conducted at the Littoral,  
253 Environment and Societies Joint Research Unit stable isotope facility (CNRS - University of  
254 La Rochelle, France). The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values are expressed in  $\delta$  notation as deviations from  
255 standards (Vienna Pee Dee Belemnite for  $\delta^{13}\text{C}$  and  $\text{N}_2$  in air for  $\delta^{15}\text{N}$ ), in ‰, according to the  
256 formula:

$$\delta X_{\text{sample}} = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000$$

257  
258 where X is  $^{13}\text{C}$  or  $^{15}\text{N}$ ,  $R_{\text{sample}}$  is the isotopic ratio of the sample and  $R_{\text{standard}}$  is the isotopic ratio  
259 of the standard. Calibration was carried out using reference materials (USGS-61, -62, -63 for  
260 both carbon and nitrogen). The analytical precision of the measurements was < 0.10‰ for  
261 carbon and nitrogen based on analyses of USGS-61 and USGS-63 used as laboratory internal  
262 standards.

263

#### 264 **2.2.5. Cytometry and imagery analyses**

265 For flow cytometry analyses, seawater was sampled with Niskin and Go-Flo bottles at the  
266 CML. Seawater was filtered through a silk mesh filter with 100- $\mu\text{m}$  pore size and then  
267 immediately fixed with a 2% paraformaldehyde solution. Samples were incubated for 15 min  
268 at 4 °C in the dark and then stored in liquid nitrogen onboard and at -80 °C in the laboratory  
269 until analysis. The autotrophic pico- and nanoplankton were analyzed using a CyFlow®Space  
270 flow cytometer (SysmexPartec) equipped with a blue diode pumped solid-state laser (20 mW;  
271 488 nm) and a red diode laser (25 mW; 638 nm). Seawater samples were thawed in the dark,  
272 filtered through a nylon mesh filter with a porosity of 30  $\mu\text{m}$  (CellTrics®, SysmexPartec), and  
273 mixed with flow check high-intensity beads of 2- $\mu\text{m}$  diameter (Polysciences, USA). Cells  
274 were characterized based on their scatter and fluorescence signals (Khammari et al., 2018)  
275 and data were analyzed with the FloMax software (Sysmex Partec), which directly calculates  
276 the cell concentration (cells  $\text{cm}^{-3}$ ) of the resolved cell groups. Carbon biomass of each cell  
277 group was estimated according to Khammari et al., (2020). The contributions of zooplankton,  
278 phytoplankton (microalgae), and detritus components to the total Plankton  $\text{DW}$  were estimated

279 using imagery methods (FlowCAM and ZOOSCAN) according to Fierro-González et al.  
280 (2023).

281

### 282 **2.3. Bayesian mixing model**

283 The contributions of the different size-fractions of phytoplankton (0.7–2.7, 2.7–20 and 20–60  
284 µm) as food resources to zooplankton size-fractions and their confidence intervals were  
285 estimated using a Bayesian mixing model using the R package MIXSIAR (Parnell et al.,  
286 2013; <https://github.com/brianstock/MixSIAR>). This modeling approach incorporates  
287 variability of potential food source isotopic compositions for consumers and of trophic  
288 fractionation factors (TFF) and generates probability distributions of food source  
289 contributions. The consumers (i.e., zooplankton) were grouped in the 60–500, 500–2000, and  
290 > 2000-µm size-fractions based on statistical differences in their isotopic compositions.  
291 Zooplankton size-fractions with similar isotopic compositions were thus considered to  
292 consume the same food resources. Contributions were computed using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values.  
293 As there is no well-established set of TFFs for plankton, we computed mixing model  
294 estimates using the mean TFF values of  $1.70 \pm 0.38$  ‰ for  $\delta^{13}\text{C}$  and  $2.40 \pm 0.26$  ‰ for  $\delta^{15}\text{N}$   
295 (mean  $\pm$  standard error (SE)), as established by Tiselius and Fransson (2016).

296

### 297 **2.4. Trophic level**

298 The trophic level (TL) of consumers was calculated following the equation proposed by Post  
299 (2002):

$$300 \quad \text{TL} = \left( \frac{\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}}{\text{TFF } \delta^{15}\text{N}} \right) + 1$$

301 where  $\delta^{15}\text{N}_{\text{consumer}}$  is the isotopic composition of the consumer,  $\delta^{15}\text{N}_{\text{baseline}}$  is the isotopic  
302 composition of the size-fraction 0.7–2.7 µm considered as baseline with a trophic level of 1  
303 and TFF  $\delta^{15}\text{N}$  was fixed to  $2.40 \pm 0.26$  ‰ (Tiselius and Fransson, 2016). TL of each size  
304 fraction was weighted to its respective biomass per station ( $\text{TL}_B$ ):

$$305 \quad \text{TL}_B = \frac{\sum_i^n (\text{TL}_i * \% \text{Biomass}_i)}{100}$$

306 where  $I$  is represented by each size fraction from 60–200 to > 2000 µm and  $n$  is the number of  
307 size-fractions.

308

## 2.5. Data treatment

The effect of size-fractions and geographical area on the  $SPM_{DW}$ ,  $Plankton_{DW}$ , POC, PON, C/N, carbon biomass of phytoplankton, biochemical composition, energy content, isotopic composition and trophic levels were tested by means of one-way ANOVA or non-parametric Kruskal-Wallis tests after testing for normality and homogeneity of variances, followed by appropriate paired comparison tests, using the software Statistica 12. Spearman's rank order correlation tests were used to assess the significance of the correlations between our results and some environmental variables (Tedetti et al., 2023).

## 3. Results

### 3.1. Plankton dry weight, TChl $a$ , POC, PON and C:N

Significant differences in  $SPM_{DW}$  were observed between the different size-fractions ( $H = 23.2$ ,  $p < 0.0001$ ) (Table 1). When considering all stations, the highest mean  $SPM_{DW}$  was measured in the 2.7–20  $\mu m$  size-fraction ( $0.18 \pm 0.04$  mg DW L $^{-1}$ ,  $n = 10$ ) and the lowest in the 20–60  $\mu m$  fraction ( $0.04 \pm 0.02$  mg DW L $^{-1}$ ,  $n = 10$ ). Generally, these concentrations decreased from coastal stations to offshore stations, except for St9, which exhibited the highest  $SPM_{DW}$  in the 2.7–20  $\mu m$  size-fraction (Table 1). The size-fractions 0.7–2.7 and 2.7–20  $\mu m$  presented the lowest values at St15. The highest  $SPM_{DW}$  in the 20–60- $\mu m$  size-fraction were observed at St17, St19 and St4. TChl $a$  concentrations in the  $> 0.7$ - $\mu m$  fraction ranged from 0.21 (St17) to 1.54  $\mu g$  L $^{-1}$  (St9) with a mean value of  $0.76 \pm 0.14$   $\mu g$  L $^{-1}$  ( $n = 10$ ) (Table 1). The 60–200 and 200–500  $\mu m$  zooplankton size-fractions showed the highest  $Plankton_{DW}$  (Table 1). POC and PON concentrations increased with phytoplankton size with the lowest values in the 0.7–2.7  $\mu m$  size-fraction (11.4 and respectively 2.1  $\mu g$  C L $^{-1}$ ) and the highest ones in the 0.7–60  $\mu m$  size-fraction (42.8 and respectively 6.9  $\mu g$  C L $^{-1}$ ) (Table S2). The lowest POC and PON values were observed at St11 for the 0.7–2.7  $\mu m$  size-fraction and at St2 for the 2.7–20  $\mu m$  size-fraction (Table S2). The C:N ratios in the 0.7 to 60  $\mu m$  size-fractions ranged from 5.7 at St19 to 8.5 at St9. The 0.7–2.7  $\mu m$  size-fraction presented significantly lower C:N ratios than the 2.7–20- $\mu m$  and the 20–60  $\mu m$  size-fractions (Table S2).

### 3.2. Planktonic group composition

342 Different plankton groups contributed to the biomass of the different size-fractions. The size-  
343 fraction 0.7–2.7  $\mu\text{m}$  was on average dominated in biomass by *Synechococcus* spp. (4.6  $\mu\text{g C}$   
344  $\text{L}^{-1}$  or  $\sim 52\%$ ) and picoeukaryotes (4.0  $\mu\text{g C L}^{-1}$  or  $\sim 45\%$ ) (Table S3). The size-fraction 2.7–  
345 20  $\mu\text{m}$  was dominated in biomass by the nanoeukaryotes (20.0  $\mu\text{g C L}^{-1}$   $\sim 88\%$ ) and  
346 represented the highest biomass among size-fractions. The highest cumulated biomass in the  
347 range 0.7–20  $\mu\text{m}$  was found at St1, St9 and St19 (Table S3). POC concentration and the  
348 carbon biomass of phytoplankton size-fractions between 0.7 and 20  $\mu\text{m}$  showed a significant  
349 linear correlation ( $R^2 = 0.66$ ;  $p = 0.018$ ) (Fig. S1). Carbon biomass estimated by flow  
350 cytometry represented around 86% of the POC measured on filters ( $y = 0.86x + 11.86$ ). Total  
351 biomass was dominated by detritus and phytoplankton in the 60–200 and 200–500  $\mu\text{m}$  size-  
352 fractions (68.8 and 59.2%, respectively), which decreased with the increasing size-fractions  
353 (10.5% in the  $> 2000\text{-}\mu\text{m}$  size-fraction) (Table S4). Copepods dominated in the zooplankton  
354 biomass in the 60 to 2000  $\mu\text{m}$  size-fractions (between 54.3% and 91.9%) while crustaceans  
355 and gelatinous dominated the  $> 2000 \mu\text{m}$  size-fraction (Table S4).

356

### 357 **3.3. Biochemical and energy content**

358 The Mediterranean plankton sampled had for all size-fractions and stations combined, except  
359 the 0.7–60- $\mu\text{m}$  fraction, mean dry weight concentrations ( $\pm$  SE) of  $222.6 \pm 6.9 \mu\text{g mg}^{-1}$  DW ( $n$   
360  $= 204$ ) for proteins,  $96.9 \pm 6.5 \mu\text{g mg}^{-1}$  DW ( $n = 203$ ) for carbohydrates,  $35.1 \pm 1.5 \mu\text{g mg}^{-1}$   
361 DW ( $n = 197$ ) for lipids and an  $E_i$  of  $7.7 \pm 0.2 \text{ kJ g}^{-1}$  DW ( $n = 196$ ).

362

#### 363 **3.3.1. Differences between plankton size-fractions**

364 Considering all stations combined, the mean concentration of proteins increased with size and  
365 was significantly higher in large fractions of zooplankton (500–1000 and 1000–2000  $\mu\text{m}$ )  
366 than in small fractions of phytoplankton (0.7–2.7 and 2.7–20  $\mu\text{m}$ ). The highest mean protein  
367 concentration was recorded in the 1000–2000  $\mu\text{m}$  size-fraction and the lowest in the largest ( $>$   
368 2000  $\mu\text{m}$ ) size-fraction (Fig. 2A). The mean concentration in carbohydrates decreased with  
369 size. The concentrations measured in phytoplankton (0.7–60 and 20–60  $\mu\text{m}$ ) were  
370 significantly higher than those of the large zooplankton (1000–2000 and  $> 2000 \mu\text{m}$ ) (Fig.  
371 2B). The mean concentration in lipids was quite homogeneous between size-fractions, with  
372 the highest values measured in the size-fractions 20–60 and 1000–2000  $\mu\text{m}$ , and lowest in the  
373 size-fractions 0.7–2.7 and  $> 2000 \mu\text{m}$  (Fig. 2C). Energy content showed an increasing trend  
374 with size for both phyto- and zooplankton size-fractions. The highest values were measured in

375 the 20–60  $\mu\text{m}$  and 1000–2000  $\mu\text{m}$  size-fractions, respectively, and the lowest in the size-  
376 fractions 0.7–2.7 and  $> 2000 \mu\text{m}$ . (Fig. 2D).

377

### 378 **3.3.2. Differences between stations**

379 To investigate the differences between stations, the size-fractions were grouped in two  
380 fractions: the phytoplankton fraction (fractions between 0.7 and 60  $\mu\text{m}$ ) and the zooplankton  
381 fraction (fractions between 60 and 500  $\mu\text{m}$  that were sampled at all the stations). The highest  
382 mean protein concentrations in phyto- and zooplankton fractions were recorded at St9, St11  
383 and St15, and the lowest at St17 (Fig. 3A, B). The highest mean carbohydrate concentrations  
384 were observed at St9 for the phytoplankton (Fig. 3C). The highest mean lipid concentrations  
385 and energy values for phyto- and zooplankton were measured at St1, St2, St9 and St11, and  
386 the lowest at St3, St4 and St17 (Fig. 3E–H). Overall, greater differences appeared between  
387 stations than between size-fractions for most of these biochemical compounds (Table S5).  
388  $E_{\text{TS}}$  ranged from 1.17  $\text{kJ m}^{-3}$  at St3 to 6.30  $\text{kJ m}^{-3}$  at St9 with a mean value ( $\pm$  SE) of  $2.37 \pm$   
389  $0.49 \text{ kJ m}^{-3}$  ( $n = 10$ ) (Fig. 4). High  $E_{\text{TS}}$  were also observed at coastal stations St1, St4, St17  
390 and St19. The 0.7–2.7 and 2.7–20  $\mu\text{m}$  size-fractions represented the largest energetic  
391 reservoirs with mean values of  $0.65 \pm 0.09 \text{ kJ m}^{-3}$  ( $n = 10$ ) and  $1.16 \pm 0.37 \text{ kJ m}^{-3}$  ( $n = 10$ ),  
392 respectively (Fig. 4). The 200–500- $\mu\text{m}$  fraction represented the largest energy reservoir for  
393 the zooplankton with a mean of 0.164  $\text{kJ m}^{-3}$ . Although the 0.7–2.7 and 2.7–20  $\mu\text{m}$  fractions  
394 had lower  $E_i$  (6.2 and 6.3  $\text{kJ g}^{-1}$  DW, respectively) than those measured in the  $> 60 \mu\text{m}$  size-  
395 fractions (between 7.0 and 9.5  $\text{kJ g}^{-1}$  DW) (Fig. 2), their dry weight was about one order of  
396 magnitude higher (Tables 1 and S2), thus enhancing their major contribution of  
397 phytoplankton to the total plankton energy amount available in the system (Fig. 4).

398

### 399 **3.4. Stable isotope compositions ( $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ )**

400 For all size fractions and stations combined, except the 0.7–60  $\mu\text{m}$  fraction, the plankton  $\delta^{13}\text{C}$   
401 values ranged from  $-26.6$  to  $-17.4 \text{ ‰}$ , with a mean of  $-23.0 \pm 0.1 \text{ ‰}$  ( $n = 136$ ), whereas the  
402  $\delta^{15}\text{N}$  values ranged from  $-0.6$  to  $5.7 \text{ ‰}$ , with a mean of  $2.6 \pm 0.1 \text{ ‰}$  ( $n = 136$ ).

403

#### 404 **3.4.1. Differences between plankton size-fractions**

405 Considering all stations combined, the mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values increased with size,  
406 especially in the fractions ranging from 0.7 to 60  $\mu\text{m}$  (Fig. 5, Table S6). Significantly higher  
407 mean  $\delta^{13}\text{C}$  values were reported in the 20–60  $\mu\text{m}$  fraction than in the 0.7–2.7  $\mu\text{m}$  fraction. The  
408 mean  $\delta^{15}\text{N}$  values of the size-fractions from 0.7 to 60  $\mu\text{m}$  were all significantly different. Size-

409 fractions between 60 and 2000  $\mu\text{m}$  showed slightly higher  $\delta^{13}\text{C}$  values than those of smaller  
410 fractions. The highest mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were measured in the 1000 to > 2000  $\mu\text{m}$   
411 size-fractions (Fig. 5, Table S6).

412

### 413 **3.4.2. Differences between stations**

414 As for the biochemical composition, the size-fractions were grouped into two fractions: the  
415 phytoplankton fraction (fractions between 0.7 and 60  $\mu\text{m}$ ) and the zooplankton fraction  
416 (fractions between 60 and 500  $\mu\text{m}$  that were sampled at all the stations). The mean  $\delta^{13}\text{C}$  and  
417  $\delta^{15}\text{N}$  values followed the same spatial variations between phyto- and zooplankton fractions  
418 (Fig. 6A-D). For both phyto- and zooplankton, the highest mean  $\delta^{13}\text{C}$  values were measured  
419 at St4 and St17. The highest mean  $\delta^{15}\text{N}$  values were detected in phytoplankton at St4, while  
420 the lowest ones were observed at St9. In zooplankton, the highest mean  $\delta^{15}\text{N}$  values were  
421 measured at St10, and the lowest ones at St9, St17, and St19 (Fig. 6A-D). Overall, in contrast  
422 to the biochemical composition, greater differences were highlighted between size-fractions  
423 than between stations for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (Table S5).

424

### 425 **3.5. Trophic levels**

426 For all zooplankton size-fractions (60 to > 2000  $\mu\text{m}$ ) and stations combined, the TL ranged  
427 from 1.5 to 3.6 with a mean of  $2.2 \pm 0.1$  ( $n = 76$ ). When considering all stations combined,  
428 mean TL significantly increased with size ( $F = 5.2$ ,  $p = 0.001$ ) (Fig. 7). The highest mean  
429 TL ( $2.6 \pm 0.2$ ,  $n = 10$ ) was measured for the 1000–2000  $\mu\text{m}$  size-fraction and the lowest TL  
430 ( $1.9 \pm 0.1$ ,  $n = 20$ ) in the 60–200  $\mu\text{m}$  fraction. For the 60–200, 200–500, and 500–1000  $\mu\text{m}$   
431 size-fractions, differences in mean TLs were overall significant between stations ( $H = 18.7$ ,  $p$   
432  $= 0.027$ ;  $H = 18.9$ ,  $p = 0.026$  and  $H = 16.3$ ,  $p = 0.037$ , respectively) with the highest mean  
433 trophic levels by size-fraction at St10. Mean TL weighted by the plankton biomass ( $\text{TL}_B$ ) had  
434 values larger than 2 at St2, St3 in northern coastal waters, and at St9, St10 and St11 in  
435 offshore waters (Fig. 8). The cumulated biomass of the zooplankton groups (60 to > 2000  $\mu\text{m}$ )  
436 of the sampled stations was significantly and negatively correlated with  $\text{TL}_B$  ( $R^2 = 0.61$ ,  $p =$   
437  $0.020$ ) (Fig. S2).

438

### 439 **3.6. Trophic flows in the plankton food web**

440 The Mediterranean plankton food web analysis highlighted size predation (Fig. 9, Fig. S3).  
441 For all stations combined, the 0.7–2.7  $\mu\text{m}$  fraction was mainly consumed by the 60–500- $\mu\text{m}$   
442 fraction, while the consumption of the 2.7–20  $\mu\text{m}$  fraction was similar between the 60–500

443 and 500–2000- $\mu\text{m}$  fractions. The  $> 2000$   $\mu\text{m}$  size-fraction mainly consumed the 20–60  $\mu\text{m}$   
444 size fraction (Fig. 9, Fig. S3).

445

## 446 **4. Discussion**

447

### 448 **4.1. Plankton biochemical content**

449 The present description of the plankton biochemical content along a north-south transect in  
450 the Mediterranean Sea appears to be unique to our knowledge. The biochemistry of phyto-  
451 and zooplankton has been extensively documented in many marine environments but remains  
452 little observed in the Mediterranean Sea (Morris and Hopkins, 1983; Danovaro et al., 2000;  
453 Yilmaz and Besiktepe, 2010; Chen et al., 2019).

454 Jónasdóttir (2019) summarizes the biochemistry of phytoplankton by a protein / carbohydrate  
455 / lipid average ratio of 5 / 3 / 2 (with a range of 40–60, 17–40, and 16–26%), similar to Ríos et  
456 al. (1998) who found a ratio of 4.9 / 3.2 / 1.9. In our study, the mean ratio of the size-fractions  
457 between 0.7 and 60  $\mu\text{m}$  was on average 5.6 / 3.6 / 0.9, therefore with relatively higher proteins  
458 and lower lipids compared to previous ratios. The biochemical ratio in the  $> 60$   $\mu\text{m}$  size-  
459 fractions was 6.9 / 2.0 / 1.1, reflecting higher protein and lower carbohydrate contents  
460 compared to phytoplankton. The higher proportion of protein to carbohydrate is a good  
461 indicator of the nitrogen availability in the environment whereas the inverse pattern may  
462 reflect nitrogen-limited environments for both phyto- (Fabiano et al., 1999; Danovaro et al.,  
463 2000; Yilmaz and Besiktepe, 2010; Kim et al., 2019) and zooplankton (Bhat et al., 1993).  
464 Chen et al. (2019) found in spring time in the Bay of Marseille (in the same location as our  
465 station St4), for the size-fraction 200–500  $\mu\text{m}$ , carbohydrate concentrations (62.4 to 66.7 mg  
466  $\text{g}^{-1}$ ) similar to ours, while their concentrations in lipids (98.3 to 102.8 mg  $\text{g}^{-1}$ ) and proteins  
467 (292.7 to 335.7 mg  $\text{g}^{-1}$ ) were higher.

468 The protein and lipid concentrations were higher in zooplankton than in phytoplankton.  
469 Within the zooplankton, an increase in proteins with size was observed, in agreement with  
470 Guisande (2006). Most of the organisms in our samples between 60 and 2000  $\mu\text{m}$  were  
471 composed of copepods, and, consequently, the different fractions corresponding to different  
472 life-stages of the same group (Fierro-González et al., 2023) may explain the size influence on  
473 their biochemical content. The highest concentrations of carbohydrates and lipids reported in  
474 the 20–60  $\mu\text{m}$  size-fraction can be related to a mixed composition of microphyto- and  
475 microzooplanktonic organisms, such as diatoms and metazoan eggs (Danovaro et al., 2000;  
476 Chen et al., 2019). However, an underestimation of the  $\text{SPM}_{\text{DW}}$  in the 20–60  $\mu\text{m}$  fraction with



477 respect to that in the size-fractions from 0.7 to 60  $\mu\text{m}$  – due to different estimation methods  
478 (see section 2.2.2) – may explain the higher biochemical concentrations measured in the 20–  
479 60  $\mu\text{m}$  fractions. Finally, the lowest protein, carbohydrate, and lipid concentrations observed  
480 in the  $> 2000\text{-}\mu\text{m}$  fraction were probably related to the dominance in this fraction of filter  
481 feeder organisms, such as salps and siphonophores (Bănaru et al., 2014; Hunt et al., 2017;  
482 Chen et al., 2019; Fierro-González et al., 2023).

483 Organic contaminants have been shown to have a strong chemical affinity for lipids or  
484 proteins (Mason et al., 1995; Wu and Wang, 2011, Frouin et al., 2013). Therefore, without  
485 considering the size of the organisms (which is also an important factor in the accumulation  
486 of contaminants in biota, in particular, phytoplankton), we can assume that the concentrations  
487 of organic contaminants in zooplankton of stations St1, St2, St9 and St11 (which contains  
488 more lipids and proteins) may be higher than those in the zooplankton of stations St3, St4 and  
489 St17 (which have less lipids and proteins). The biochemical content of the plankton size  
490 fractions can change due to variations of the composition of the plankton community and the  
491 nutrient inputs linked to the physical and chemical environment, thus affecting the entire  
492 trophodynamics of the ecosystem (Chen et al., 2019, 2021; Tedetti et al., 2023).

493

#### 494 **4.2. Plankton total energy amount ( $E_{\text{TS}}$ )**

495 The  $E_{\text{T}}$  decreased with size due to plankton biomass reduction with size. In our study, the  $E_{\text{T}}$   
496 in  $\text{SPM}_{\text{DW}}$  were lower than previously measured in other areas (Mayzaud et al., 1989; Fabiano  
497 et al., 1999; Kim et al., 2019). This is most likely due to the lower phytoplankton biomass  
498 reported in the oligotrophic Mediterranean Sea, highlighting their low qualitative values even  
499 if spatial and seasonal variations may occur. In the eastern Mediterranean basin, the  $E_{\text{i}}$   
500 measured in zooplankton by Danovaro et al., (2000) were even lower than in our study,  
501 probably related to higher oligotrophy in their study area. In the Bay of Marseille, the  $E_{\text{T}}$   
502 measured at St4 were higher for us than those recorded in similar zooplankton size-fractions  
503 during the same season in 2017 by Chen et al. (2019). Plankton showed higher  $E_{\text{TS}}$  at St1, St4,  
504 St9 and St19. At these stations, where bloom conditions prevailed, trophic regimes were  
505 probably responsible for enhanced biomass (Mayot et al., 2017; Chen et al., 2019; Tedetti et  
506 al., 2023) (Table S1), which may have impacted their  $E_{\text{TS}}$ . The 0.7–2.7, 2.7–20, and 200–500-  
507  $\mu\text{m}$  size-fractions represented the largest energetic reservoir in the Mediterranean phyto-, and  
508 zooplankton compartments. Our study highlights their importance as major potential sources  
509 of contaminants for their consumers.

510

### 4.3. Plankton stable isotopes ratios and composition

The fractions comprised between 0.7 and 60  $\mu\text{m}$  corresponded to  $\text{SPM}_{\text{DW}}$  made up of a complex mixture of living, detrital and lithogenic material, difficult to separate (Lam et al., 2015; Tedetti et al., 2023). The main limitation of food web studies relying of stable isotope ratios is to establish an acceptable baseline, using samples mainly composed of primary producers (Harmelin-Vivien et al., 2008; Tamelander et al., 2009). In our study, pico- and nanoplankton dominated the  $\text{SPM}_{\text{DW}}$  biomass which was composed of around 86% of photosynthetic organisms, as confirmed by cytometry results (Boudriga et al., 2022). Moreover, their low C:N ratios suggest a composition dominated by living photosynthetic organisms.

Few studies have measured isotopic compositions of the smallest size-fractions of plankton (Wainright and Fry, 1994; Tamelander et al., 2009), and even fewer have separated them by size (Rau et al., 1990; Rolff, 2000; Im et al., 2015; Hunt et al., 2017; Décima, 2022). The size-fractions from 0.7 to 60  $\mu\text{m}$  (without considering the 0.7–60  $\mu\text{m}$  fraction) have similar  $\delta^{13}\text{C}$  values but their  $\delta^{15}\text{N}$  values are rather low ( $-23.9 \pm 0.2 \text{‰}$  and  $1.4 \pm 0.16 \text{‰}$ , respectively) compared to those measured in other oceanic basins (from  $-28$  to  $-17 \text{‰}$  and from 1 to 12  $\text{‰}$ , respectively) (Wainright and Fry, 1994; Rolff, 2000; Tamelander et al., 2009) and in the Mediterranean Sea (from  $-25$  to  $-22 \text{‰}$  and from 1 to 6  $\text{‰}$ , respectively) (Rau et al., 1990; Harmelin-Vivien et al., 2008; Hunt et al., 2017; Liénart et al., 2017).

Several processes may explain the low  $\delta^{15}\text{N}$  values of the plankton in our study: 1) in the convection areas subjected to algae blooms (such as St9), nutrients made of light isotopes are preferentially uptaken by phytoplankton (Wainright and Fry, 1994; Rolff, 2000; Tamelander et al., 2009), 2) in water with poor nutrient content, ammonium, the main nitrogen source emitted through excretion and recycling, has lower  $\delta^{15}\text{N}$  values (Checkely and Miller, 1989), and 3) the high proportion of diazotrophs (atmospheric nitrogen fixer) in oligotrophic waters may lower  $\delta^{15}\text{N}$  values (Pantoja et al., 2002; Montoya et al., 2002; Koppelman et al., 2003).

Within the 0.7 and 60  $\mu\text{m}$  size-fractions,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values significantly increased with size from pico-, nano- to microplankton, similar to previous studies (Im et al., 2015; Hunt et al., 2017). Differences between primary producers can be related to differences in the isotopic composition of inorganic nitrogen sources and/or fractionation between molecules made of heavy and light isotopes during physiological processes (Ostrom and Fry, 1993). A large contribution of cyanobacteria, mainly composed of *Synechococcus* spp. may lower  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of SPM in the 0.7–2.7  $\mu\text{m}$  size-fraction (Rau et al., 1990; Rolff, 2000; Hunt et al., 2017). These differences in the composition may also suggest predation within the 0.7–60  $\mu\text{m}$

545 fraction (Onodera et al., 2018; Armengol et al., 2019). However, an increase in  $\delta^{15}\text{N}$  values  
546 with the size has already been observed in autotrophs (Karsh et al., 2003; Hunt et al., 2017).  
547 The group composed of size-fractions larger than 60  $\mu\text{m}$  and dominated by zooplankton,  
548 mainly copepods (Fierro-González et al., 2023), presented higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values than  
549 phytoplankton.  
550 The isotopic compositions reported here for the 200–500  $\mu\text{m}$  size-fractions ( $-22.6 \pm 0.4 \text{ ‰}$   
551 and  $3.2 \pm 0.2 \text{ ‰}$ , for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively) were rather in the lower range of previous  
552 estimates in different oceanic basins (from  $-22$  to  $-19\text{‰}$  and from  $2$  to  $8\text{‰}$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$   
553 values, respectively) (Fry and Quiñones, 1994; Bode et al., 2007; Yang et al., 2017). Overall,  
554 the isotopic compositions measured in the different zooplankton size-fractions were within  
555 the same range as those reported in the ultra-oligotrophic eastern Mediterranean basin  
556 (Koppelman et al., 2009; Denda and Christiansen, 2010) and in the more productive area of  
557 the Gulf of Lion (Espinasse et al., 2014; Bănaru et al., 2014; Hunt et al., 2017).  
558 Within the zooplankton size-fractions,  $\delta^{15}\text{N}$  values increased with size, up to the 1000–2000  
559  $\mu\text{m}$  fraction, underlining an enhancement of the predation with size (Fry and Quiñones, 1994;  
560 Rolff, 2000; Bănaru et al., 2014; Espinasse et al., 2014; Hunt et al., 2017). The  $\delta^{15}\text{N}$  values  
561 increased with the size-fractions, which may be due to the succession of the different life  
562 stages of copepods, coinciding with the pattern observed in their biochemical composition  
563 (Espinasse et al., 2014; Chen et al., 2019) related to metabolic changes during the lifespan  
564 (Guisande, 2006), adaptative foraging (Kozak et al., 2020), ontogenetics (Mauchline, 1998;  
565 Im et al., 2015) or all these processes combined. Fierro-González et al. (2023) reported an  
566 increase in the proportion of carnivores with size. However, in the largest size-fraction ( $>$   
567 2000  $\mu\text{m}$ ), gelatinous organisms were generally overrepresented with respect to other  
568 fractions, leading to higher  $\delta^{13}\text{C}$  and lower  $\delta^{15}\text{N}$  values due probably to distinct food sources  
569 from smaller fractions (Bănaru et al., 2014; Espinasse et al., 2014).

570

#### 571 **4.4. Spatial variation in plankton isotopic compositions**

572 The highest  $\delta^{15}\text{N}$  values in phytoplankton were recorded at St4, located in the Bay of  
573 Marseille, which is highly impacted by anthropogenic and terrestrial inputs. These inputs may  
574 induce, in case of declining nitrates related to intense bloom events, an increase of the  $\delta^{15}\text{N}$   
575 values (Raimbault et al., 2008; Fey et al., 2021). Moreover, the effluents of the Marseille  
576 sewage treatment plant may be  $^{15}\text{N}$ -enriched in the inorganic nitrogen pool due to bacterial  
577 denitrification (Wainright and Fry, 1994; Cabana and Rasmussen, 1996). The high  $\delta^{13}\text{C}$   
578 values measured in phyto- and zooplankton in the Bay of Marseille (St3 and St4) and in the

579 Gulf of Gabès (St17 and St19) may be due to higher growth rates and nutrient availability in  
580 these productive areas (Laws et al., 1995; Bidigare et al., 1997), as well as to inputs of  
581 sedimentary organic matter in the water column during sediment resuspension events (Table  
582 S1). Moreover, the low  $\delta^{15}\text{N}$  values measured on the Tunisian coasts support this hypothesis  
583 and may be related to seagrass detritus (Cresson et al., 2012). St9, located at the border of the  
584 convective area of the Northwestern Mediterranean Sea, was characterized by a post-bloom  
585 event during the campaign (Tedetti et al., 2023) and displayed the lowest  $\delta^{15}\text{N}$  values in  
586 phyto- and zooplanktonic organisms. The highest C:N measured at this station may suggest a  
587 higher detrital organic matter content and a higher microbial production of regenerated  
588 isotopically lighter ammonium compared to the other stations (Maguer et al., 2000).  
589 The relatively high  $\delta^{13}\text{C}$  (and  $\delta^{15}\text{N}$ ) values measured in phyto- and zooplankton in the Bay of  
590 Marseille and the Gulf of Gabès may also be related to various inputs (sediment resuspension,  
591 effluents, etc.), and be the sign of higher levels of contaminants which could derive from the  
592 same sources. To support this hypothesis, higher trace metal concentrations have been  
593 reported in these coastal stations compared to other MERITE-HIPPOCAMPE stations  
594 (Chifflet et al., 2023).

595

#### 596 **4.5. Trophic levels and food web implications**

597 The TLs determined in this study, ranging from 1.5 to 3.6, increased with size and spread out  
598 over 2 TLs. TLs lower than 2 may be related to a mixture of primary producers and  
599 consumers mainly found at some stations in the 60–200  $\mu\text{m}$  size-fraction, related to clogging  
600 of the sampling device caused by phytoplankton. Further improvements in sampling methods  
601 by using larger mesh-size nets for zooplankton size-fractions collection may avoid potential  
602 clogging during bloom events and the presence of phytoplankton within the 60–200  $\mu\text{m}$  size-  
603 fraction.

604 When biomass is averaged to the TL of zooplankton ( $\text{TL}_B$ ), higher values are obtained at the  
605 coastal (St2, and St3), and offshore (St9, St10, and St11) stations. High adaptability in food  
606 habits of zooplankton is well known and omnivory seems to be the most common trophic  
607 pathway (Fierro-González et al., 2023). Higher TLs are generally reached in microbial food  
608 webs, often observed in oligotrophic regimes (Søreide et al., 2006; Kürten et al., 2013). St10  
609 and St11 contained carnivorous plankton, such as chaetognaths which may explain the higher  
610 TLs of the zooplankton community observed in these areas (Fierro-González et al., 2023). It  
611 has been suggested that the TFF between phytoplankton and protozoans is equal to 0,  
612 contributing to an underestimation of the number of TLs in planktonic food webs (Gutiérrez-

613 Rodríguez et al., 2014). However, in this work, we suggest that the higher TLs of plankton  
614 were probably related to the microbial food web.

615 Coastal stations (St1, St4, St15, St17 and St19) were characterized by lower TL<sub>B</sub>. The  
616 lower TL of plankton in productive systems is classic in herbivore food webs, dominated by  
617 larger phytoplankton organisms readily available to zooplankton (Sommer et al., 2002;  
618 Fileman et al., 2007). Food chain length decreases in productive ecosystems due to an  
619 adaptive foraging of consumers which selects the most abundant low TL resources (Kondoh  
620 and Ninomiya, 2009). Detritus and phytoplankton were dominant in these stations in the 60–  
621 200 µm size-fraction contributing to lowering TL<sub>B</sub> values (Fierro-González et al., 2023).

622 In addition, the zooplankton biomass was related to the trophic pathways. A negative  
623 relationship between the TL<sub>B</sub> and the zooplankton biomass was observed during this study.  
624 Higher biomasses of zooplankton have been measured at coastal stations relative to offshore  
625 areas in relation to their primary production (Champalbert, 1996). Where TLs were high (St9,  
626 St10 and St11), large size fractions (500–1000 and 1000–2000 µm) were also well  
627 represented, accounting for 27 to 54% of the total zooplankton biomass. Espinasse et al.  
628 (2014) have already highlighted the overrepresentation of large plankton organisms in  
629 moderately productive areas, while Décima (2022) have reported an inverse relationship  
630 between food chain length and productivity in zooplankton. Although located in the offshore  
631 area, St9 was characterized by a still productive post-bloom situation (Tedetti et al., 2023)  
632 with high TL<sub>B</sub>. Usually, during post-bloom, diatoms give way to inedible algae not consumed  
633 by zooplankton organisms and the source of organic matter is obtained through the cell lysis,  
634 fuelling microbial loop and enhancing food steps (Sommer et al., 2002). High C:N ratios  
635 observed at St9 may indicate heterotrophy within the 0.7–60 µm fractions (Harmelin-Vivien  
636 et al., 2008). The post-bloom situation may induce a decrease of the resources and thus  
637 mesoplankton preying on microplankton (Levinsen et al., 2000; Basedow et al., 2016). Hence,  
638 the results reported here highlight different trophodynamic scenarios in the Mediterranean  
639 plankton food webs and their control on planktonic biomasses, as hypothesized by Fry and  
640 Quiñones (1994).

641 Contrasting carbon fluxes can impact contaminant transfer. The ability of each contaminant to  
642 bioaccumulate can lead to different scenarios. In low-productive ecosystems, organic matter  
643 fluxes go through more trophic steps, which can favor a higher transfer of contaminants that  
644 will bioaccumulate such as methylmercury, PCBs or Cd (Tiano et al., 2014; Schartup et al.,  
645 2018; Chouvelon et al., 2019). Conversely, in productive ecosystems, direct access to organic  
646 matter sources and reduced food steps favors higher transfer of contaminants with little or no

647 capacity to bioaccumulate, such as the numerous trace elements Co, Ni, Cu, Ag, Pb, and Zn  
648 (Chouvelon et al., 2019).

649

#### 650 **4.6. Plankton food web flows**

651 The difference in stable isotope composition between phytoplankton size-fractions made them  
652 relevant candidates for mixing model analysis of their relative contributions to zooplankton  
653 biomass (Phillips et al., 2014; Hunt et al., 2017). Overall, the contribution of the 0.7–2.7- $\mu\text{m}$   
654 size-fraction to the diet of the 60–500  $\mu\text{m}$  size fraction underlines the role of the  
655 microzooplankton (60–200  $\mu\text{m}$ ) and of the small mesozooplankton (200–500  $\mu\text{m}$ ) in the  
656 transfer of organic matter from the baseline to higher trophic level consumers. The  
657 picoplankton size fraction was mainly composed of *Synechococcus* spp., the most abundant  
658 phytoplankton organism in the Mediterranean Sea that sustains primary production (Boudriga  
659 et al., 2022). In fact, during the MERITE-HIPPOCAMPE campaign, picoplankton accounted  
660 for, on average, 27% of the total biomass of phytoplankton.

661 Classically, we consider that nanoflagellates and microzooplankton (from 2 to 200  $\mu\text{m}$  size-  
662 fractions) may represent intermediate food steps (Ryther, 1969; Calbet and Landry, 1999)  
663 ensuring the link between the 0.7–2.7  $\mu\text{m}$  fraction and mesozooplankton (200–2000  $\mu\text{m}$ )  
664 (Sommer et al., 2000). The 60 to 500  $\mu\text{m}$  size-fractions were constituted of a large percentage  
665 of phytoplankton and detritus that would have contributed to lowering their stable isotope  
666 ratios. This may have consequences with regard to the mixing model results and may explain  
667 the high percentage of picoplankton estimated in the diet of 60–500  $\mu\text{m}$  size-fraction.

668 However, in agreement with our results, and despite their small size, recent studies  
669 demonstrated that small copepods may feed on picoplankton (Motwani and Gorokhova, 2013;  
670 Im et al., 2015; Major et al., 2017).

671 Primary producers were also dominant in the 2.7–20  $\mu\text{m}$  fractions, representing 69% of the  
672 phytoplanktonic biomass and about half of the total food supply to both the 60–500 and the  
673 500–2000  $\mu\text{m}$  size-fractions. Nanoplankton was mainly composed of nanoeukaryotes and its  
674 contribution to the planktonic food web seems essential, in agreement with the results of Hunt  
675 et al. (2017). Finally, the 20–60  $\mu\text{m}$  fraction has low biomass and represents an important  
676 contribution only to the diet of the > 2000  $\mu\text{m}$  size-fractions. TFFs for plankton should be  
677 experimentally determined and a higher number of replicates should be analyzed to improve  
678 model results and to reduce their variability.

679 Differences in contaminant accumulation have been reported in phytoplankton size-fractions.  
680 Trace metals reflected, for each element, contrasted accumulation patterns between small and

681 large phytoplankton fractions (Chifflet et al., 2023). Higher methylmercury concentrations  
682 were reported during a picoplanktonic bloom, probably due to a higher surface to volume  
683 ratio, favoring uptake (Heimbürger et al., 2010). In addition, for PCBs, a higher accumulation  
684 was observed in smaller cells (Axelman et al., 1997). The different carbon size-fractions of  
685 food sources can thus influence the transfer of contaminants and concentrations in  
686 zooplankton consumers.

687

## 688 **5. Conclusions**

689 During the MERITE-HIPPOCAMPE campaign, plankton size-fractions revealed contrasted  
690 biochemical and isotopic compositions related to their size, composition and location.  
691 Carbohydrate concentrations were the highest in phytoplankton (between 0.7 and 60  $\mu\text{m}$  size-  
692 fractions) with respect to zooplankton ( $> 60 \mu\text{m}$  size-fractions), which displayed high protein  
693 and lipid contents increasing with size. The affinity of proteins and lipids for contaminants  
694 makes zooplankton more sensitive to their accumulation (regardless of the size of organisms).  
695 Due to the high amount of energy contained in their biomass, the pico- and nanoplankton  
696 represents a major food resource in Mediterranean ecosystems fueling the zooplankton food  
697 webs and an essential pathway for contaminants due to the combination of small size and high  
698 energetic content. In the zooplankton community, the 200–500  $\mu\text{m}$  size-fraction, dominated  
699 by copepods, showed the highest energy amount, which explains their role as essential food  
700 resource for many planktivorous fishes. Spatial variations of isotopic compositions of  
701 plankton size-fractions were also observed, revealing different carbon sources between the  
702 coast and the offshore areas, and between the Bay of Gabès (southern coast) and the Bay of  
703 Toulon (northern coast), and resulting in a different exposure to contaminants. Trophic levels  
704 revealed increasing predation with size, which can result in the biomagnification of  
705 contaminants. Trophic pathways in planktonic food webs displayed spatial variations  
706 influenced by the availability of phytoplankton resources. Higher predation occurred in low  
707 productive areas where the zooplankton community reached the highest mean trophic levels,  
708 increasing the potential exposure of planktonic food webs to contaminants. Our findings on  
709 the spatial variations of the biomass, biochemical composition, and the role of the different  
710 plankton size-fractions in the food web, as well as the different flows of organic matter in the  
711 pelagic food webs, are an essential step for the comprehension of the transfer of contaminants  
712 in the Mediterranean pelagic food webs.

713

714

715 **Author contribution statement**

716 *Conception and design of study: DB, MT, FC, MP,*

717 *Acquisition of data: JATO, MeTe, LG, PF, BL, GG, IB, MB, AZ, MT, SC*

718 *Analysis and/or interpretation of data: JATO, DB, MT, TG, CC, SC*

719 *Drafting of the manuscript: JATO, DB, MT*

720 *Revising/editing of the manuscript: JATO, DB, MT, FC, BL*

721 *Project administration and funding acquisition: DB, MT, FC, MP*

722

723 **Acknowledgements**

724 The authors wish to thank the crew of the R/V *Antea* and the various platforms of the

725 Mediterranean Institute of Oceanography having contributed to the data acquisition:

726 Plateforme Analytique de Chimie des Environnements Marins (PACEM) for the POC/PON

727 measurements, Plateforme Régionale de Cytométrie pour la Microbiologie (PRECYM) for

728 cytometric analyses, Microscopie et Imagerie numérique (MIM) for identification expertise

729 and the Service Atmosphère-Mer (SAM) for the technical and operational tasks. The authors

730 thank the LIENSs joint research unit (CNRS - La Rochelle University) for the measurement

731 of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. The MERITE-HIPPOCAMPE project has been funded by the cross-

732 disciplinary *Pollution & Contaminants* axis of the CNRS-INSU MISTRALS program (joint

733 action of the MERMEX-MERITE and CHARMEX subprograms) and received support from

734 the IRD French-Tunisian International Joint Laboratory (LMI) COSYS-Med. We are grateful

735 for the additional funding received from IFREMER, the MIO Action Sud and Transverse

736 Axis programs (CONTAM Transverse Axis), and from the IRD Ocean Department. This

737 study received funding by the CONTAMPUMP project (ANR JCJC #19-CE34-0001-01).

738 Finally, we warmly thank three anonymous Reviewers for their very relevant and useful

739 comments and corrections on the manuscript, as well as Michael Paul for the English

740 corrections.

741

742 **Supplementary information**

743 Supplementary material related to this article is available online at: xxx

744

745 **References**

746 Alekseenko, E., Thouvenin, B., Tronczyński, J., Carlotti, F., Garreau, P., Tixier, C., Baklouti,

747 M., 2018. Modeling of PCB trophic transfer in the Gulf of Lions; 3D coupled model



748 application. *Marine Pollution Bulletin* 128, 140–155.  
749 <https://doi.org/10.1016/j.marpolbul.2018.01.008>

750 Armengol, L., Calbet, A., Franchy, G., Rodríguez-Santos, A., Hernández-León, S., 2019.  
751 Planktonic food web structure and trophic transfer efficiency along a productivity  
752 gradient in the tropical and subtropical Atlantic Ocean. *Scientific Reports* 9, 2044.  
753 <https://doi.org/10.1038/s41598-019-38507-9>

754 Axelman, J., Broman, D., Näf, C., 1997. Field Measurements of PCB Partitioning between  
755 Water and Planktonic Organisms: Influence of Growth, Particle Size, and  
756 Solute–Solvent Interactions. *Environmental Science & Technology* 31, 665–669.  
757 <https://doi.org/10.1021/es960088+>

758 Bănar, D., Carlotti, F., Barani, A., Grégori, G., Neffati, N., Harmelin-Vivien, M., 2014.  
759 Seasonal variation of stable isotope ratios of size-fractionated zooplankton in the Bay of  
760 Marseille (NW Mediterranean Sea). *Journal of Plankton Research* 36, 145–156.  
761 <https://doi.org/10.1093/plankt/fbt083>

762 Bănar, D., Diaz, F., Verley, P., Campbell, R., Navarro, J., Yohia, C., Oliveros-Ramos, R.,  
763 Mellon-Duval, C., Shin, Y.-J., 2019. Implementation of an end-to-end model of the Gulf  
764 of Lions ecosystem (NW Mediterranean Sea). I. Parameterization, calibration and  
765 evaluation. *Ecological Modelling* 401, 1–19.  
766 <https://doi.org/10.1016/j.ecolmodel.2019.03.005>

767 Bănar, D., Mellon-Duval, C., Roos, D., Bigot, J.-L., Souplet, A., Jadaud, A., Beaubrun, P.,  
768 Fromentin, J.-M., 2013. Trophic structure in the Gulf of Lions marine ecosystem (north-  
769 western Mediterranean Sea) and fishing impacts. *Journal of Marine Systems* 111–112,  
770 45–68. <https://doi.org/10.1016/j.jmarsys.2012.09.010>

771 Banse, K., Mosher, S., 1980. Adult Body Mass and Annual Production/Biomass Relationships  
772 of Field Populations. *Ecological Monographs* 50, 355–379.  
773 <https://doi.org/10.2307/2937256>

774 Basedow, S.L., de Silva, N.A.L., Bode, A., van Beusekom, J., 2016. Trophic positions of  
775 mesozooplankton across the North Atlantic: estimates derived from biovolume spectrum  
776 theories and stable isotope analyses. *Journal of Plankton Research* 38, 1364–1378.  
777 <https://doi.org/10.1093/plankt/fbw070>

778 Bhat, K.L., Rayadurga, S., Ansari, Z.A., 1993. Biochemical composition of zooplankton from  
779 the northern Arabian Sea. *Pakistan Journal of Marine Sciences* 2, 17–22.

780 Bidigare, R.R., Fluegge, A., Freeman, K.H., Hanson, K.L., Hayes, J.M., Hollander, D.,  
781 Jasper, J.P., King, L.L., Laws, E.A., Milder, J., Millero, F.J., Pancost, R., Popp, B.N.,

782 Steinberg, P.A., Wakeham, S.G., 1997. Consistent fractionation of <sup>13</sup>C in nature and in  
783 the laboratory: Growth-rate effects in some haptophyte algae. *Global Biogeochemical*  
784 *Cycles* 11, 279–292. <https://doi.org/10.1029/96GB03939>

785 Bishop, J.K.B., Edmond, J.M., Ketten, D.R., Bacon, M.P., Silker, W.B., 1977. The chemistry,  
786 biology, and vertical flux of particulate matter from the upper 400 m of the equatorial  
787 Atlantic Ocean. *Deep Sea Research* 24, 511–548. [https://doi.org/10.1016/0146-](https://doi.org/10.1016/0146-6291(77)90526-4)  
788 [6291\(77\)90526-4](https://doi.org/10.1016/0146-6291(77)90526-4)

789 Bishop, J.K.B., Lam, P.J., Wood, T.J., 2012. Getting good particles: Accurate sampling of  
790 particles by large volume in-situ filtration: Getting good particles. *Limnology and*  
791 *Oceanography: Methods* 10, 681–710. <https://doi.org/10.4319/lom.2012.10.681>

792 Bligh, E.G., Dyer, W.J., 1959. A rapid method of total lipid extraction and purification.  
793 *Canadian Journal of Biochemistry and Physiology* 37, 911–917.  
794 <https://doi.org/10.1139/o59-099>

795 Bode, A., Alvarez-Ossorio, M.T., Cunha, M.E., Garrido, S., Peleteiro, J.B., Porteiro, C.,  
796 Valdés, L., Varela, M., 2007. Stable nitrogen isotope studies of the pelagic food web on  
797 the Atlantic shelf of the Iberian Peninsula. *Progress in Oceanography*, 74, 115–131.  
798 <https://doi.org/10.1016/j.pocean.2007.04.005>

799 Boudriga, I., Thyssen, M., Zouari, A., Garcia, N., Tedetti, M., Bel Hassen, M., 2022.  
800 Ultraphytoplankton community structure in subsurface waters along a North-South  
801 Mediterranean transect. *Marine Pollution Bulletin* 182, 113977.  
802 <https://doi.org/10.1016/j.marpolbul.2022.113977>

803 Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a Metabolic  
804 Theory of Ecology. *Ecology* 85, 1771–1789. <https://doi.org/10.1890/03-9000>

805 Cabana, G., Rasmussen, J.B., 1994. Modelling food chain structure and contaminant  
806 bioaccumulation using stable nitrogen isotopes. *Nature* 372, 255–257.  
807 <https://doi.org/10.1038/372255a0>

808 Cabana, G., Rasmussen, J.B., 1996. Comparison of aquatic food chains using nitrogen  
809 isotopes. *Proceedings of the National Academy of Sciences* 93, 10844–10847.  
810 <https://doi.org/10.1073/pnas.93.20.10844>

811 Calbet, A., Landry, M.R., 1999. Mesozooplankton influences on the microbial food web:  
812 Direct and indirect trophic interactions in the oligotrophic open ocean. *Limnology and*  
813 *Oceanography* 44, 1370–1380. <https://doi.org/10.4319/lo.1999.44.6.1370>

814 Carlotti, F., Thibault-Botha, D., Nowaczyk, A., Lefèvre, D., 2008. Zooplankton community  
815 structure, biomass and role in carbon fluxes during the second half of a phytoplankton

816 bloom in the eastern sector of the Kerguelen Shelf (January–February 2005). *Deep Sea*  
817 *Research Part II: Topical Studies in Oceanography*, 55, 720–733.  
818 <https://doi.org/10.1016/j.dsr2.2007.12.010>

819 Champalbert, G., 1996. Characteristics of zooplankton standing stock and communities in the  
820 western Mediterranean Sea: relations to hydrology. *Scientia Marina* 60, 97–113.

821 Checkley, D.M., Miller, C.A., 1989. Nitrogen isotope fractionation by oceanic zooplankton.  
822 *Deep Sea Research Part A. Oceanographic Research Papers* 36, 1449–1456.  
823 [https://doi.org/10.1016/0198-0149\(89\)90050-2](https://doi.org/10.1016/0198-0149(89)90050-2)

824 Chen, C.-T., Bănaru, D., Carlotti, F., Faucheux, M., Harmelin-Vivien, M., 2019. Seasonal  
825 variation in biochemical and energy content of size-fractionated zooplankton in the Bay  
826 of Marseille (North-Western Mediterranean Sea). *Journal of Marine Systems* 199,  
827 103223. <https://doi.org/10.1016/j.jmarsys.2019.103223>

828 Chen, C.-T., Carlotti, F., Harmelin-Vivien, M., Guilloux, L., Bănaru, D., 2021. Temporal  
829 variation in prey selection by adult European sardine (*Sardina pilchardus*) in the NW  
830 Mediterranean Sea. *Progress in Oceanography* 196, 102617.  
831 <https://doi.org/10.1016/j.pocean.2021.102617>

832 Chen, C.-T., Carlotti, F., Harmelin-Vivien, M., Lebreton, B., Guillou, G., Vassallo, L., Le  
833 Bihan, M., Bănaru, D., 2022. Diet and trophic interactions of Mediterranean  
834 planktivorous fishes. *Marine Biology* 169, 119. [https://doi.org/10.1007/s00227-022-](https://doi.org/10.1007/s00227-022-04103-1)  
835 [04103-1](https://doi.org/10.1007/s00227-022-04103-1)

836 Chifflet, S., Briant, N., Tesán-Onrubia, J.A., Zaaboub, N., Amri, S., Radakovitch, O., Bănaru,  
837 D., Tedetti, M., 2023. Distribution and accumulation of trace metal in the planktonic food  
838 web of the Mediterranean Sea (MERITE-HIPPOCAMPE campaign). *Marine Pollution*  
839 *Bulletin* 186, 114384. <https://doi.org/10.1016/j.marpolbul.2022.114384>.

840 Chouvelon, T., Strady, E., Harmelin-Vivien, M., Radakovitch, O., Brach-Papa, C., Crochet,  
841 S., Knoery, J., Rozuel, E., Thomas, B., Tronczynski, J., Chiffolleau, J.-F., 2019. Patterns  
842 of trace metal bioaccumulation and trophic transfer in a phytoplankton-zooplankton-small  
843 pelagic fish marine food web. *Marine Pollution Bulletin* 146, 1013–1030.  
844 <https://doi.org/10.1016/j.marpolbul.2019.07.047>

845 Cohen, J.E., Pimm, S.L., Yodzis, P., Saldana, J., 1993. Body Sizes of Animal Predators and  
846 Animal Prey in Food Webs. *The Journal of Animal Ecology* 62, 67.  
847 <https://doi.org/10.2307/5483>

848 Cossa, D., Knoery, J., Bănaru, D., Harmelin-Vivien, M., Sonke, J.E., Hedgecock, I.M., Bravo,  
849 A.G., Rosati, G., Canu, D., Horvat, M., Sprovieri, F., Pirrone, N., Heimbürger-Boavida,

850 L.-E., 2022. Mediterranean Mercury Assessment 2022: An Updated Budget, Health  
851 Consequences, and Research Perspectives. *Environmental Science & Technology* 56,  
852 3840–3862. <https://doi.org/10.1021/acs.est.1c03044>

853 Cresson, P., Ruitton, S., Fontaine, M.-F., Harmelin-Vivien, M., 2012. Spatio-temporal  
854 variation of suspended and sedimentary organic matter quality in the Bay of Marseilles  
855 (NW Mediterranean) assessed by biochemical and isotopic analyses. *Marine Pollution*  
856 *Bulletin* 64, 1112–1121. <https://doi.org/10.1016/j.marpolbul.2012.04.003>

857 Cresson, P., Chouvelon, T., Bustamante, P., Bănaru, D., Baudrier, J., Le Loc'h, F., Mauffret,  
858 A., Mialet, B., Spitz, J., Wessel, N., Briand, M.J., Denamiel, M., Doray, M., Guillou, G.,  
859 Jadaud, A., Lazard, C., Prieur, S., Rouquette, M., Saraux, C., Serre, S., Timmerman, C.-  
860 A., Verin, Y., Harmelin-Vivien, M., 2020. Primary production and depth drive different  
861 trophic structure and functioning of fish assemblages in French marine ecosystems.  
862 *Progress in Oceanography* 186, 102343. <https://doi.org/10.1016/j.pocean.2020.102343>

863 Danovaro, R., Dell'Anno, A., Pusceddu, A., Marrale, D., Della Croce, N., Fabiano, M.,  
864 Tselepidis, A., 2000. Biochemical composition of pico-, nano- and micro-particulate  
865 organic matter and bacterioplankton biomass in the oligotrophic Cretan Sea (NE  
866 Mediterranean). *Progress in Oceanography* 46, 279–310. [https://doi.org/10.1016/S0079-](https://doi.org/10.1016/S0079-6611(00)00023-9)  
867 [6611\(00\)00023-9](https://doi.org/10.1016/S0079-6611(00)00023-9)

868 Décima, M., 2022. Zooplankton trophic structure and ecosystem productivity. *Marine*  
869 *Ecology Progress Series* 692, 23–42. <https://doi.org/10.3354/meps14077>

870 Denda, A., Christiansen, B., 2010. Zooplankton at a seamount in the eastern Mediterranean:  
871 distribution and trophic interactions. *Journal of the Marine Biological Association of the*  
872 *United Kingdom* 91, 33–49. <https://doi.org/10.1017/S0025315410001153>

873 DuBois, Michel., Gilles, K.A., Hamilton, J.K., Rebers, P.A., Smith, Fred., 1956. Colorimetric  
874 Method for Determination of Sugars and Related Substances. *Analytical Chemistry* 28,  
875 350–356. <https://doi.org/10.1021/ac60111a017>

876 Durrieu de Madron, X., Guieu, C., Sempéré, R., Conan, P., Cossa, D., D'Ortenzio, F.,  
877 Estournel, C., Gazeau, F., Rabouille, C., Stemmann, L., Bonnet, S., Diaz, F., Koubbi, P.,  
878 Radakovitch, O., Babin, M., Baklouti, M., Bancon-Montigny, C., Belviso, S.,  
879 Bensoussan, N., Bonsang, B., Bouloubassi, I., Brunet, C., Cadiou, J.-F., Carlotti, F.,  
880 Chami, M., Charmasson, S., Charrière, B., Dachs, J., Doxaran, D., Dutay, J.-C., Elbaz-  
881 Poulichet, F., Eléaume, M., Eyrolles, F., Fernandez, C., Fowler, S., Francour, P.,  
882 Gaertner, J.C., Galzin, R., Gasparini, S., Ghiglione, J.-F., Gonzalez, J.-L., Goyet, C.,  
883 Guidi, L., Guizien, K., Heimbürger, L.-E., Jacquet, S.H.M., Jeffrey, W.H., Joux, F., Le

884 Hir, P., Leblanc, K., Lefèvre, D., Lejeusne, C., Lemé, R., Loÿe-Pilot, M.-D., Mallet, M.,  
885 Méjanelle, L., Mélin, F., Mellon, C., Mérigot, B., Merle, P.-L., Migon, C., Miller, W.L.,  
886 Mortier, L., Mostajir, B., Mousseau, L., Moutin, T., Para, J., Pérez, T., Petrenko, A.,  
887 Poggiale, J.-C., Prieur, L., Pujo-Pay, M., Pulido-Villena, Raimbault, P., Rees, A.P.,  
888 Ridame, C., Rontani, J.-F., Ruiz Pino, D., Sicre, M.A., Taillandier, V., Tamburini, C.,  
889 Tanaka, T., Taupier-Letage, I., Tedetti, M., Testor, P., Thébault, H., Thouvenin, B.,  
890 Touratier, F., Tronczynski, J., Ulses, C., Van Wambeke, F., Vantrepotte, V., Vaz, S.,  
891 Verney, R., 2011. Marine ecosystems' responses to climatic and anthropogenic forcings  
892 in the Mediterranean. *Progress in Oceanography* 91, 97–166.  
893 <https://doi.org/10.1016/j.pocean.2011.02.003>

894 Espinasse, B., Harmelin-Vivien, M., Tiano, M., Guilloux, L., Carlotti, F., 2014. Patterns of  
895 variations in C and N stable isotope ratios in size-fractionated zooplankton in the Gulf of  
896 Lion, NW Mediterranean Sea. *Journal of Plankton Research* 36, 1204–1215.  
897 <https://doi.org/10.1093/plankt/fbu043>

898 Fabiano, M., Danovaro, R., Povero, P., 1999. Vertical Distribution and Biochemical  
899 Composition of Pico- and Microparticulate Organic Matter in the Ross Sea (Antarctica),  
900 in: Spezie, G., Manzella, G.M.R. (Eds.), *Oceanography of the Ross Sea Antarctica*.  
901 Springer Milan, Milano, pp. 233–246. [https://doi.org/10.1007/978-88-470-2250-8\\_16](https://doi.org/10.1007/978-88-470-2250-8_16)

902 Fan, C.-W., Reinfelder, J.R., 2003. Phenanthrene Accumulation Kinetics in Marine Diatoms.  
903 *Environmental Science & Technology* 37, 3405–3412. <https://doi.org/10.1021/es026367g>

904 Fey, P., Parravicini, V., Bănar, D., Dierking, J., Galzin, R., Lebreton, B., Meziane, T.,  
905 Polunin, N.V.C., Zubia, M., Letourneur, Y., 2021. Multi-trophic markers illuminate the  
906 understanding of the functioning of a remote, low coral cover Marquesan coral reef food  
907 web. *Scientific Reports* 11, 20950. <https://doi.org/10.1038/s41598-021-00348-w>

908 Fierro-González, P., Pagano, M., Guilloux, L., Makhlof, N., Tedetti, M., Carlotti, F., 2023.  
909 Zooplankton biomass, size structure, and associated metabolic fluxes with focus on its  
910 roles at the chlorophyll maximum layer during the plankton-contaminant MERITE-  
911 HIPPOCAMPE cruise. Submitted to this special issue.

912 Fileman, E., Smith, T., Harris, R., 2007. Grazing by *Calanus helgolandicus* and Para-  
913 *Pseudocalanus* spp. on phytoplankton and protozooplankton during the spring bloom in  
914 the Celtic Sea. *Journal of Experimental Marine Biology and Ecology* 348, 70–84.  
915 <https://doi.org/10.1016/j.jembe.2007.04.003>

916 Frouin, H., Dangerfield, N., Macdonald, R.W., Galbraith, M., Crewe, N., Shaw, P., Mackas,  
917 D., Ross, P.S., 2013. Partitioning and bioaccumulation of PCBs and PBDEs in marine

918 plankton from the Strait of Georgia, British Columbia, Canada. *Progress in*  
919 *Oceanography*, Strait of Georgia Ecosystem Research Initiative (ERI) 115, 65–75.  
920 <https://doi.org/10.1016/j.pocean.2013.05.023>

921 Fry, B., Quiñones, R.B., 1994. Biomass spectra and stable isotope indicators of trophic level  
922 in zooplankton of the northwest Atlantic. *Marine Ecology Progress Series* 112, 201–204.

923 Guisande, C., 2006. Biochemical fingerprints in zooplankton. *Limnetica* 25, 369–376.

924 Gutiérrez-Rodríguez, A., Décima, M., Popp, B.N., Landry, M.R., 2014. Isotopic invisibility of  
925 protozoan trophic steps in marine food webs. *Limnology and Oceanography* 59, 1590–  
926 1598. <https://doi.org/10.4319/lo.2014.59.5.1590>

927 Harmelin-Vivien, M., Bănar, D., Dromard, C.R., Ourgaud, M., Carlotti, F., 2019.  
928 Biochemical composition and energy content of size-fractionated zooplankton east of the  
929 Kerguelen Islands. *Polar Biology* 42, 603–617. [https://doi.org/10.1007/s00300-019-](https://doi.org/10.1007/s00300-019-02458-8)  
930 [02458-8](https://doi.org/10.1007/s00300-019-02458-8)

931 Harmelin-Vivien, M., Loizeau, V., Mellon, C., Beker, B., Arlhac, D., Bodiguel, X., Ferraton,  
932 F., Hermand, R., Philippon, X., Salen-Picard, C., 2008. Comparison of C and N stable  
933 isotope ratios between surface particulate organic matter and microphytoplankton in the  
934 Gulf of Lions (NW Mediterranean). *Continental Shelf Research*, 28, 1911–1919.  
935 <https://doi.org/10.1016/j.csr.2008.03.002>

936 Heimbürger, L.-E., Cossa, D., Marty, J.-C., Migon, C., Averty, B., Dufour, A., Ras, J., 2010.  
937 Methyl mercury distributions in relation to the presence of nano- and picophytoplankton  
938 in an oceanic water column (Ligurian Sea, North-western Mediterranean). *Geochimica et*  
939 *Cosmochimica Acta* 74, 5549–5559. <https://doi.org/10.1016/j.gca.2010.06.036>

940 Hirst, A.G., Kiørboe, T., 2002. Mortality of marine planktonic copepods: global rates and  
941 patterns. *Marine Ecology Progress Series* 230, 195–209.  
942 <https://doi.org/10.3354/meps230195>

943 Hunt, B.P.V., Carlotti, F., Donoso, K., Pagano, M., D’Ortenzio, F., Taillandier, V., Conan, P.,  
944 2017. Trophic pathways of phytoplankton size classes through the zooplankton food web  
945 over the spring transition period in the north-west Mediterranean Sea. *Journal of*  
946 *Geophysical Research: Oceans* 122, 6309–6324. <https://doi.org/10.1002/2016JC012658>

947 Im, D.-H., Wi, J.H., Suh, H.-L., 2015. Evidence for ontogenetic feeding strategies in four  
948 calanoid copepods in the East Sea (Japan Sea) in summer, revealed by stable isotope  
949 analysis. *Ocean Science Journal* 50, 481–490. <https://doi.org/10.1007/s12601-015-0044-y>

950 Jónasdóttir, S.H., 2019. Fatty Acid Profiles and Production in Marine Phytoplankton. *Marine*  
951 *Drugs* 17, 151. <https://doi.org/10.3390/md17030151>

952 Karsh, K.L., Trull, T.W., Lourey, M.J., Sigman, D.M., 2003. Relationship of nitrogen isotope  
953 fractionation to phytoplankton size and iron availability during the Southern Ocean Iron  
954 RElease Experiment (SOIREE). *Limnology and Oceanography* 48, 1058–1068.  
955 <https://doi.org/10.4319/lo.2003.48.3.1058>

956 Khammeri, Y., Bellaaj-Zouari, A., Hamza, A., Medhioub, W., Sahli, E., Akrouf, F., Barraji,  
957 N., Ben Kacem, M.Y., Bel Hassen, M., 2020. Ultraphytoplankton community  
958 composition in Southwestern and Eastern Mediterranean Basin: Relationships to water  
959 mass properties and nutrients. *Journal of Sea Research* 158, 101875.  
960 <https://doi.org/10.1016/j.seares.2020.101875>

961 Khammeri, Y., Hamza, I.S., Zouari, A.B., Hamza, A., Sahli, E., Akrouf, F., Ben Kacem,  
962 M.Y., Messaoudi, S., Hassen, M.B., 2018. Atmospheric bulk deposition of dissolved  
963 nitrogen, phosphorus and silicate in the Gulf of Gabès (South Ionian Basin); implications  
964 for marine heterotrophic prokaryotes and ultraphytoplankton. *Continental Shelf Research*  
965 159, 1–11. <https://doi.org/10.1016/j.csr.2018.03.003>

966 Kim, Y., Lee, Jang Han, Kang, J.J., Lee, Jae Hyung, Lee, H.W., Kang, C.K., Lee, S.H., 2019.  
967 River discharge effects on the contribution of small-sized phytoplankton to the total  
968 biochemical composition of POM in the Gwangyang Bay, Korea. *Estuarine, Coastal and*  
969 *Shelf Science* 226, 106293. <https://doi.org/10.1016/j.ecss.2019.106293>

970 Kondoh, M., Ninomiya, K., 2009. Food-chain length and adaptive foraging. *Proceedings of*  
971 *the Royal Society B: Biological Sciences* 276, 3113–3121.  
972 <https://doi.org/10.1098/rspb.2009.0482>

973 Koppelman, R., Weikert, H., Lahajnar, N., 2003. Vertical distribution of mesozooplankton  
974 and its  $\delta^{15}\text{N}$  signature at a deep-sea site in the Levantine Sea (eastern Mediterranean) in  
975 April 1999. *Journal of Geophysical Research: Oceans* 108.  
976 <https://doi.org/10.1029/2002JC001351>

977 Koppelman, R., Böttger-Schnack, R., Möbius, J., Weikert, H., 2009. Trophic relationships of  
978 zooplankton in the eastern Mediterranean based on stable isotope measurements. *Journal*  
979 *of Plankton Research* 31, 669–686. <https://doi.org/10.1093/plankt/fbp013>

980 Kozak, E.R., Franco-Gordo, C., Godínez-Domínguez, E., Suárez-Morales, E., Ambriz-  
981 Arreola, I., 2020. Seasonal variability of stable isotope values and niche size in tropical  
982 calanoid copepods and zooplankton size fractions. *Marine Biology* 167, 37.  
983 <https://doi.org/10.1007/s00227-020-3653-7>

984 Krasakopoulou, E., Karageorgis, A.P., 2005. Spatial and temporal distribution patterns of  
985 suspended particulate matter and particulate organic carbon in the Saronikos Gulf

986 (eastern Mediterranean, Greece). *Geo-Marine Letters* 25, 343–359.  
987 <https://doi.org/10.1007/s00367-005-0007-x>

988 Kürten, B., Painting, S.J., Struck, U., Polunin, N.V.C., Middelburg, J.J., 2013. Tracking  
989 seasonal changes in North Sea zooplankton trophic dynamics using stable isotopes.  
990 *Biogeochemistry* 113, 167–187. <https://doi.org/10.1007/s10533-011-9630-y>

991 Lam, P.J., Ohnemus, D.C., Auro, M.E., 2015. Size-fractionated major particle composition  
992 and concentrations from the US GEOTRACES North Atlantic Zonal Transect. *Deep Sea*  
993 *Research Part II: Topical Studies in Oceanography*, 116, 303–320.  
994 <https://doi.org/10.1016/j.dsr2.2014.11.020>

995 Laws, E.A., Popp, B.N., Bidigare, R.R., Kennicutt, M.C., Macko, S.A., 1995. Dependence of  
996 phytoplankton carbon isotopic composition on growth rate and [CO<sub>2</sub>]<sub>aq</sub>: Theoretical  
997 considerations and experimental results. *Geochimica et Cosmochimica Acta* 59, 1131–  
998 1138. [https://doi.org/10.1016/0016-7037\(95\)00030-4](https://doi.org/10.1016/0016-7037(95)00030-4)

999 Leblanc, K., Quéguiner, B., Diaz, F., Cornet, V., Michel-Rodriguez, M., Durrieu de Madron,  
1000 X., Bowler, C., Malviya, S., Thyssen, M., Grégori, G., Rembauville, M., Grosso, O.,  
1001 Poulain, J., de Vargas, C., Pujo-Pay, M., Conan, P., 2018. Nanoplanktonic diatoms are  
1002 globally overlooked but play a role in spring blooms and carbon export. *Nature*  
1003 *Communications* 9, 953. <https://doi.org/10.1038/s41467-018-03376-9>

1004 Levinson, H., Turner, J.T., Nielsen, T.G., Hansen, B.W., 2000. On the trophic coupling  
1005 between protists and copepods in arctic marine ecosystems. *Marine Ecology Progress*  
1006 *Series* 204, 65–77. <https://doi.org/10.3354/meps204065>

1007 Liénart, C., Savoye, N., Bozec, Y., Breton, E., Conan, P., David, V., Feunteun, E., Grangeré,  
1008 K., Kerhervé, P., Lebreton, B., Lefebvre, S., L'Helguen, S., Mousseau, L., Raimbault, P.,  
1009 Richard, P., Riera, P., Sauriau, P.-G., Schaal, G., Aubert, F., Aubin, S., Bichon, S.,  
1010 Boinet, C., Bourasseau, L., Bréret, M., Caparros, J., Cariou, T., Charlier, K., Claquin, P.,  
1011 Cornille, V., Corre, A.-M., Costes, L., Crispi, O., Crouvoisier, M., Czamanski, M., Del  
1012 Amo, Y., Derriennic, H., Dindinaud, F., Durozier, M., Hanquiez, V., Nowaczyk, A.,  
1013 Devesa, J., Ferreira, S., Fournier, M., Garcia, F., Garcia, N., Geslin, S., Grossteffan, E.,  
1014 Gueux, A., Guillaudeau, J., Guillou, G., Joly, O., Lachaussée, N., Lafont, M.,  
1015 Lamoureux, J., Lecuyer, E., Lehodey, J.-P., Lemeille, D., Leroux, C., Macé, E., Maria,  
1016 E., Pineau, P., Petit, F., Pujo-Pay, M., Rimelin-Maury, P., Sultan, E., 2017. Dynamics of  
1017 particulate organic matter composition in coastal systems: A spatio-temporal study at  
1018 multi-systems scale. *Progress in Oceanography* 156, 221–239.  
1019 <https://doi.org/10.1016/j.pocean.2017.03.001>



1020 Liénart, C., Savoye, N., David, V., Ramond, P., Rodriguez Tress, P., Hanquiez, V., Marieu,  
1021 V., Aubert, F., Aubin, S., Bichon, S., Boinet, C., Bourasseau, L., Bozec, Y., Bréret, M.,  
1022 Breton, E., Caparros, J., Cariou, T., Claquin, P., Conan, P., Corre, A.-M., Costes, L.,  
1023 Crouvoisier, M., Del Amo, Y., Derriennic, H., Dindinaud, F., Duran, R., Durozier, M.,  
1024 Devesa, J., Ferreira, S., Feunteun, E., Garcia, N., Geslin, S., Grossteffan, E., Gueux, A.,  
1025 Guillaudeau, J., Guillou, G., Jolly, O., Lachaussée, N., Lafont, M., Lagadec, V.,  
1026 Lamoureux, J., Lauga, B., Lebreton, B., Lecuyer, E., Lehodey, J.-P., Leroux, C.,  
1027 L’Helguen, S., Macé, E., Maria, E., Mousseau, L., Nowaczyk, A., Pineau, P., Petit, F.,  
1028 Pujo-Pay, M., Raimbault, P., Rimmelin-Maury, P., Rouaud, V., Sauriau, P.-G., Sultan, E.,  
1029 Susperregui, N., 2018. Dynamics of particulate organic matter composition in coastal  
1030 systems: Forcing of spatio-temporal variability at multi-systems scale. *Progress in*  
1031 *Oceanography* 162, 271–289. <https://doi.org/10.1016/j.pocean.2018.02.026>

1032 Ljungström, G., Claireaux, M., Fiksen, Ø., Jørgensen, C., 2020. Body size adaptations under  
1033 climate change: zooplankton community more important than temperature or food  
1034 abundance in model of a zooplanktivorous fish. *Marine Ecology Progress Series* 636, 1–  
1035 18. <https://doi.org/10.3354/meps13241>

1036 Lowry, O.H., Rosebrough, N.J., Farr, A.L., Randall, R.J., 1951. Protein measurement with the  
1037 Folin phenol reagent. *Journal of Biological Chemistry* 193, 265–275.

1038 Maguer, J.-F., L’helguen, S., Le Corre, P., 2000. Nitrogen Uptake by Phytoplankton in a  
1039 Shallow Water Tidal Front. *Estuarine, Coastal and Shelf Science* 51, 349–357.  
1040 <https://doi.org/10.1006/ecss.2000.0678>

1041 Major, Y., Kifle, D., Niedrist, G.H., Sommaruga, R., 2017. An isotopic analysis of the  
1042 phytoplankton–zooplankton link in a highly eutrophic tropical reservoir dominated by  
1043 cyanobacteria. *Journal of Plankton Research* 39, 220–231.  
1044 <https://doi.org/10.1093/plankt/fbx007>

1045 Mason, R.P., Reinfelder, J.R., Morel, F.M.M., 1995. Bioaccumulation of mercury and  
1046 methylmercury. *Water Air Soil Pollut* 80, 915–921. <https://doi.org/10.1007/BF01189744>

1047 Mauchline, J., 1998. The biology of Calanoid copepods. In: Blaxter, J.H.S., Southward, A.J.,  
1048 Tyler, P.A.(Eds.), *Advances in Marine Biology*, 245–292. Academic Press, San Diego,  
1049 USA.

1050 Mayot, N., D’Ortenzio, F., Uitz, J., Gentili, B., Ras, J., Vellucci, V., Golbol, M., Antoine, D.,  
1051 Claustre, H., 2017. Influence of the Phytoplankton Community Structure on the Spring  
1052 and Annual Primary Production in the Northwestern Mediterranean Sea. *Journal of*  
1053 *Geophysical Research: Oceans* 122, 9918–9936. <https://doi.org/10.1002/2016JC012668>

1054 Mayzaud, P., Chanut, J., Ackman, R., 1989. Seasonal changes of the biochemical composition  
1055 of marine particulate matter with special reference to fatty acids and sterols. *Marine*  
1056 *Ecology Progress Series* 56, 189–204. <https://doi.org/10.3354/meps056189>

1057 Montoya, J.P., Carpenter, E.J., Capone, D.G., 2002. Nitrogen fixation and nitrogen isotope  
1058 abundances in zooplankton of the oligotrophic North Atlantic. *Limnology and*  
1059 *Oceanography* 47, 1617–1628. <https://doi.org/10.4319/lo.2002.47.6.1617>

1060 Morris, M.J., Hopkins, T.L., 1983. Biochemical composition of crustacean zooplankton from  
1061 the eastern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology* 69, 1–  
1062 19.

1063 Motwani, N.H., Gorokhova, E., 2013. Mesozooplankton Grazing on Picocyanobacteria in the  
1064 Baltic Sea as Inferred from Molecular Diet Analysis. *PLOS ONE* 8, e79230.  
1065 <https://doi.org/10.1371/journal.pone.0079230>

1066 Onodera, T., Kanaya, G., Hatamoto, M., Kohzu, A., Iguchi, A., Takimoto, Y., Yamaguchi, T.,  
1067 Mizuochi, M., Syutsubo, K., 2018. Evaluation of trophic transfer in the microbial food  
1068 web during sludge degradation based on <sup>13</sup>C and <sup>15</sup>N natural abundance. *Water*  
1069 *Research* 146, 30–36. <https://doi.org/10.1016/j.watres.2018.09.016>

1070 Ostrom, P. H., Fry, B., 1993. Sources and cycling of organic matter within modern and  
1071 prehistoric food webs. *Organic geochemistry*, 785-798. Springer, Boston, MA.

1072 Pantoja, S., Repeta, D.J., Sachs, J.P., Sigman, D.M., 2002. Stable isotope constraints on the  
1073 nitrogen cycle of the Mediterranean Sea water column. *Deep Sea Research Part I:*  
1074 *Oceanographic Research Papers* 49, 1609–1621. [https://doi.org/10.1016/S0967-](https://doi.org/10.1016/S0967-0637(02)00066-3)  
1075 [0637\(02\)00066-3](https://doi.org/10.1016/S0967-0637(02)00066-3)

1076 Parnell, A.C., Phillips, D.L., Bearhop, S., Semmens, B.X., Ward, E.J., Moore, J.W., Jackson,  
1077 A.L., Grey, J., Kelly, D.J., Inger, R., 2013. Bayesian stable isotope mixing models.  
1078 *Environmetrics* 24, 387–399. <https://doi.org/10.1002/env.2221>

1079 Peterson, B.J., Howarth, R.W., Garritt, R.H., 1985. Multiple stable isotopes used to trace the  
1080 flow of organic matter in estuarine food webs. *Science* 227, 1361–1363.  
1081 <https://doi.org/10.1126/science.227.4692.1361>

1082 Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens,  
1083 B.X., Ward, E.J., 2014. Best practices for use of stable isotope mixing models in food-  
1084 web studies. *Canadian Journal of Zoology* 92, 823–835. [https://doi.org/10.1139/cjz-2014-](https://doi.org/10.1139/cjz-2014-0127)  
1085 [0127](https://doi.org/10.1139/cjz-2014-0127)

1086 Pinnegar, J.K., Polunin, N.V.C., 1999. Differential fractionation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  among  
1087 fish tissues: implications for the study of trophic interactions. *Functional Ecology* 13,  
1088 225–231. <https://doi.org/10.1046/j.1365-2435.1999.00301.x>

1089 Post, D.M., 2002. Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and  
1090 Assumptions. *Ecology* 83, 703–718. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2)

1092 Postel, L., Fock, H., Hagen, W., 2000. 4 - Biomass and abundance, In: Harris, R., Wiebe, P.,  
1093 Lenz, J., Skjoldal, H.R., Huntley, M. (Eds.), *ICES Zooplankton Methodology Manual*.  
1094 Academic Press, London, pp. 83–192. <https://doi.org/10.1016/B978-012327645-2/50005-0>

1096 Raimbault, P., Diaz, F., Pouvesle, W., Boudjellal, B., 1999. Simultaneous determination of  
1097 particulate organic carbon, nitrogen and phosphorus collected on filters, using a semi-  
1098 automatic wet-oxidation method. *Marine Ecology Progress Series* 180, 289.

1099 Raimbault, P., Garcia, N., Cerutti, F., 2008. Distribution of inorganic and organic nutrients in  
1100 the South Pacific Ocean; evidence for long-term accumulation of organic matter in  
1101 nitrogen-depleted waters. *Biogeosciences* 5, 281–298. <https://doi.org/10.5194/bg-5-281-2008>

1103 Rau, G., Teysse, J., Rassoulzadegan, F., Fowler, S., 1990. C-13/C-12 and N-15/N-14  
1104 variations among size-fractionated marine particles - implications for their origin and  
1105 trophic relationships. *Marine Ecology Progress Series* 59(1/2), 33–38.

1106 Ríos, A.F., Fraga, F., Pérez, F.F., Figueiras, F.G., 1998. Chemical composition of  
1107 phytoplankton and Particulate Organic Matter in the Ría de Vigo (NW Spain). *Scientia*  
1108 *Marina* 62 (3), 257–271 <https://doi.org/10.3989/scimar.1998.62n3257>

1109 Rolff, C., 2000. Seasonal variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of size-fractionated plankton at a  
1110 coastal station in the northern Baltic proper. *Marine Ecology Progress Series* 203, 47–65.  
1111 <https://doi.org/10.3354/meps203047>

1112 Ryther, J.H., 1969. Photosynthesis and Fish Production in the Sea. *Science* 166, 72–76.  
1113 <https://doi.org/10.1126/science.166.3901.72>

1114 Schartup, A.T., Qureshi, A., Dassuncao, C., Thackray, C.P., Harding, G., Sunderland, E.M.,  
1115 2018. A Model for Methylmercury Uptake and Trophic Transfer by Marine Plankton.  
1116 *Environmental Science & Technology* 52, 654–662.  
1117 <https://doi.org/10.1021/acs.est.7b03821>

1118 Sommer, F., Stibor, H., Sommer, U., Velimirov, B., 2000. Grazing by mesozooplankton from  
1119 Kiel Bight, Baltic Sea, on different sized algae and natural seston size fractions. *Marine*  
1120 *Ecology Progress Series* 199, 43–53. <https://doi.org/10.3354/meps199043>

1121 Sommer, U., Stibor, H., Katchakis, A., Sommer, F., Hansen, T., 2002. Pelagic food web  
1122 configurations at different levels of nutrient richness and their implications for the ratio  
1123 fish production:primary production, in: Vadstein, O., Olsen, Y. (Eds.), *Sustainable*  
1124 *Increase of Marine Harvesting: Fundamental Mechanisms and New Concepts*. Springer  
1125 Netherlands, Dordrecht, pp. 11–20. [https://doi.org/10.1007/978-94-017-3190-4\\_2](https://doi.org/10.1007/978-94-017-3190-4_2)

1126 Søreide, J.E., Hop, H., Carroll, M.L., Falk-Petersen, S., Hegseth, E.N., 2006. Seasonal food  
1127 web structures and sympagic–pelagic coupling in the European Arctic revealed by stable  
1128 isotopes and a two-source food web model. *Progress in Oceanography* 71, 59–87.  
1129 <https://doi.org/10.1016/j.pocean.2006.06.001>

1130 Tamelander, T., Kivimäe, C., Bellerby, R.G.J., Renaud, P.E., Kristiansen, S., 2009. Base-line  
1131 variations in stable isotope values in an Arctic marine ecosystem: effects of carbon and  
1132 nitrogen uptake by phytoplankton. *Hydrobiologia* 630, 63–73.  
1133 <https://doi.org/10.1007/s10750-009-9780-2>

1134 Tao, Y., Yu, J., Liu, X., Xue, B., Wang, S., 2018. Factors affecting annual occurrence,  
1135 bioaccumulation, and biomagnification of polycyclic aromatic hydrocarbons in plankton  
1136 food webs of subtropical eutrophic lakes. *Water Research* 132, 1–11.  
1137 <https://doi.org/10.1016/j.watres.2017.12.053>

1138 Tedetti, M., Tronczynski, J., 2019. HIPPOCAMPE cruise, RV Antea.  
1139 <https://doi.org/10.17600/18000900>

1140 Tedetti, M., Tronczynski, J., Carlotti, J.F., Pagano, M., Ben Ismail, S., Sammari, C., Bel  
1141 Hassen, M., Desboeufs, K., Poindron, C., Chifflet, S., Bellaaj Zouari, A., Abdennadher,  
1142 M., Amri, S., Bănar, D., Ben Abdallah, L., Bhairy, N., Boudriga, I., Bourin, A., Brach-  
1143 Papa, C., Briant, N., Cabrol, L., Chevalier, C., Chouba, L., Coudray, S., Daly Yahia, M.  
1144 N., de Garidel Thoron, T., Dufour, A., Dutay, J-C., Espinasse, B., Fierro-González, P.,  
1145 Fournier, M., Garcia, N., Giner, F., Guigue, C., Guilloux, L., Hamza, A., Heimbürger-  
1146 Boavida, L-E., Jacquet, S., Knoery, J., Lajnef, R., Makhlof Belkahia, N., Malengros, D.,  
1147 Martinot, P.L., Bosse, A., Mazur, J-C., Meddeb, M., Misson, B., Pringault, O.,  
1148 Quéméneur, M., Radakovitch, O., Raimbault, P., Ravel, R., Rossi, R., Rwawi, C., Sakka  
1149 Hlaili, A., Tesán-Onrubia, J.A., Thomas, B., Thyssen, M., Zaaboub, N., Garnier, C.,  
1150 2023. Contamination of planktonic food webs in the Mediterranean Sea: Setting the

1151 frame for the MERITE-HIPPOCAMPE oceanographic cruise (spring 2019). *Marine*  
1152 *Pollution Bulletin*. In press in this special issue.

1153 Tiano, M., Tronczyński, J., Harmelin-Vivien, M., Tixier, C., Carlotti, F., 2014. PCB  
1154 concentrations in plankton size classes, a temporal study in Marseille Bay, Western  
1155 Mediterranean Sea. *Marine Pollution Bulletin* 89, 331–339.  
1156 <https://doi.org/10.1016/j.marpolbul.2014.09.040>

1157 Tiselius, P., Fransson, K., 2016. Daily changes in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  stable isotopes in copepods:  
1158 equilibrium dynamics and variations of trophic level in the field. *Journal of Plankton*  
1159 *Research* 38, 751–761. <https://doi.org/10.1093/plankt/fbv048>

1160 Trimble, S.M., Baskaran, M., 2005. The role of suspended particulate matter in  $^{234}\text{Th}$   
1161 scavenging and  $^{234}\text{Th}$ -derived export fluxes of POC in the Canada Basin of the Arctic  
1162 Ocean. *Marine Chemistry* 96, 1–19. <https://doi.org/10.1016/j.marchem.2004.10.003>

1163 Vander Zanden, M.J.V., Rasmussen, J.B., 2001. Variation in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  trophic  
1164 fractionation: Implications for aquatic food web studies. *Limnology and Oceanography*  
1165 46, 2061–2066. <https://doi.org/10.4319/lo.2001.46.8.2061>

1166 Wainright, S.C., Fry, B., 1994. Seasonal variation of the stable isotopic compositions of  
1167 coastal marine plankton from Woods Hole, Massachusetts and Georges Bank. *Estuaries*  
1168 17, 552–560. <https://doi.org/10.2307/1352403>

1169 Wu, Y., Wang, W.-X., 2011. Accumulation, subcellular distribution and toxicity of inorganic  
1170 mercury and methylmercury in marine phytoplankton. *Environmental Pollution, Nitrogen*  
1171 *Deposition, Critical Loads and Biodiversity* 159, 3097–3105.  
1172 <https://doi.org/10.1016/j.envpol.2011.04.012>

1173 Yang, G., Li, C., Guilini, K., Wang, X., Wang, Y., 2017. Regional patterns of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$   
1174 stable isotopes of size-fractionated zooplankton in the western tropical North Pacific  
1175 Ocean. *Deep Sea Research Part I: Oceanographic Research Papers* 120, 39–47.  
1176 <https://doi.org/10.1016/j.dsr.2016.12.007>

1177 Yılmaz, A.Z., Besiktepe, S., 2010. Annual variations in biochemical composition of size  
1178 fractionated particulate matter and zooplankton abundance and biomass in Mersin Bay,  
1179 NE Mediterranean Sea. *Journal of Marine Systems* 81, 260–271.  
1180 <https://doi.org/10.1016/j.jmarsys.2010.01.002>

1181

1182 Figure captions

1183

1184 **Figure 1.** Location of the ten sampling stations of the MERITE-HIPPOCAMPE campaign in the Mediterranean  
1185 Sea (April-Mai 2019).

1186

1187 **Figure 2.** Boxplot of the concentrations of A) proteins, B) carbohydrates, C) lipids ( $\mu\text{g mg}^{-1}$  DW) and D) energy  
1188 content ( $E_i$ ) ( $\text{kJ g}^{-1}$  DW) in the different plankton size-fractions (fractions between 0.7 and 60  $\mu\text{m}$  in green and >  
1189 60  $\mu\text{m}$  in orange) for all stations combined. H = Kruskal–Wallis non-parametric test and the associated p-value  
1190 for the respective biochemical compounds: H = 43.5,  $p < 0.0001$ ; H = 110.6,  $p < 0.001$ ; H = 41.8,  $p < 0.0001$  and  
1191 H = 51.7,  $p < 0.0001$ . Mean values with different letters are significantly different ( $p < 0.05$ ). The mean and  
1192 median values are represented by a cross and a horizontal line, respectively, and the box length is defined as the  
1193 interquartile range. The minimum and maximum values are represented by whiskers. Mean values with different  
1194 post-hoc letters are significantly different ( $p < 0.05$ ).

1195

1196 **Figure 3.** Boxplot of the concentrations of A, B) proteins, C, D) carbohydrates, E, F) lipids ( $\mu\text{g mg}^{-1}$  DW) and  
1197 G, H) energy content ( $E_i$ ) ( $\text{kJ g}^{-1}$  DW) in the phyto- (fractions between 0.7 and 60  $\mu\text{m}$  – in green) and  
1198 zooplankton (fractions between 60 and 500  $\mu\text{m}$  – in orange) fractions for each station. H = Kruskal–Wallis non-  
1199 parametric test and the associated p-value for the respective biochemical compounds for phytoplankton (H =  
1200 43.4,  $p < 0.0001$ ; H = 30.6,  $p < 0.0001$ ; H = 34.9,  $p < 0.0001$  and H = 42.9,  $p < 0.0001$ ) and for zooplankton (H  
1201 = 43.8,  $p < 0.0001$ ; H = 22.9,  $p < 0.006$ ; H = 38.8,  $p < 0.0001$  and H = 38.8,  $p < 0.0001$ ). Stations are grouped  
1202 by geographical area: St1, St2, St3 and St4 for the Northern coast, St9, St10 and St11 for the offshore area, and  
1203 St15, St17 and St19 for the Southern coast. The mean and median values were represented by a cross and a  
1204 horizontal line, respectively, and the box length is defined as the interquartile range. The minimum and  
1205 maximum values are represented by whiskers. Mean values with different post-hoc letters are significantly  
1206 different ( $p < 0.05$ ).

1207

1208 **Figure 4.** Total amount of energy provided by plankton ( $E_T$  in  $\text{kJ m}^{-3}$ ) for each of the size-fractions by station.  
1209 Stations are grouped by geographical area: St1, St2, St3 and St4 for the Northern coast, St9, St10 and St11 for  
1210 the offshore area, and St15, St17 and St19 for the Southern coast.

1211

1212 **Figure 5.** Mean ( $\pm$  standard error, SE) stable isotope compositions ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, ‰) in the different  
1213 plankton size-fractions for all stations combined. Green dots correspond to the phytoplankton size-fractions  
1214 (from 0.7 to 60  $\mu\text{m}$ ), while the orange dots correspond to zooplankton size-fractions (> 60  $\mu\text{m}$ ).

1215

1216 **Figures 6.** Boxplot of the A, B)  $\delta^{13}\text{C}$  and C, D)  $\delta^{15}\text{N}$  values (‰) in the phyto- (fractions between 0.7 and 60  $\mu\text{m}$   
1217 – in green) and zooplankton (fractions between 60 and 500  $\mu\text{m}$  – in orange) fractions for each station. Stations  
1218 are grouped by geographical area: St1, St2, St3 and St4 for the Northern coast, St9, St10 and St11 for the  
1219 offshore area, and St15, St17 and St19 for the Southern coast. Kruskal–Wallis non-parametric test were  
1220 performed for A) (H = 25.5,  $p < 0.05$ ), C) (H = 24.1,  $p < 0.05$ ) and D) (H = 33.5,  $p < 0.0001$ ), and one-way

1221 ANOVA test was performed for B) ( $F = 4.4$ ,  $p < 0.0001$ ). The mean and median values are represented by a  
1222 cross and a horizontal line, respectively, and the box length is defined as the interquartile range. The minimum  
1223 and maximum values are represented by whiskers. Mean values with different post-hoc letters are significantly  
1224 different ( $p < 0.05$ ).

1225

1226 **Figure 7.** Boxplot of the trophic levels (TL) of the zooplankton size-fractions (60 to  $> 2000 \mu\text{m}$ ). The median  
1227 value is represented by a horizontal line and the box length is defined as the interquartile range. The minimum  
1228 and maximum values are represented by whiskers. One-way ANOVA test ( $F = 5.17$ ,  $p = 0.001$ ). Superscript  
1229 letters represent Newman-Keuls post-hoc groups and values with the different letters are significantly different  
1230 ( $p < 0.05$ ).

1231

1232 **Figure 8.** Trophic levels (TL) of the zooplankton size-fractions (60 to  $> 2000 \mu\text{m}$ ) and mean TL weighted by  
1233 their biomass ( $\text{TL}_B$ ) for each station. Stations are gathered by geographical area: St1, St2, St3 and St4 for the  
1234 Northern coast, St9, St10 and St11 for the offshore area, and St15, St17 and St19 for the Southern coast.

1235

1236 **Figure 9.** Relative contributions of  $0.7\text{--}2.7 \mu\text{m}$  (pico-),  $2.7\text{--}20 \mu\text{m}$  (nano-), and  $20\text{--}60 \mu\text{m}$  (microplankton) as  
1237 food resources for three zooplankton size-fractions. Arrows indicate the trophic transfer between pico-POM  
1238 nano-POM, and micro-POM fractions and zooplankton size fractions:  $60\text{--}500 \mu\text{m}$  (in green),  $500\text{--}2000 \mu\text{m}$  (in  
1239 blue) and  $> 2000 \mu\text{m}$  (in orange). Their thickness is proportional to relative contribution in percentage, indicated  
1240 close to the corresponding arrow.

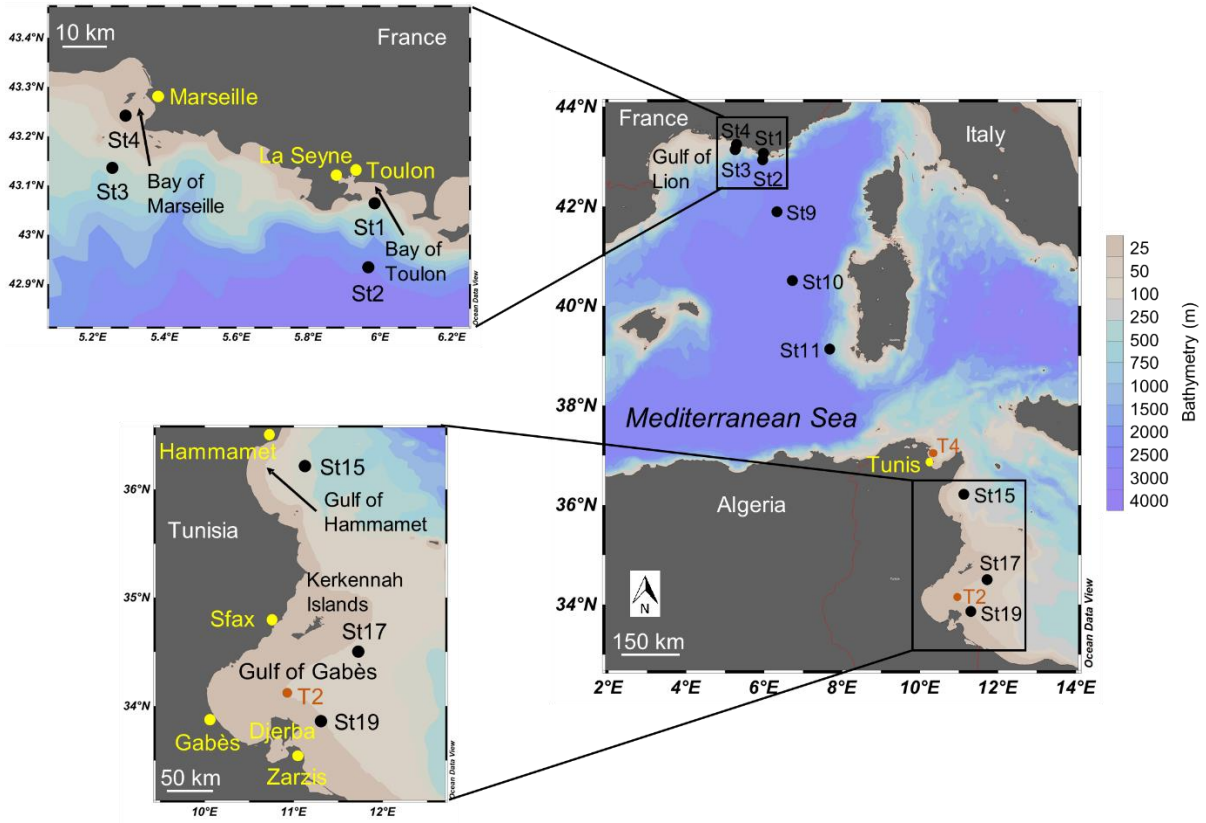
1241

1242 **Table 1.** Suspended particulate matter and plankton dry weight ( $\text{SPM}_{\text{DW}}$  and  $\text{Plankton}_{\text{DW}}$ , in  $\text{mg DW L}^{-1}$ ) for the  
1243 different plankton size-fractions and stations, as well as total chlorophyll *a* concentration ( $\text{TChl}_a$ ,  $\mu\text{g L}^{-1}$ ) for the  
1244  $> 0.7\text{-}\mu\text{m}$  fraction. Kruskal-Wallis test and the associated *p*-value for  $\text{SPM}_{\text{DW}}$  ( $H = 23.15$ ,  $p < 0.0001$ ) and  
1245  $\text{Plankton}_{\text{DW}}$  ( $H = 28.51$ ,  $p < 0.0001$ ). Superscript letters represent rank comparison groups and values with  
1246 different letters are significantly different ( $p < 0.05$ ). St = station, SE = standard-error, *n* = number of samples.

1247

1248 **Figures**

1249

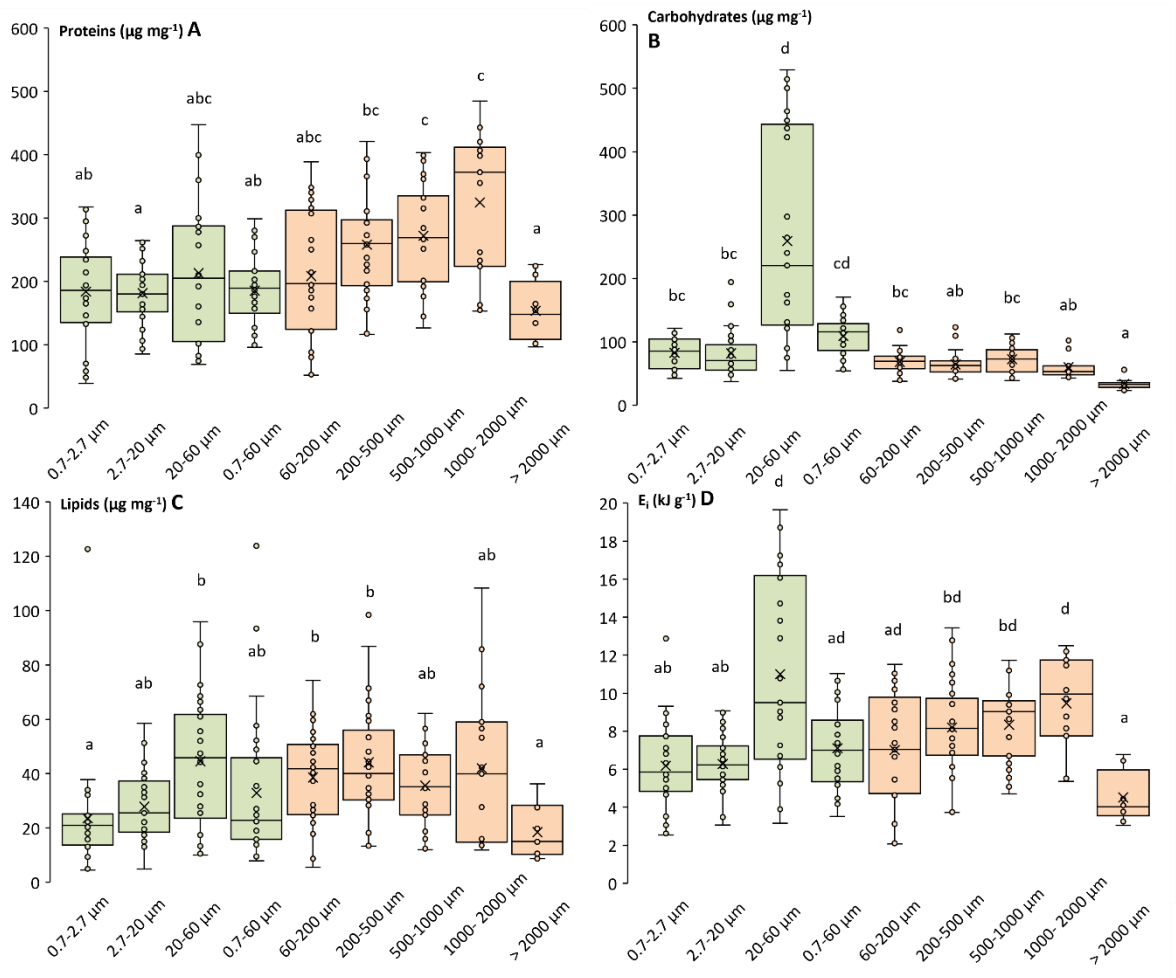


1250

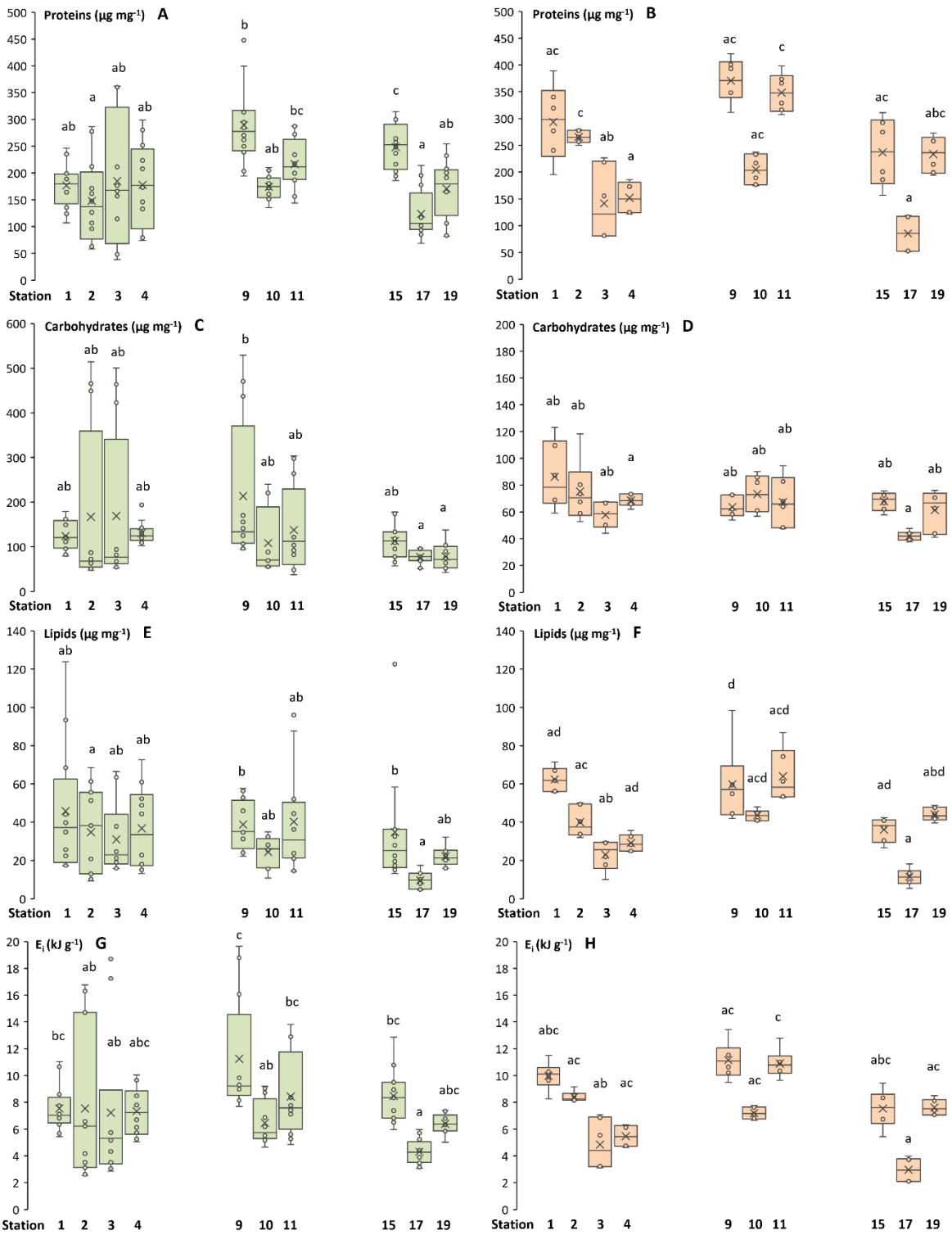
1251 **Figure 1**

1252





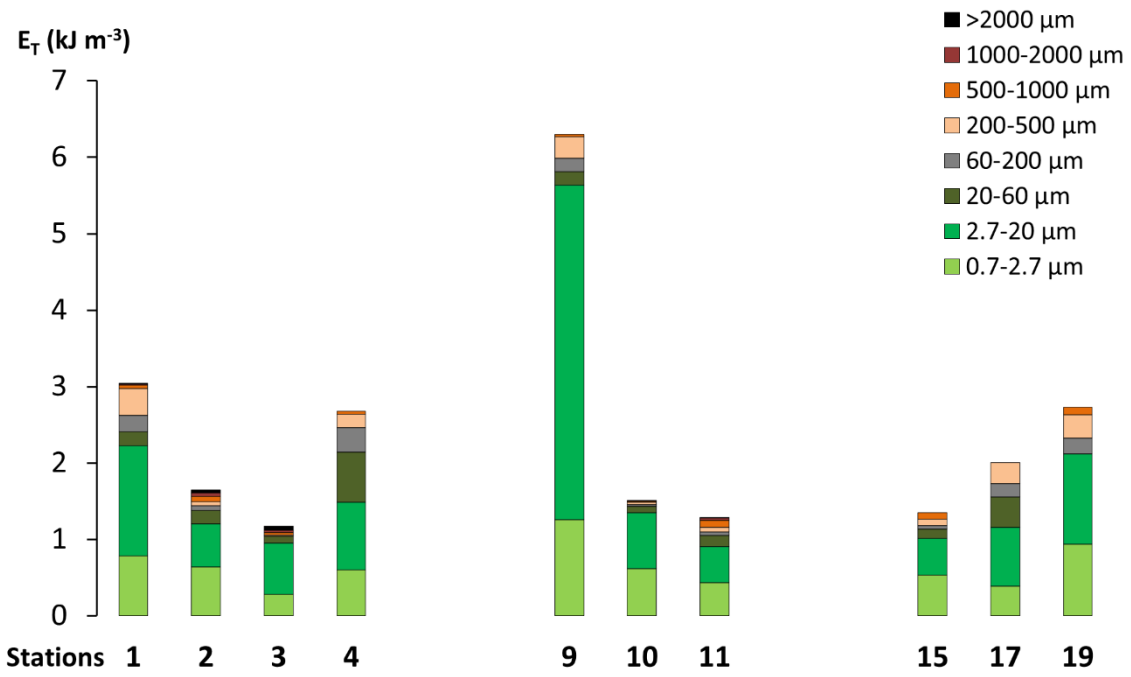
1255 **Figure 2**



1256

1257

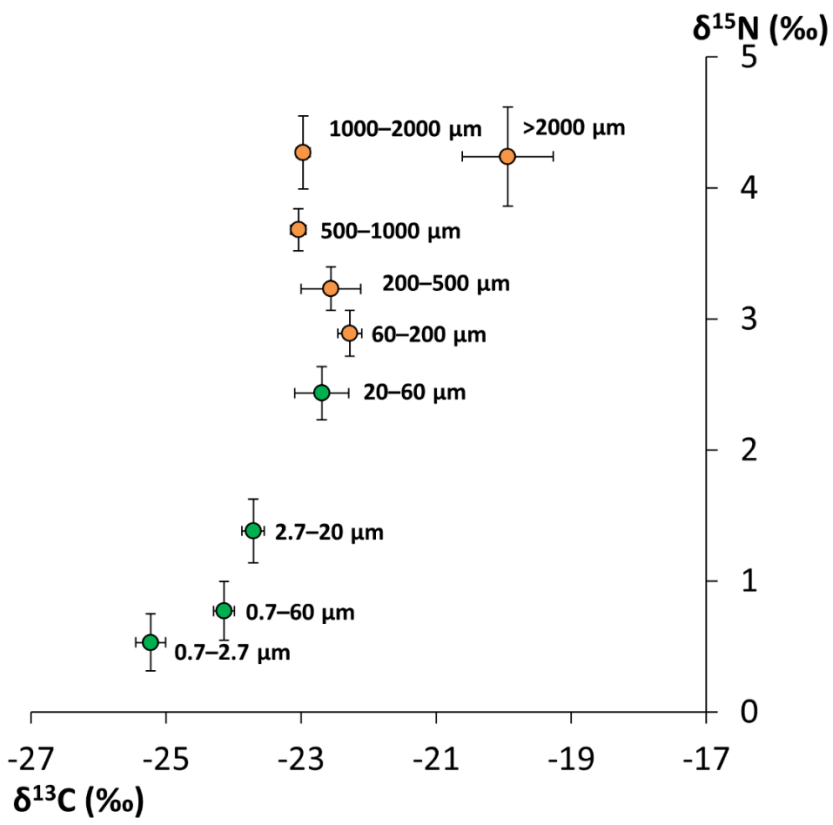
**Figure 3**



1258

1259 **Figure 4**

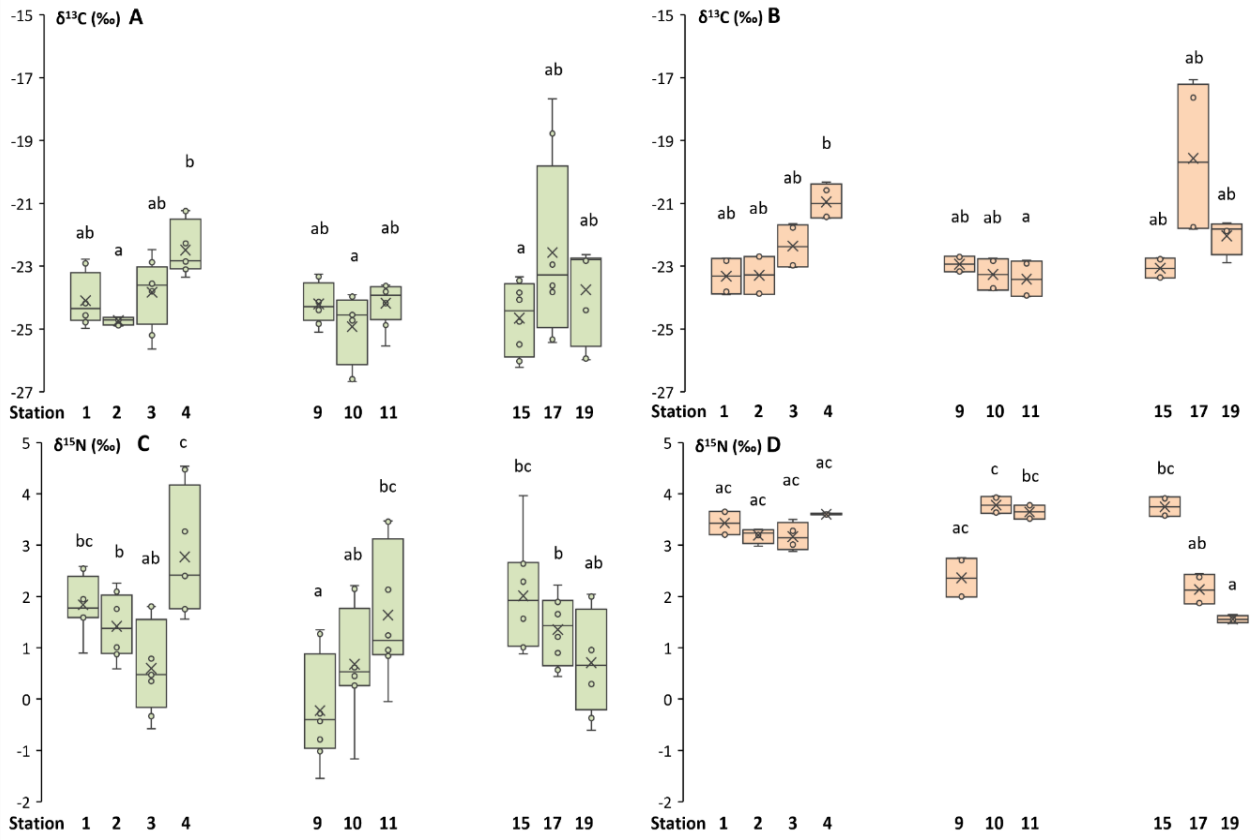
1260



1261

1262 **Figure 5**

1263

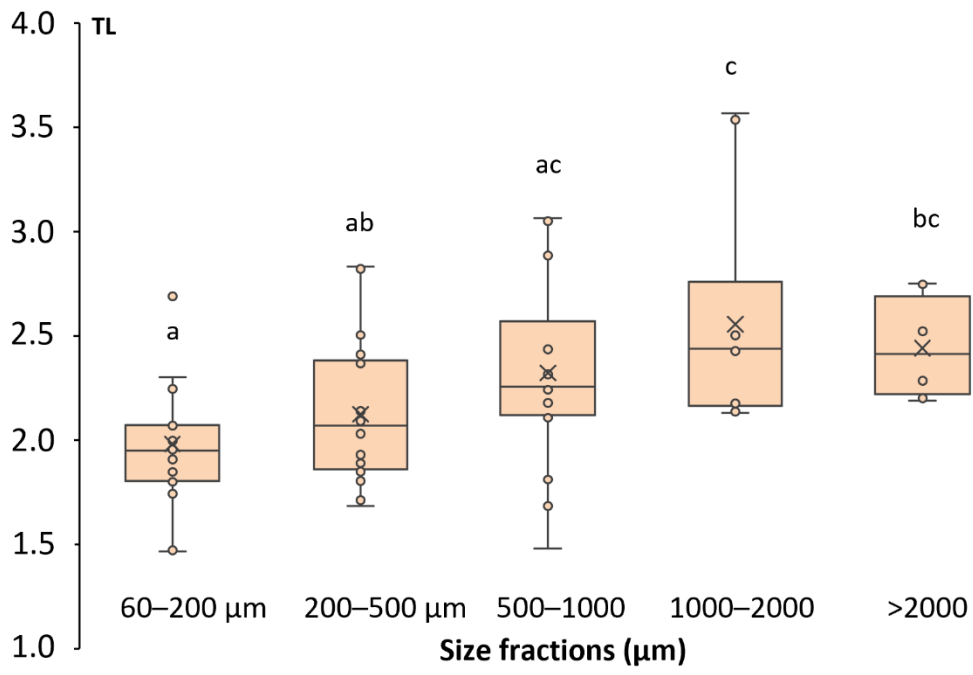


1264

1265 **Figure 6**

1266

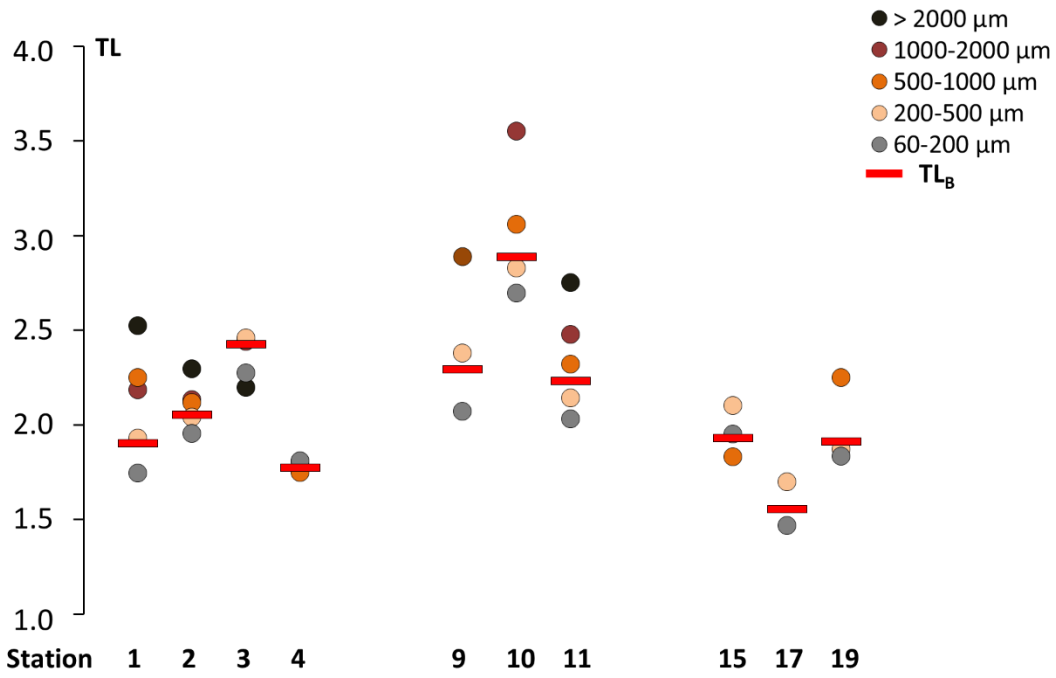
1267



1268

1269 **Figure 7**

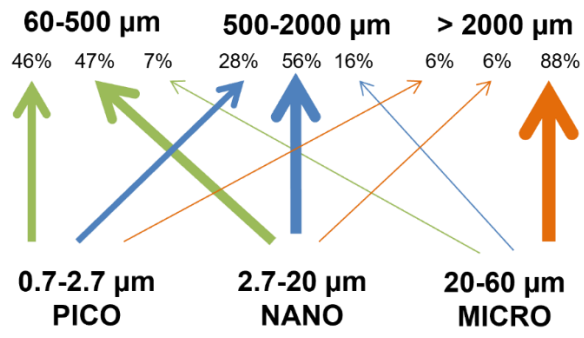
1270



1271

1272 **Figure 8**

1273



1274

1275 **Figure 9**

1276



1277 **Tables**1278 **Table 1.**

Stations	St1	St2	St3	St4	St9	St10	St11	St15	St17	St19	n	Mean $\pm$ SE		
Size-fractions	SPM <sub>DW</sub> (mg DW L <sup>-1</sup> )													
0.7–2.7 $\mu$ m	0.11	0.23	0.09	0.11	0.14	0.12	0.06	0.05	0.07	0.16	10	0.11	$\pm$ 0.02	ab
2.7–20 $\mu$ m	0.24	0.09	0.12	0.11	0.53	0.13	0.09	0.07	0.23	0.17	10	0.18	$\pm$ 0.04	bc
20–60 $\mu$ m	0.03	0.01	0.00	0.11	0.01	0.01	0.01	0.01	0.11	0.11	10	0.04	$\pm$ 0.02	a
0.7–60 $\mu$ m	0.35	0.32	0.21	0.22	0.67	0.25	0.15	0.12	0.29	0.34	10	0.29	$\pm$ 0.05	c
TChla (> 0.7 $\mu$ m) ( $\mu$ g L <sup>-1</sup> )	0.77	0.38	0.68	0.98	1.54	0.55	0.38	0.67	0.21	1.45	10	0.76	$\pm$ 0.14	
	Plankton <sub>DW</sub> (mg DW L <sup>-1</sup> )													
60–200 $\mu$ m	0.020	0.007	0.002	0.068	0.017	0.003	0.004	0.006	0.083	0.029	10	0.024	$\pm$ 0.027	ab
200–500 $\mu$ m	0.037	0.007	0.002	0.028	0.023	0.004	0.005	0.010	0.072	0.038	10	0.023	$\pm$ 0.021	ab
500–1000 $\mu$ m	0.005	0.007	0.004	0.007	0.004	0.002	0.009	0.009	0.002	0.011	10	0.006	$\pm$ 0.003	b
1000–2000 $\mu$ m	0.002	0.005	0.007	0.002	0.0002	0.001	0.002	0.001		0.0000	10	0.002	$\pm$ 0.002	a
> 2000 $\mu$ m	0.0004	0.005	0.013			0.0001	0.0004	0.001		0.0002	10	0.003	$\pm$ 0.005	a
Sum														
60–>2000 $\mu$ m	0.064	0.031	0.028	0.105	0.044	0.011	0.020	0.026	0.157	0.078	50	0.057	$\pm$ 0.019	

1279