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## Patterns of mesozooplankton community composition and vertical fluxes in the global ocean

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2 [ocean](#)

3

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25 **Abstract**

26 Vertical variations in physical and chemical conditions drive changes in marine  
27 zooplankton community composition. In turn, zooplankton communities play a critical role in  
28 regulating the transfer of organic matter produced in the surface ocean to deeper layers. Yet,  
29 the links between zooplankton community composition and the strength of vertical fluxes of  
30 particles remain elusive, especially on a global scale. Here, we provide a comprehensive  
31 analysis of variations in zooplankton community composition and vertical particle flux in the  
32 upper kilometer of the global ocean. Zooplankton samples were collected across five depth  
33 layers and vertical particle fluxes were assessed using continuous profiles of the Underwater  
34 Vision Profiler (UVP5) at 57 stations covering seven ocean basins. Zooplankton samples  
35 were analysed using a Zooscan and individual organisms were classified into 19 groups for  
36 the quantitative analyses. Zooplankton abundance, biomass and vertical particle flux  
37 decreased from the surface to 1000m depth at all latitudes. The zooplankton abundance  
38 decrease rate was stronger at sites characterised by oxygen minima ( $< 5\mu\text{mol O}_2.\text{kg}^{-1}$ ) where  
39 most zooplankton groups showed a marked decline in abundance, except the jellyfishes,  
40 molluscs, annelids, large protists and a few copepod families. The attenuation rate of vertical  
41 particle fluxes was weaker at such oxygen-depleted sites. Canonical redundancy analyses  
42 showed that the epipelagic zooplankton community composition depended on the  
43 temperature, on the phytoplankton size distribution and the surface large particulate organic  
44 matter while oxygen was an additional important factor for structuring zooplankton in the  
45 mesopelagic. Our results further suggest that future changes in surface phytoplankton size and  
46 taxa composition and mesopelagic oxygen loss might lead to profound shift in zooplankton  
47 abundance and community structure in both the euphotic and mesopelagic ocean. These  
48 changes may affect the vertical export and hereby the strength of the biological carbon pump

49

50

51 **Keywords: Zooplankton, biological carbon pump, Epipelagic, Mesopelagic, Community structure,**  
52 **Particle flux, Attenuation rates, Oxygen Minimum Zone.**

## 53 Introduction

54           The upper kilometer of the ocean constitutes a habitat where most of the organic  
55 carbon produced by the phytoplankton in the epipelagic layer (0-200m) sinks into the  
56 mesopelagic layer (200-1000m) while being progressively consumed and respired. Within the  
57 wide size spectrum of planktonic organisms (0.02 $\mu$ m-2m), mesozooplankton (0.2-20mm) are  
58 a pivotal component of marine trophic webs impacting the Biological Carbon Pump (BCP)  
59 through their feeding, vertical migration, and the production of faecal pellets (Steinberg and  
60 Landry, 2017). In a context of global climate change, zooplankton communities experience  
61 increasingly stressful conditions through global warming, ocean acidification and  
62 deoxygenation (Oschlies et al., 2018; Schmidtko et al., 2017), enhanced water column  
63 stratification in the open ocean and modifications in phytoplankton production and  
64 community structure (Coma et al., 2009; Kwiatkowski et al., 2019; Richardson, 2008). Long  
65 term field surveys have shown how changes in climatic conditions lead to large shifts in  
66 surface zooplankton composition (Beaugrand et al., 2019). Future climate warming could  
67 further reduce macronutrient supplies in the upper ocean and could therefore lead to a decline  
68 in biomass in the tropical open ocean or could cause positive trophic amplification in the  
69 polar ocean (Chust et al., 2014). Such changes in biomass may be amplified in the  
70 zooplankton through trophodynamic effects, which could greatly alter the fluxes of organic  
71 matter into the deeper mesopelagic layers. Modifications of the quantity and quality of the  
72 vertical particle flux produced in the surface layers could trigger substantial changes in  
73 mesozooplankton abundance and composition. In addition, the expansion of Oxygen  
74 Minimum Zones (OMZ) (Schmidtko et al., 2017; Stramma et al., 2010) may further constrain  
75 the spatial distribution of the numerous zooplankton taxa that are sensitive to dissolved  
76 oxygen levels (Ekau et al., 2010; Kiko et al., 2020; Kiko and Hauss, 2019; Seibel, 2011;  
77 Wishner et al., 2020, 2018). Therefore, understanding the variations of zooplankton biomass  
78 and diversity in the epi- and mesopelagic is essential to better understand the impact of global  
79 climate change on the properties of marine ecosystems.

80           However, mesopelagic zooplankton communities remain critically under-sampled  
81 compared to the epipelagic ones, as most collections are in the first 200m of the water  
82 column (Everett et al., 2017). The mesopelagic is still considered a “dark hole” (Robinson et  
83 al., 2010; St John et al., 2016) as the gaps in sampling lead to critical holes in knowledge  
84 regarding the functioning of mesopelagic ecosystems and how they are controlled by the  
85 organic matter fluxing from the euphotic zone. Local to regional field studies reported that the  
86 abundance of mesozooplankton decreases exponentially with depth, in parallel with

87 substantial changes in species diversity and genus composition that remain poorly resolved  
88 (Bode et al., 2018; Brugnano et al., 2012; Hernández-León et al., 2020; Koppelman et al.,  
89 2005; Kosobokova and Hopcroft, 2010; Yamaguchi et al., 2004). Some studies reported  
90 increases in diversity with depth, with maxima in the meso- to bathypelagic layers (Bode et  
91 al., 2018; Gaard et al., 2008; Kosobokova and Hopcroft, 2010; Yamaguchi et al., 2004),  
92 whereas other studies reported either the opposite diversity pattern or even an absence of  
93 vertical patterns due to large spatio-temporal variability (Gaard et al., 2008; Hidalgo et al.,  
94 2012; Palomares-García et al., 2013; Wishner et al., 2008). Such mismatch between  
95 observations might be related to the wide range of environmental conditions sampled using a  
96 variety of sampling gears that make inter-comparisons difficult. One recent global analysis of  
97 zooplankton vertical distribution in inter-tropical regions showed that in this narrow  
98 latitudinal band the vertical dimension was the main structuring pattern suggesting that  
99 midwater processes mediated by zooplankton may not change between oceans at those  
100 latitudes (Fernández de Puelles et al., 2019). How these changes relate to the vertical flux and  
101 also across the full latitudinal band is poorly understood because plankton observations and  
102 biogeochemical studies have usually been carried out by distinct scientific communities.  
103 Recent interdisciplinary cruises have taken place, providing more integrated knowledge on  
104 the importance of zooplankton to carbon sequestration (Guidi et al., 2016; Kiko et al., 2020;  
105 Steinberg and Landry, 2017; Stukel et al., 2019). No global study has yet been able to analyse  
106 community-level variations in zooplankton abundances, biomass and community composition  
107 in conjunction with assessments of vertical particle flux in the upper kilometre of the global  
108 ocean.

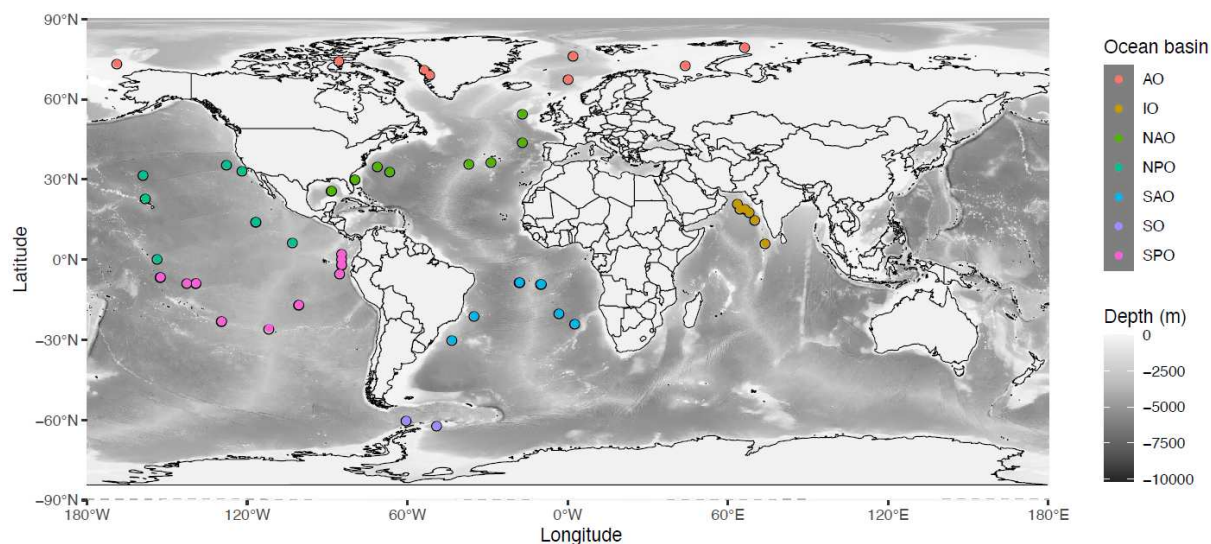
109 Here, a homogeneous dataset of community-level zooplankton images generated from  
110 the TARA Oceans expeditions is explored together with associated measurements of their  
111 contextual environmental conditions to: (i) test whether zooplankton communities present  
112 consistent vertical variations in abundance and composition across the oceans and in different  
113 latitudinal bands, and (ii) investigate the main drivers of such vertical gradients and how they  
114 are coupled to the surface phytoplankton and estimates of particle flux. The TARA Oceans  
115 expedition collected over 35000 samples encompassing the whole plankton community (i.e.,  
116 from viruses to jellyfish) across the global ocean from 2009 to 2013 (Karsenti et al., 2011).  
117 Previous studies that analysed the TARA Oceans imaging dataset explored the global  
118 latitudinal gradients in richness and composition for the whole plankton community focusing  
119 on surface waters (Ibarbalz et al., 2019; Brandao et al., in press). Here, we aim to describe the  
120 community composition of mesozooplankton down to 1000m depth on a global scale. As the

121 imaging techniques used here cannot achieve a species-level identification of the zooplankton  
122 community composition, our approach is rather oriented towards larger taxonomic and /or  
123 functional groups that may be associated with broad ecological and biogeochemical functions.

## 124 [Materials and methods](#)

### 125 **Sampling sites and environmental variables**

126 TARA Oceans took place between 2009 and 2013. Among the 210 stations that were  
127 sampled, 57 stations covering 7 ocean basins (Fig. 1) were sampled with a Multinet (Pesant et  
128 al., 2015; Roullier et al., 2014), a sampling device with five nets that allows for depth-  
129 stratified sampling (see below).



130  
131 **Fig. 1:** Location of the 57 stations sampled with the Multinet, grouped by ocean basin: AO=Arctic  
132 Ocean, IO=Indian Ocean, NAO=North Atlantic Ocean, NPO=North Pacific Ocean, SAO=South  
133 Atlantic Ocean, SO=Southern Ocean or Austral Ocean, SPO=South Pacific Ocean.

134  
135 A CTD rosette equipped with optical sensors was deployed to measure the physico-  
136 chemical parameters within the water column. Temperature and conductivity were measured  
137 from the surface to a maximum of 1300 m depth using a Seabird 911 CTD mounted on a Sea-  
138 Bird Carousel sampler with 10 Niskin bottles. The following additional sensors were mounted  
139 to measure optical properties related to relevant biogeochemical variables: fluorometer  
140 (Wetlab ECO-AFL/FL model), dissolved oxygen sensor (model SBE 43), nitrate sensor  
141 (ISUS with a maximum rating depth of 1000m Satlantic SA), a 25 cm transmissometer for  
142 particles 0.5–20  $\mu\text{m}$  (WETLabs), a one-wavelength backscatter meter for particles 0.5–10  $\mu\text{m}$

143 (WETLabs), and an Underwater Vision Profiler 5 (UVP5) for particles >150  $\mu\text{m}$  and  
144 zooplankton >600  $\mu\text{m}$  (Hydroptic). Assuming that particle sinking speed increases with size,  
145 those particles detected through the backscattering will be referred to as suspended particulate  
146 matter (SPM, particles < 10 $\mu\text{m}$  in Equivalent Spherical Diameter), while the ones detected by  
147 the UVP5 (>150 $\mu\text{m}$  in Equivalent Spherical Diameter) will be referred as particles. Vertical  
148 particle mass flux (in mg Dry Weight  $\text{m}^{-2} \text{d}^{-1}$ ) was calculated from the particle size spectra  
149 detected by the UVP5 as in (Guidi et al., 2008). Based on the High Pressure Liquid  
150 Chromatography (HPLC) analysis of water collected with Niskin bottles, we used the method  
151 of (Uitz et al., 2006) to estimate the contribution (%) of three pigment size classes  
152 (microphytoplankton, nanophytoplankton, and picophytoplankton;  $f_{\text{micro}}$ ,  $f_{\text{nano}}$ , and  $f_{\text{pico}}$ ,  
153 respectively) to total phytoplankton biomass in the epipelagic layer. According to the authors,  
154 such grouping allows for the description of the broad community composition with  $f_{\text{micro}}$   
155 dominated by diatoms,  $f_{\text{nano}}$  by chromophytes, cryptophytes and nanoflagellates and  $f_{\text{pico}}$   
156 by cyanobacteria, green flagellates and prochlorophytes. The median value of all hydrological  
157 and optical data together with imaging data were calculated for each of the five horizontal  
158 layers sampled by the Multinet for future data processing. The samples were classified as  
159 anoxic, hypoxic and normoxic according to the oxygen minimum value measured within the  
160 towed layer. We used a threshold of 5  $\mu\text{mol kg}^{-1}$  to classify the stations as anoxic (Roullier  
161 et al., 2014) and 58.5  $\mu\text{mol kg}^{-1}$  (Bode et al., 2018) to classify them as hypoxic.

## 162 **Zooplankton sampling, digitization, biomass estimates**

163 A Hydrobios Multinet (with a 300 $\mu\text{m}$  mesh and an aperture of 0.25 $\text{m}^2$ ) was used to  
164 sample zooplankton (Roullier et al., 2014; Pesant et al., 2015) in five distinct water layers  
165 ranging from the surface to occasionally 1300 m depth. The five depth layers were locally  
166 defined as a function of the vertical structure of the water column according to the profiles of  
167 temperature, salinity, fluorescence, nutrients, oxygen, and particulate matter (Pesant et al.,  
168 2015). The Multinet was equipped with a flowmeter to measure the volume of seawater  
169 filtered by each net tow (Pesant et al., 2015). Day and night net tows were conducted at ten  
170 stations. Sampling at the other stations occurred at day or night, depending on cruise schedule  
171 and operational constraints. Once collected, the samples were preserved in a solution of  
172 buffered formaldehyde-Borax solution (4%). In the laboratory, the samples were rinsed and  
173 split with a Motoda box (MOTODA, 1959). The final split was analysed with the Zooscan  
174 imaging system (Gorsky et al., 2010) which allowed a rapid and semi-automatic analysis of  
175 zooplankton samples. Few tens of morphological attributes (max and min length, area, grey

176 leves, ...) are measured on each object and used for the initial prediction. In total, nearly  
177 400,000 images of living zooplankton and detritus and their associated morphological data  
178 were obtained by the Zooscan. These images were imported into Ecotaxa, an online platform  
179 which allows an automatic prediction of the taxonomic classification of each single image  
180 followed by a manual validation/correction. The organisms were then identified manually  
181 down to the order, sometimes to the family and rarely down to the genus level. All copepods  
182 were sorted at the family level apart from the smallest copepods that cannot be recognised at  
183 the family level from the image. They were all grouped into one category called Other-  
184 copepoda or other-Calanoidea if their morphological features permitted classifying them as  
185 Calanoidea. This initial sorting allowed classifying zooplankton into 119 taxa. As many taxa  
186 showed a very small contribution to total zooplankton abundance, the 119 taxa were grouped  
187 into 19 taxonomic groups (Table 1). Those include all the major zooplankton groups that are  
188 frequently observed in the oceans. To investigate vertical patterns in mesozooplankton  
189 abundance, these 19 groups were further aggregated into eight groups representing a  
190 combination of taxonomic and functional classification (Table 1).

191 Once the zooplankton images were sorted, Ecotaxa enabled us to extract the  
192 concentration and the biovolume of each mesozooplankton group at every station and for  
193 every net tow, while accounting for the Motoda fraction and the volume sampled. The  
194 biovolume was computed for each individual zooplankton using the minor and major length  
195 axes assuming a prolate ellipsoidal shape (Gorsky et al., 2010). The biomass was calculated  
196 for the 8 large groups using the equations for the different taxa :

$$197 \quad \text{Body Weight}(\mu\text{C}) = aS^b \quad (1)$$

198 where  $S$  is body area in  $\text{mm}^2$ . Taxon-specific area-to-dry mass conversion factors  
199 (Lehette and Hernandez-Leon, 2009) and dry mass to carbon (C) conversion factors (Kjørboe,  
200 2013) were used to calculate the biomass and C content of each zooplankton organism  
201 scanned. Taxonomic units and biomass conversion factors used are listed in Table 2. For large  
202 protists the conversion factor was adjusted to  $0.08 \text{ mgC mm}^{-3}$  (Biard et al., 2016).

203 Shannon diversity index ( $H'$ ) was calculated based on the relative abundances of the  
204 119 taxa for each sample as follows:

$$205 \quad H' = -\sum_i^n p_i \log p_i \quad (2)$$

206 where  $p_i$  is relative abundance of each taxa in one sample and  $\log$  is the natural  
207 logarithm.

208



## 209 **Analyzing the vertical distribution of zooplankton and particles**

210 Vertical attenuation rates of zooplankton (abundance and biomass) and estimated  
211 particle fluxes were estimated, from the five sampled layers for zooplankton and from the 5  
212 meter resolution profile of estimated vertical flux using the following equation :

$$213 \quad X = X_0(Z/Z_0)^b \quad (3)$$

214 where  $X$  represents the zooplankton abundance, the zooplankton biomass or the  
215 particle vertical flux at the depth level  $Z$ ,  $X_0$  the zooplankton biomass or abundance and  
216 vertical particle flux at the depth  $Z_0$  (chosen as median depth of the surface net) and  $b$  the  
217 slope taken as a proxy of the attenuation rate of zooplankton biomass zooplankton abundance  
218 or particle flux. In the rest of the manuscript, A\_zoo represents the slope  $b$  of vertical profile  
219 for zooplankton abundance, B\_zoo the slope  $b$  of vertical profile for zooplankton biomass,  
220 A\_flux the slope  $b$  of vertical profile for particle flux, and P\_flux1, P\_flux2 and P\_flux3 the  
221 particle flux in respectively the epipelagic, upper and lower mesopelagic. To analyse  
222 latitudinal patterns in attenuation rates, the slope values were separated into three latitudinal  
223 bands based on the latitudinal position of their corresponding sampling stations: intertropical  
224 ( $0^\circ$ - $30^\circ$ ), temperate ( $30^\circ$ - $60^\circ$ ) and polar ( $60^\circ$ - $90^\circ$ ). The intertropical stations gathered both  
225 OMZ and non-OMZ stations, which allowed us to analyse the effect of oxygen depletion on  
226 zooplankton and particles. Non-parametric variance analyses (Kruskal and Wallis tests) were  
227 performed to test for differences in slope values (i.e. zooplankton and particles attenuation  
228 rates) between latitudinal bands.

## 229 **Multivariate analysis of community composition**

230 To explore the response of zooplankton community composition to environmental  
231 drivers across depth layers, the non-interpolated abundances of the 19 taxonomic groups  
232 mentioned above were aggregated into three layers: the epipelagic layer (0-200m), the upper  
233 mesopelagic layer (200-500m) and the lower mesopelagic layer (500-1000m). To analyse  
234 separately the three depth layers, the samples collected in overlapping layers (18.59% of the  
235 total samples) were not included in the statistical analysis (Table S1). To characterise the  
236 environmental conditions of each layer at each sampling station the median values of the  
237 following contextual environmental variables were used: temperature (T), salinity (S), oxygen  
238 ( $O_2$ ), nitrate concentration ( $NO_3$ ), chlorophyll  $a$  concentration (Chl\_ $a$ ), phytoplankton size  
239 fractions ( $f_{micro}$ ,  $f_{nano}$ , and  $f_{pico}$ ), concentration of suspended particles (SPM) and particle  
240 flux (P\_Flux). The measurements of all these environmental variables are available on  
241 PANGAEA (<https://doi.org/10.1594/PANGAEA.840721>).

242 To estimate the strength of the Diel Vertical Migration (DVM) at 10 stations, pairwise  
243 Wilcoxon tests were performed to compare in each layers the abundance and biomass of each  
244 taxa between day and night. For those 10 same pairs of stations, we used an analysis of  
245 similarities (ANOSIM) to test for significant variations in community composition between  
246 day and night samples. The ANOSIM tested whether the inter-groups difference (day and  
247 night groups) was higher than the intra-groups difference, by providing an R coefficient. An R  
248 coefficient close to one suggests dissimilarity between groups, while R value close to zero  
249 suggests an even distribution of high and low ranks within and between groups. An R value  
250 below zero suggests that dissimilarities are greater within groups than between groups (Clarke  
251 and Gorley, 2001). ANOSIM tests were performed within each layer using log-transformed  
252 (where log is the natural logarithm) abundances and Bray-Curtis distance among stations.

253 For each depth layer, a canonical redundancy analysis (RDA) was performed based on  
254 the abundances of the 19 mesozooplankton groups and the above-mentioned environmental  
255 variables to explore the explanatory power of these variables in structuring the  
256 mesozooplankton community. The RDA is an extension of the multiple regression analysis  
257 applied to multivariate data (Legendre and Legendre, 1998). It allows representing the  
258 response variables (abundances of the 19 mesozooplankton groups) in a “constrained”  
259 reduced space, i.e., constructed from the explanatory variables (the environmental variables).  
260 For each RDA, the following variables were used as “supplementary variables” of the  
261 analysis in order to visualize their correlation with the environmental structuring of the  
262 mesozooplankton community (i.e., to visualise their position in the RDA space): attenuation  
263 of particle flux (A\_flux), attenuation of zooplankton abundance (A\_zoo), attenuation of  
264 zooplankton biomass (B\_zoo) and the Shannon index ( $H'$ ). Beforehand, a Hellinger  
265 transformation was performed on the mesozooplankton abundances. A preliminary RDA  
266 based on all samples together showed a very strong effect of depth on mesozooplankton  
267 community composition (Fig. S1). Therefore, to avoid such a strong effect of depth on the  
268 community composition analysis, three separate RDAs were performed on each of the three  
269 layers defined above. Significant axes were identified using the Kaiser-Guttman criterion  
270 (Legendre and Legendre, 1998).

271 Data manipulation and statistical analyses were performed with Matlab 2018b  
272 (MATLAB 9.5) for the vertical profiles of abundance and biomass and statistical test  
273 (Wilcoxon test, Kruskal-wallis test), R environment v3.5.1 (using the following packages:  
274 vegan version 2.5-5, ggplot2 version 3.1.1, ggrepel version 0.8.0 and ggfortify version 0.4.7)

275 for the redundancy analysis and PRIMER6 (Version 6.1.12) and PERMANOVA+ (Version  
276 1.0.2) for the ANOSIM test.

## 277 Results

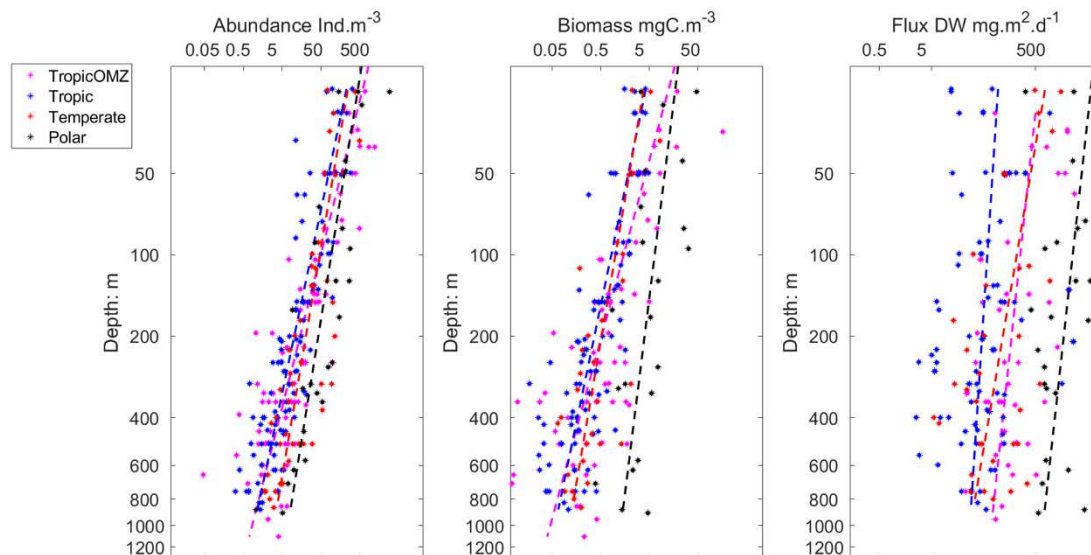
### 278 **Day night variability**

279 In each layer, the comparison between day/night of the taxonomic groups indicated  
280 that only a few groups (Euphausiidae, Metridinidae, Corycaeidae and Cnidaria for abundance;  
281 Eumalacostraca and Ostracoda for biomass) showed significant differences in either the  
282 surface layer or the upper mesopelagic layer (Table S1). Nonetheless, the ANOSIM found no  
283 significant differences in the community composition between the day and night samples at  
284 the community-level (R0-200m = -0.039; R200-500m = -0.008; R500-1100m = -0.006). The  
285 same analyses based on biomass also indicated no significant differences (R0-200m = 0.018;  
286 R200-500m = -0.051; R500-1100m = 0.087). As a consequence, all further analyses were  
287 carried out without making any distinctions between day and night samples.

### 288 **Vertical patterns in zooplankton total abundance and biomass and particle flux**

289 On a global scale, zooplankton abundance and biomass decreased exponentially with  
290 depth (Fig. 2) in the different latitudinal bins. Abundance and biomass decrease rate with  
291 depth and were correlated ( $r^2=0.342$ ,  $p=4.6*10^{-5}$ ) but the biomass attenuation rate estimates  
292 were systematically lower than the attenuation based on the abundance profiles. On average,  
293 polar waters showed increased zooplankton abundance and biomass compared to the stations  
294 located in the tropics. In the epipelagic layer, abundances and biomass ranged from 1 to 5000  
295 ind  $m^{-3}$  and 0.05 to 200 mg C  $m^{-3}$  while in the mesopelagic they were reduced to 0.05 to 450  
296 ind  $m^{-3}$  and 0.005 to 40 mg C  $m^{-3}$ . Copepods were the most abundant being 85% and 65% of  
297 the abundance and biomass in the epipelagic, 85 and 76% in the upper mesopelagic and 95%  
298 and 97% in the lower pelagic (Table 3). The estimated vertical flux also decreased with depth  
299 in all latitudinal bands. On average, polar waters showed higher fluxes compared to the  
300 stations located in the tropics.

301

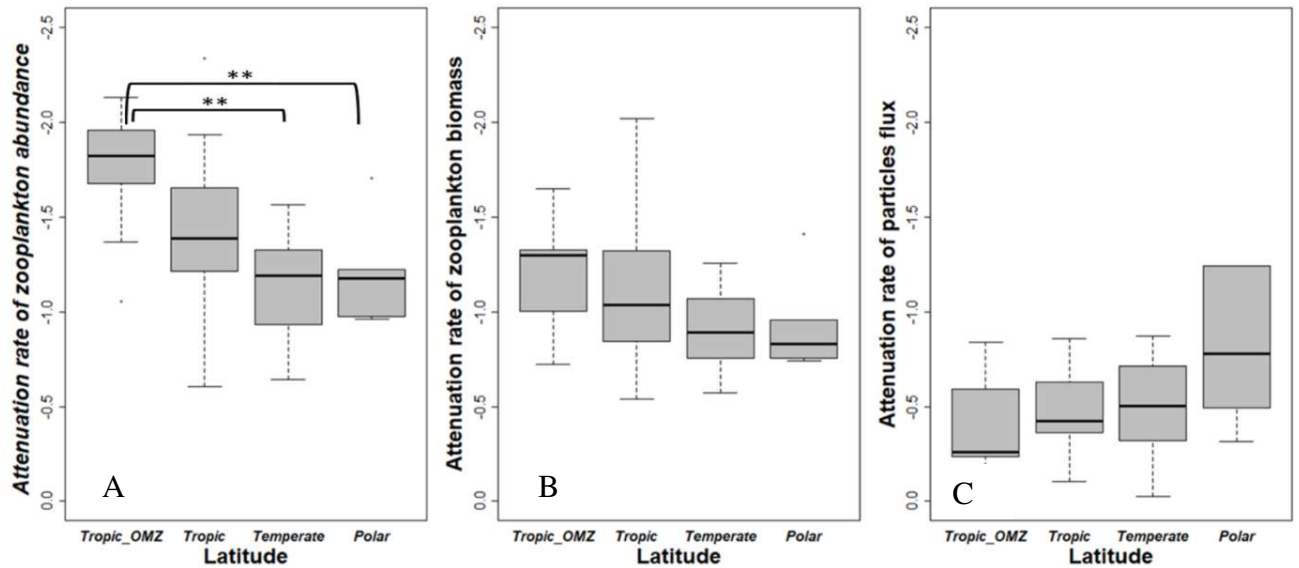


302

303 Fig. 2: Vertical distribution of zooplankton biomass, abundance and particle flux in different  
 304 latitudinal bands. Dotted lines represent the fitted regression for each latitudinal band (equation 3).  
 305 The parameters are given in table 4.

306

307 The attenuation rates of zooplankton abundance and biomass with depth were stronger than  
 308 the attenuation rates of the vertical particle flux (Fig. 3A, B and C, Table 4). The decrease  
 309 rates in zooplankton vertical abundance and biomass are more pronounced in OMZ stations  
 310 compared to the non-OMZ stations. Yet, such difference was found to be significant only  
 311 when the vertical decrease rates were calculated from abundances. In general, zooplankton  
 312 attenuation rates decreased with latitude whereas the attenuation rates of particle fluxes  
 313 increased with latitude (Fig. 3, Table 3). A non-parametric variance analysis (Kruskal-Wallis  
 314 test) of the attenuation rate revealed significant differences in the attenuation rates of  
 315 zooplankton abundances between the anoxic tropical stations and the temperate and polar  
 316 ones, but not with the other tropical stations (Table 4). No statistical difference between  
 317 regions was found. The attenuation rate of vertical flux was weaker at the OMZ sites  
 318 compared to the non OMZ ones but this difference was not significant (Fig. 3B).



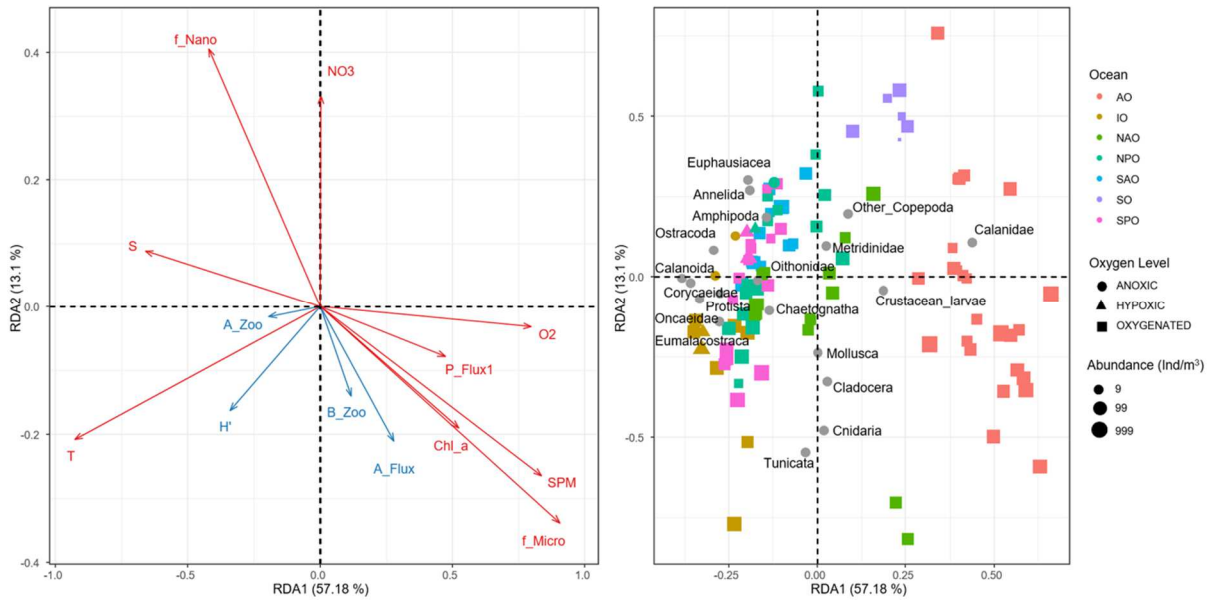
319  
 320 Fig. 3: Distributions of attenuation rates per latitudinal band (Tropical, Tropical OMZ, Temperate,  
 321 and Polar). A: Attenuation rate of zooplankton abundance (A\_zoo). B: Attenuation rate of zooplankton  
 322 biomass (B\_zoo). C: Attenuation rate of particle flux (A\_flux). (\*\*) means significant Kruskal-Wallis  
 323 test with  $p < 0.01$  (Table 5).

324

### 325 Structuring of the epipelagic community composition.

326 In the epipelagic layer (0 – 200 m depth), the environmental variables explained  
 327 32.71% of the total variance in mesozooplankton groups' abundances. The first RDA axis  
 328 (RDA1, 57.18 % of constrained variance) opposed the samples from polar waters, and  
 329 especially those from the Arctic dominated by Calanidae and crustacean larvae (RDA1 > 0),  
 330 to the tropical samples presenting more even contributions from most of the remaining  
 331 groups: Protista, Eumalacostraca, Annelida, Amphipoda, Corycaeidae, Chaetognatha,  
 332 Euphausiacea, Oithonidae, Ostracoda, Oncaeidae, Calanoida (RDA1 < 0). RDA1 was  
 333 negatively scored by temperature and salinity and positively scored by vertical particle flux,  
 334 microphytoplankton contribution, suspended particle concentration, dissolved oxygen  
 335 concentration and chlorophyll *a* concentration. Among the supplementary variables, the  
 336 attenuations of the particle flux and of the zooplankton biomass were positively correlated  
 337 with RDA1, while the attenuation of the zooplankton abundance and the Shannon index were  
 338 negatively correlated to RDA1. RDA2 (13.1% of constrained variance) opposed the samples  
 339 from the Indian Ocean and North Atlantic Ocean that present higher abundances of Cnidaria,  
 340 Mollusca, Tunicata and Cladocera (RDA2 < 0) to those samples from the Southern Ocean  
 341 presenting higher abundances of Annelida, Euphausiacea, Amphipoda and Other Copepoda

342 (RDA2 > 0). RDA2 was positively scored by nitrate concentrations and the relative  
 343 contribution of nanophytoplankton. It was negatively scored by the concentration of  
 344 suspended particles and the relative contribution of microphytoplankton. All supplementary  
 345 variables were negatively correlated with RDA2.  
 346



347  
 348  
 349 **Fig. 4: RDA on the epipelagic communities with the factors in the left panel and samples and taxa in**  
 350 **the right panel. Each colored dot corresponds to a sample, i.e., one net at one depth at one station**  
 351 **while the taxa are given as grey dots. The red arrows correspond to the quantitative environmental**  
 352 **variables in RDA space: f\_pico, f\_nano and f\_micro correspond to the relative contribution (%) of**  
 353 **pico-, nano- and micro-phytoplankton to total phytoplankton biomass, O2 = dissolved oxygen**  
 354 **concentration ( $\mu\text{mol/kg}$ ), Chl\_a = Chlorophyll a concentration ( $\text{mg/m}^3$ ), SPM = suspended particles**  
 355 **matter ( $\text{m}^3/\text{sr}$ ), T = temperature ( $^\circ\text{C}$ ), Sal = salinity, NO3 = nitrate concentration ( $\text{mol/kg}$ ), Z = depth**  
 356 **(m) and P\_Flux= particulate flux ( $\text{mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ). Grey dots mark the projection of the zooplankton**  
 357 **groups abundance ( $\text{ind}\cdot\text{m}^{-3}$ ). Supplementary variables estimated for the epipelagic layer are**  
 358 **represented with blue arrows: attenuation of particle flux (A\_flux), attenuation of zooplankton**  
 359 **abundance (A\_zoo), attenuation of zooplankton biomass (B\_zoo) and the Shannon index ( $H'$ ). Colors**  
 360 **correspond to the ocean basin where the samples were taken: AO = Arctic Ocean, IO = Indian Ocean,**  
 361 **NAO = North Atlantic Ocean, NPO = North Pacific Ocean, SAO = South Atlantic Ocean, SO =**  
 362 **Southern Ocean, SPO = South Pacific Ocean. Shapes illustrate oxygen level, Anoxic:  $[\text{O}_2] < 5\mu\text{mol/kg}$ ;**  
 363 **Hypoxic:  $5\mu\text{mol/kg} < [\text{O}_2] < 58.5\mu\text{mol/kg}$  and oxygenated:  $[\text{O}_2] > 58.5\mu\text{mol/kg}$ .**

364 **Structuring of the upper mesopelagic community composition.**

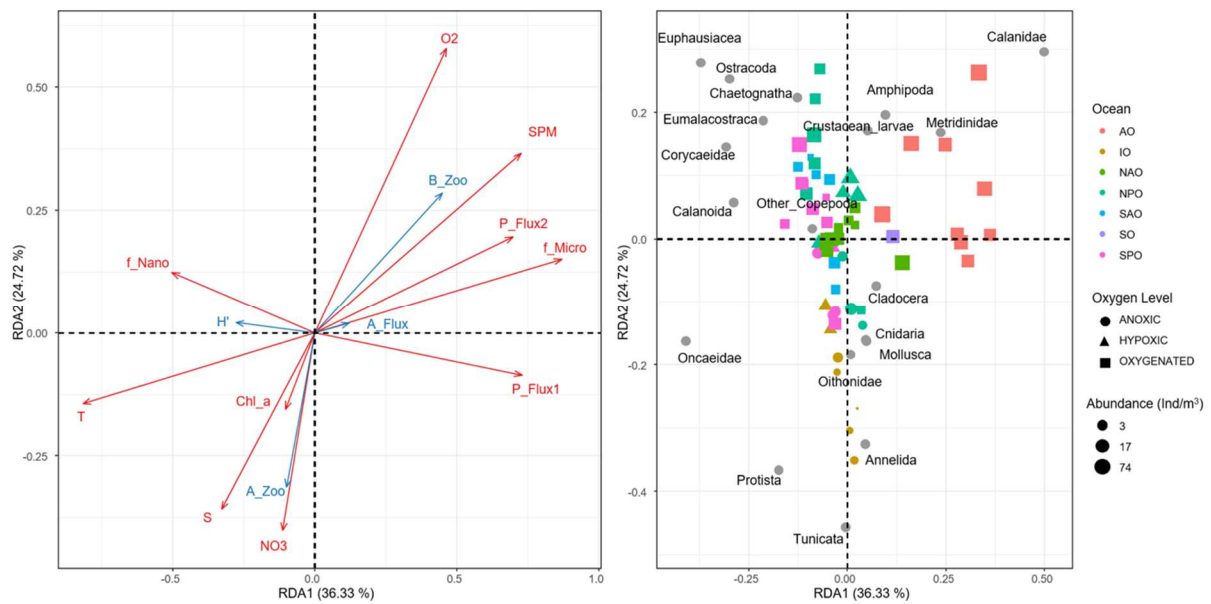
365 In the upper mesopelagic layer (200 to 500 m depth), the environmental variables  
 366 explained 29% of the total variance in mesozooplankton groups' abundances. Again, the first

367 RDA axis (RDA1, 36.33% of constrained variance) mainly opposed the polar samples  
368 dominated by Calanidae copepods, and characterized by higher concentrations of suspended  
369 particle, particle flux (both from surface and upper mesopelagic layer), and higher dissolved  
370 oxygen concentrations (RDA1 > 0), from the samples characterized by more diverse  
371 zooplankton communities (mainly Corycaeidae, small Calanoida, Oncaeidae) and correlated  
372 to higher temperature, higher salinity and a higher relative contribution of the  
373 nanophytoplankton (RDA1 < 0). Similarly, to what was observed for the epipelagic layer,  
374 among the supplementary variables, the attenuations of the particle flux and of zooplankton  
375 biomass were positively correlated with RDA1, while the attenuation of zooplankton  
376 abundance and the Shannon index were negatively correlated to RDA1. RDA2 (24.72% of  
377 constrained variance) opposed the anoxic samples from the Indian Ocean presenting higher  
378 abundances of Tunicata, Annelida, Protista, Mollusca, Oithonidae and Cnidaria (RDA2 < 0)  
379 to the oxygenated ones displaying higher abundances of Ostracoda, Eumalacostraca,  
380 crustacean larvae, other Copepoda, Chaetognatha and Euphausiacea (RDA2 > 0). Samples  
381 from the Arctic Ocean were dominated by large copepods from the Calanidae and  
382 Metridinidae families. Samples from the Pacific and Atlantic Oceans were dominated by  
383 other Copepoda, Eumalacostraca, Ostracoda, Euphausiacea, Chaetognatha and crustacean  
384 larvae. Higher attenuation rates of zooplankton biomass and particle flux were found in polar  
385 samples whereas higher zooplankton attenuation rates were found in warmer waters,  
386 especially at OMZ stations. Again, samples from the tropical upper mesopelagic layers  
387 displayed more diverse communities the extra-tropical regions. The distribution of the  
388 supplementary variables along RDA2 differed from what was observed for the epipelagic  
389 layer, as the supplementary variables, except the attenuation of the zooplankton abundances,  
390 were positively correlated to RDA2.

391

392



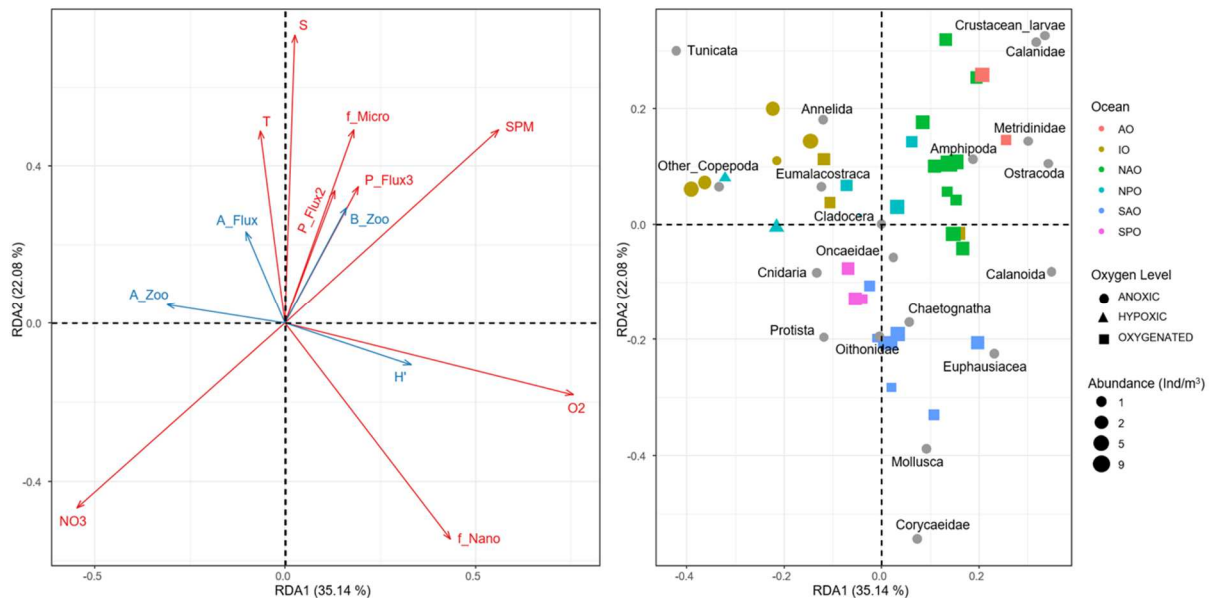


393  
 394 Fig. 5: RDA performed on the upper mesopelagic abundances with the factors in the left panel and  
 395 samples and taxa in the right panel. Each colored dot corresponds to a sample, i.e., one net at one  
 396 depth at one station while the taxa are given as grey dots. The orange arrows correspond to the  
 397 quantitative environmental variables (see legend of Fig. 4). Anoxic:  $[O_2] < 5\mu\text{mol/kg}$ ; Hypoxic:  
 398  $5\mu\text{mol/kg} < [O_2] < 58.5\mu\text{mol/kg}$  and oxygenated:  $[O_2] > 58.5\mu\text{mol/kg}$ . Supplementary variables  
 399 estimated for the upper mesopelagic layer are represented with blue arrows: attenuation of particle flux  
 400 (A\_flux), attenuation of zooplankton abundance (A\_zoo), attenuation of zooplankton biomass (B\_zoo)  
 401 and the Shannon index ( $H'$ ).

## 402 Structuring of the lower mesopelagic community composition

403 In the lower mesopelagic layers (500 to 1000 m depth), the environmental variables  
 404 explained 29.46 % of the total variance in mesozooplankton groups' abundances. The first  
 405 RDA axis (RDA1, 35.14 % of constrained variance) opposed the stations from the Arctic and  
 406 North Atlantic Oceans characterized by higher dissolved oxygen concentrations, higher  
 407 suspended particle concentrations (RDA1 > 0), from the anoxic and nitrate-rich stations from  
 408 the Indian Ocean (RDA1 < 0). The former stations were characterized by higher abundances  
 409 of Calanidae, Calanoida, Metridinidae, crustacean larvae, Ostracoda and Amphipoda, whereas  
 410 the latter were characterized by higher abundances of Tunicata, Annelida, Eumalacostraca and  
 411 other Copepoda. RDA2 (22.08 % of constrained variance) separated the colder and less salty  
 412 stations of the Southern Atlantic Ocean (RDA2 < 0) from the warmer, saltier stations (RDA2  
 413 > 0) of the North Atlantic and the Indian Oceans that are characterized by less diverse  
 414 zooplankton communities. The stations that sampled the oxygenated waters of the North  
 415 Atlantic and Arctic Oceans were dominated by large copepods of the Metridinidae and  
 416 Calanidae families, as well as most of the small other Calanoida (i.e. those smaller copepods

417 that could not be recognized at a more detailed taxonomic level) in addition to Ostracoda,  
 418 Amphipoda, and crustacean larvae. Oxygenated stations from the South Atlantic Ocean  
 419 (SAO) were characterized by higher abundances of Chaetognatha, Corycaeidae,  
 420 Euphausiacea, Cnidaria, Mollusca, Oithonidae, Oncaeidae and Protista. Samples taken in the  
 421 OMZ of the Indian and North Pacific Oceans displayed higher abundances of other  
 422 Copepoda, Tunicata, Annelida, Eumalacostraca and Protista. Higher mesozooplankton  
 423 biomass and stronger particle flux attenuation rates were found in the normoxic waters while  
 424 higher zooplankton attenuation rates were observed at the stations that sampled an OMZ. The  
 425 distribution of the supplementary variables showed similar association with environmental  
 426 variables as in the upper mesopelagic.  
 427



428  
 429 Fig. 6: RDA performed on the lower mesopelagic abundances with the factors in the left panel and  
 430 samples and taxa in the right panel. Each colored dot corresponds to a sample, i.e., one net at one  
 431 depth at one station while the taxa are given as grey dots. The orange arrows correspond to the  
 432 quantitative environmental variables (see legend of Fig. 4). Anoxic:  $[O_2] < 5 \mu\text{mol/kg}$ ; Hypoxic:  
 433  $5 \mu\text{mol/kg} < [O_2] < 58.5 \mu\text{mol/kg}$  and oxygenated:  $[O_2] > 58.5 \mu\text{mol/kg}$ ). Supplementary variables  
 434 estimated for the lower mesopelagic layer are represented with blue arrows: attenuation of particle flux  
 435 (A\_flux), attenuation of zooplankton abundance (A\_zoo), attenuation of zooplankton biomass (B\_zoo)  
 436 and the Shannon index ( $H'$ ).

437

438

439 **Discussion**

440 The present global analysis of spatial patterns of the mesozooplankton community and  
441 their relationship with the strength of the vertical particle flux is based on zooplankton  
442 abundance and biomass and vertical particles flux estimated using state-of-the-art imaging  
443 techniques (Zooscan and UVP5). The rigorous quality control (see Supplementary Material)  
444 allows to depict correlations between zooplankton and particle flux, two important  
445 components of the biological carbon pump (BCP). Notably the study allows to infer global  
446 ecological patterns in the epipelagic and mesopelagic layers, the coupling between these two  
447 layers in oxygenated, hypoxic and anoxic situations. Diel Vertical Migration in zooplankton  
448 at global scale and it's relationships with particle vertical flux could not be investigated  
449 because the net sampling was not designed to address the DVM globally. However, at 10  
450 occasions, day and night sampling was performed and revealed diel variability for few taxa  
451 but no change in the community composition (see Supplementary Material). As a  
452 consequence, all further analyses were carried out without making any distinctions between  
453 day and night samples.

454 **Important environmental factors for the mesozooplankton community composition in**  
455 **the epipelagic layer**

456 High latitude marine ecosystems are characterised by a combination of lower species  
457 diversity and shorter food webs (Laws, 1985; Stempniewicz et al., 2007) sustained by higher  
458 concentrations of large microphytoplankton cells (diatoms). On the contrary, low latitude  
459 ecosystems are featured by more complex and diverse food webs (Saporiti et al., 2015; Uitz et  
460 al., 2006, p. 200) adapted to lower production rates ensured by smaller cells (i.e. pico- and  
461 nanoplankton). How the dynamics of zooplankton community composition and vertical  
462 particle flux follow this scheme remains more elusive. Previous field-based studies reported  
463 peaks in zooplankton species richness in the tropics (Rombouts et al., 2010; Rutherford et al.,  
464 1999; Yasuhara et al., 2012), which is in line with the above-mentioned theory that the  
465 tropical food-depleted regions promote more complex food-webs with higher species  
466 richness. Our RDAs results supports the view that, on a global scale, temperature and the  
467 production regime of surface ecosystems are the main drivers of zooplankton community  
468 structure in the epipelagic layer. Therefore, in the epipelagic layers, less abundant and more  
469 diverse zooplankton thrive in warm, pico- and nanophytoplankton-dominated waters contrary  
470 to the polar waters where zooplankton is much more abundant but less diverse. Polar waters  
471 are characterised by a higher contribution of microphytoplankton to total phytoplankton

472 biomass and higher concentrations of particles. Our results also indicate that the two polar  
473 communities are not completely alike, as the Arctic is dominated by calanoid copepods while  
474 euphausiids and small undetermined copepods dominate in the few stations sampled in the  
475 Southern Ocean. Such differentiation has been previously shown by several authors who  
476 found that Arctic zooplankton were dominated by *Calanus* spp. (Balazy et al., 2018; Hirche  
477 and Mumm, 1992), whereas it was shown that Antarctic zooplankton were dominated by  
478 euphausiids, small calanoids, cyclopoids (i.e. *Oithona* spp., *Oncaea* spp.) and salps (Park and  
479 Wormuth, 1993; Pinkerton et al., 2020; Quetin et al., 1996; Ross et al., 2008; Steinberg et al.,  
480 2015).

### 481 **Important environmental factors for the mesozooplankton community structure in the** 482 **mesopelagic layer**

483 The RDA displayed similar general patterns in both the upper and lower mesopelagic  
484 layers with the stations in the Indian Ocean (with low zooplankton concentration in low  
485 oxygen) and Arctic Ocean (with high zooplankton concentration in oxygenated conditions)  
486 being in all layers well separated from the other stations in the remaining ocean. The highest  
487 mesopelagic zooplankton concentrations were found at stations associated with high  
488 microphytoplankton concentrations in the epipelagic and high particle flux, suggesting a  
489 strong impact of surface production regime on the mesozooplankton in the mesopelagic  
490 (Hernández-León et al., 2020). The inter-basin differences in zooplankton concentration and  
491 community composition was slightly lower in the lower mesopelagic compared to the upper  
492 mesopelagic, probably due to the more homogeneous habitat (Fernández de Puellas et al.,  
493 2019).

494 In general, stations associated with anoxic or hypoxic conditions at midwater depth  
495 displayed lower zooplankton concentrations in the mesopelagic and different community  
496 composition from oxygenated layers. The stations that sampled the tropical OMZ showed  
497 higher proportions of gelatinous carnivorous zooplankton (Cnidaria), gelatinous filter feeders  
498 (Tunicata), Mollusca and small omnivorous grazers (Cladocera). Anoxic or strongly hypoxic  
499 conditions in the mesopelagic may have selected for those taxa adapted to low oxygen  
500 (Vaquer-Sunyer and Duarte, 2008). In mesopelagic oxygenated waters, the stations of the  
501 Tropical Pacific Ocean displayed a higher diversity stemming from the higher and relatively  
502 even abundances of large protists (i.e. Rhizaria and Foraminifera), chaetognaths, crustaceans  
503 (Ostracods, Euphausiacea, Eumalacostraca, Amphipoda), and various copepod families  
504 (Corycaeidae, Oithonidae, Oncaeidae, small Calanoida). These zooplankton communities

505 were associated with oligotrophic conditions at surface (Fig. 4), lower zooplankton  
506 abundances, lower concentrations of suspended matter, weaker particle fluxes and weaker  
507 attenuation rates (Fig. 3B) and with stronger attenuation rates of organisms' abundances (Fig.  
508 3A). Therefore, we propose that oligotrophic regimes feature a network of diverse taxa that is  
509 not efficient at using the low amount of material fluxing. Our results are consistent with  
510 previous studies suggesting that those oligotrophic regimes can be relatively efficient at  
511 exporting the slow-sinking fraction of the little carbon that is produced in the surface layers  
512 due to a low impact of zooplankton grazing on the sinking particles (Guidi et al., 2009;  
513 Henson et al., 2015). This regime could help explain why we found the lowest particle flux  
514 attenuation rates in the tropics.

### 515 **Global vertical patterns of zooplankton and particle flux**

516 The concentration and biomass of various zooplankton groups decreased with depth  
517 (Fig. S1), confirming the general trend of decreasing zooplankton abundance and biomass  
518 from the surface to 1000 m depth (Bode et al., 2018; Brugnano et al., 2012; Hernández-León  
519 et al., 2020; Koppelman et al., 2005; Kosobokova and Hopcroft, 2010; Yamaguchi et al.,  
520 2004). Among these earlier studies, two models for the attenuation of zooplankton have been  
521 proposed: an exponential or a power model. Here, we used the power model (equation 1)  
522 because it was widely used to model vertical flux attenuation rates (Martin et al., 1987).  
523 Based on this power model, we observed rates of decrease in zooplankton abundance or  
524 biomass (Fig. 3) that were in the same range as those reported in the western Pacific Ocean (-  
525 1.52 to -1.41 for abundance and -1.32 to -1.10 for biomass, (Yamaguchi et al., 2002).  
526 Zooplankton abundance decreased more rapidly with depth than biomass as the average size  
527 of organisms increased with depth, confirming that the contribution of larger species increases  
528 with depth (Homma and Yamaguchi, 2010; Yamaguchi et al., 2002). Considering a larger  
529 latitudinal band than earlier studies who found weak regional or global patterns (Hernández-  
530 León et al., 2020; Puelles et al., 2019), we showed that the rates of zooplankton attenuation  
531 vary with latitude and to a lesser extent with oxygen concentrations (Fig. 3) and also in the  
532 opposite direction of the flux attenuation.

533 Stronger surface particle fluxes and vertical attenuation rates were found at higher  
534 latitudes where primary production is mainly ensured by the microphytoplankton and weaker  
535 flux and attenuation was found in the low latitude dominated by picophytoplankton (Fig.4).  
536 Such latitudinal pattern in particle attenuation rates results from the gradient in the production  
537 regime and has been observed quasi-systematically with imaging systems on global scales

538 (Guidi et al., 2015), but also based on sediment traps (Berelson, 2001) or combining sediment  
539 traps with satellite-based estimates of primary production (Henson et al., 2012). However,  
540 several short-term experiments at selected sites from temperate to tropical latitudes of the  
541 Pacific and Atlantic, showed an opposite pattern with stronger flux and attenuation in cold  
542 and productive regions compared to inter-tropical oligotrophic (Buesseler et al., 2007; Marsay  
543 et al., 2015). The inconsistency of the observations is difficult to explain although it was  
544 noted that depth varying remineralisation due to varying temperature may reconcile the  
545 contrasted results (Marsay et al., 2015). It is possible that some of the variations arise from  
546 the use of different methodologies (instruments, time scale, global representation of the  
547 dataset) to address the complexity of the processes to be measured simultaneously.

548         Opposite pattern between the vertical attenuations of zooplankton abundance  
549 (A\_Zoo) and biomass (B\_zoo) in one hand and the vertical attenuation of flux (A\_Flux) in the  
550 other hand supports the view that the abundant zooplankton community plays a crucial role in  
551 flux attenuation in productive layers, by feeding and fragmenting the sinking material as  
552 suggested in previous studies (Dilling and Alldredge, 2000; Giering et al., 2014; Lampitt et  
553 al., 1990; Stemmann et al., 2004). However, on average and more importantly at high  
554 latitudes, zooplankton attenuation rates were stronger than the vertical flux attenuation rates  
555 (Fig. 3) indicating that zooplankton vertical zonation may be affected by other processes than  
556 the resources provided by the flux of organic matter from the epipelagic layer. In the inter-  
557 tropical OMZ regions, zooplankton vertical attenuation rates were maximum when the  
558 vertical attenuation of the particle's flux was minimum. Previous studies have reported lower  
559 flux attenuation rates in the OMZ of the Arabian Sea (Haake et al., 1992; Roullier et al.,  
560 2014), and Eastern Tropical North Pacific (Cavan et al., 2017; Van Mooy et al., 2002). Lower  
561 zooplankton activity together with reduced bacterial activity (Cram et al., 2021) allow sinking  
562 particles to transit through the OMZ core without being severely degraded (Wishner et al.,  
563 2008, 1995).

564

### 565 **Sensitivity of plankton and vertical flux to varying oxygen conditions**

566         By comparing zooplankton communities from inter-tropical stations with those from  
567 oxygenated mesopelagic layers to stations from OMZs, our analysis brought additional  
568 evidence that change in zooplankton community composition may affect the efficiency of the  
569 BCP. The zooplankton community sampled in the Indian Ocean OMZ displayed a distinct  
570 composition compared to the other samples, which is in line with the increasing number of

571 studies that document the profound impact of oxygen depletion on pelagic organisms (Ekau et  
572 al., 2010; Hauss et al., 2016; Wishner et al., 2018). Our results underlined how the OMZ can  
573 strongly reduce the abundance of several zooplankton groups (i.e. Calanoida, Euphausiacea,  
574 Amphipoda, Ostracoda) that are outcompeted by more hypoxia-tolerant ones. We found that  
575 tunicates (mostly Appendicularia), large protists (Collodaria and Foraminifera), polychaetes,  
576 Oncaeidae, Oithinidae and to a lesser extent Cnidaria (jellyfishes) may tolerate OMZ  
577 conditions, since their abundance at OMZ and at non-OMZ stations did not present significant  
578 differences. All of these zooplankton groups have been reported as being able to thrive or  
579 endure at low oxygen concentrations in various OMZs (Ekau et al., 2010; Hauss et al., 2016;  
580 Keister and Tuttle, 2013; Kiko and Hauss, 2019; Parris et al., 2014; Tutası and Escribano,  
581 2020; Werner and Buchholz, 2013; Wishner et al., 2020). Those “hypoxiphilic” or hypoxia-  
582 tolerant taxa display special adaptations that enable them to remain at extremely low oxygen  
583 concentrations where other zooplankton groups cannot, because they fail to meet their  
584 metabolic oxygen demand (Childress and Seibel, 1998; Seibel, 2011). Jellyfish and large  
585 protists benefit from their passive feeding tactics which are less oxygen-demanding than  
586 active cruising and filter feeding (Kjørboe, 2011). Indeed, hypoxia-tolerant taxa can also  
587 display behavioral adaptations that cut down the metabolic costs associated with active  
588 feeding or the active search for mates in the water column. Copepod species belonging to the  
589 Oncaeidae and Oithonidae families are known for performing ambush feeding tactics or to  
590 attach themselves on large detritus (Brun et al., 2017), which allows them to capture small  
591 preys or to feed on falling detritus at very low metabolic costs. Therefore, these less motile  
592 copepods frequently outcompete most of their calanoid congeners in OMZs and often co-  
593 occur with Appendicularia, as those discard particle-rich aggregates on which the copepods  
594 feed (Alldredge, 1972; Brun et al., 2017; Kjørboe, 2011). Other possible adaptations consist  
595 in the use of lipid storages and metabolic suppression (Wishner et al., 2020).

596         Some organisms conduct diapause in the OMZ for an extended period, allowing them  
597 to avoid foraging predators and to complete their life cycle (Arashkevich et al., 1996).  
598 Diapause reduces energetic costs and thus allows the organisms to survive in resource-  
599 depleted conditions. Metabolic suppression goes hand in hand with the diapause, but can also  
600 occur on shorter time scales, e.g. when organisms stay at OMZ depth during diel vertical  
601 migrations. Diapause and metabolic suppression are associated with reduced respiratory and  
602 locomotor activity. Feeding on and disruption of particles could therefore be reduced at OMZ  
603 depth not only due to the exclusion of many hypoxia intolerant zooplankton organisms, but  
604 also due to the reduced activity of those zooplankton organisms that can cope with OMZ

605 conditions. The zooplankton groups we found to characterize the community inhabiting the  
606 hypoxic and anoxic layers are those that commonly outcompete others in OMZs worldwide.  
607 They could benefit from the likely future expansion of OMZ (Oschlies et al., 2018) and thus  
608 become increasingly abundant with future climate change. Such changes could probably  
609 result in enhanced vertical particle flux in those regions. However, this requires further  
610 research as some of these organisms could already be living near their physiological hypoxia  
611 tolerance limits (Wishner et al., 2018).

## 612 **Conclusions**

613 We showed that consistent observations can be obtained at a global level using *in situ*  
614 camera systems and precise net sampling in various ecosystems representative of different  
615 ocean conditions. In future surveys, consistently combining these techniques with acoustic  
616 and other bio-optical sensors will allow the measurement of the vertical and horizontal  
617 distribution of organisms with greater precision. We showed that the key environmental  
618 variables driving epipelagic mesozooplankton community structure at the global scale are  
619 temperature, phytoplankton biomass and key groups/size. In the mesopelagic layer, surface  
620 phytoplankton size classes, particle concentration, temperature and oxygen availability were  
621 identified as the main drivers of mesozooplankton community structure. Our work  
622 furthermore suggests that low attenuation of zooplankton abundance and biomass go in hand  
623 with high particle flux attenuation and vice versa. Such information is crucial for the  
624 parameterization of marine ecosystem models that describe complex zooplankton-related  
625 processes based on coarse but increasingly numerous functional types. These models suggest  
626 that surface phytoplankton biomass and size classes, the flux of particles and the oxygen  
627 content in the mesopelagic layer will all be affected further by global climate change. The fact  
628 that zooplankton communities are sensitive to those factors suggests that future climatic  
629 changes may profoundly alter zooplankton communities worldwide, at the surface but also in  
630 the deeper mesopelagic layer.

631

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663

665

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1010 **Table 1: List of the 19 taxa kept for the RDA analysis.**

<b>Taxonomic groups</b>	<b>Sub groups</b>
Protista	Protista includes unrecognized protista on the images
Annelida	Images of all Annelida
Chaetognatha	Images of all Chaetognatha
Tunicata	Images of all Gelatinous filter feeders
Cnidaria	Images of all gelatinous carnivores belonging to Cnidaria
Mollusca	Images of all Pteropoda
Cladocera	Images of all Small Cladocera
Eumalacostraca	Images of all Decapoda but those distinguish at detailed taxonomic level
Euphausiacea	Images of all Euphausiacea
Amphipoda	Images of all Amphipoda
Ostracoda	Images of all Ostracoda
Crustacean_larvae	Images of all crustacean larvae
Other_Copepoda	Images of all Copepoda but those distinguish at detailed taxonomic level
Calanoida	Images of all Calanoida but those distinguish at detailed taxonomic level
Oithonidae	Images of all Oithonidae
Corycaeidae	Images of all Corycaeidae
Oncaeidae	Images of all Oncaeidae
Metridinidae	Images of all Metridinidae
Calanidae	Images of all Calanidae

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1012 **Table 2: Coefficient factors used for equation 1 taken from observed allometric relationships between**  
 1013 **body area and individual dry mass (Lehette et al., 2009). The conversion factors to carbon are taken**  
 1014 **from Kiorboe (2013).**

<b>Zooplankton category</b>	<b>Biomass Exponent (b)</b>	<b>Biomass Multiplier (a)</b>	<b>DW to C</b>
Copepods	1.59 ± 0.03	45.25	0.48
Chaetognaths	1.19 ± 0.13	23.45	0.367
Decapods	1.48 ± 0.05	49.58	0.419
Cnidaria	1.02 ± 0.38	43.17	0.132
Tunicata	1.24 ± 0.08	4.03	0.103
Pteropods	1.54 ± 0.03	43.38	0.289
Protists*		0.08 mgC mm <sup>-3</sup>	
Other (Annelids, Cladocera, Ostracoda)	1.54 ± 0.03	43.38	0.289

1015 \* for the protist we used a conversion factor between biovolume and biomass (Biard et al.,  
 1016 2016)

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Table 3: Summary of the main mesozooplankton groups global proportion of abundance and biomass:

Taxa Proportion(%)	Epipelagic		Upper Mesopelagic		Lower Mesopelagic	
	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
All copepoda	84.89	65	84.80	76.39	94.5	96.5
Chaetognatha	3.67	8.39	2.44	3.48	2.06	2.53
Crust decapoda	2.9	18.9	0.36	14.98	0.00	0.00
Cnidaria	0.7	0.96	0.19	0.24	0.00	0.00
Tunicata	0.5	0.02	0.08	0.001	0.1	0.00
Protista	1.5	0.5	0.97	0.19	0.9	0.09
Pteropoda	1.2	0.6	0.41	0.03	0.00	0.00
Other (annelids, cladocera, ostracoda)	4.2	3.09	10.05	3.23	2.38	0.87

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Table 4: Summary of the vertical attenuation rate (b: median and IC: confidence Interval) of mesozooplankton abundance and biomass and particle vertical flux (b: median value and IC: confidence Interval).

	Zooplankton abundance (ind. m <sup>-3</sup> )		Zooplankton biomass (mgC m <sup>-3</sup> )		Particle vertical flux (mgDW m <sup>-2</sup> d <sup>-1</sup> )	
	<i>b</i>	IC (95%)	<i>b</i>	IC (95%)	<i>b</i>	IC (95%)
ANOXIA_TROPIC	-1.82	-2.13 - -1.13	-1.3	-2.9 - -0.75	-0.26	-0.77- -0.19
TROPIC	-1.39	-2.46 - -0.69	-1.04	-1.92 - -0.58	-0.42	-0.78- -0.21
TEMPERATE	-1.19	-1.56 - -0.64	-0.89	-1.26 - -0.57	-0.50	-0.84- -0.11
POLAR	-1.18	-1.71 - -0.96	-0.83	-1.41 - -0.74	-0.78	-4.51- -0.36

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Table 5: Probability of H0, no difference between the groups (pairwise Kruskal-Wallis test) for total zooplankton and biomass depth attenuation rates and particle flux attenuation rate. \* Significant differences (p<0.05).

Two by two comparisons		Abundance	Biomass	Flux
Tropic-Anoxia	Tropic	0.057	0.641	0.77
Tropic-Anoxia	Temperate	0.0018*	0.189	0.82
Tropic-Anoxia	Polar	0.01*	0.238	0.09
Tropic	Temperate	0.34	0.639	0.99
Tropic	Polar	0.51	0.685	0.28
Temperate	Polar	0.99	1	0.52

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