

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

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23 Abstract

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

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50

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

53 Introduction

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

79 However, mesopelagic zooplankton communities remain critically under-sampled
80 compared to the epipelagic ones, as most collections is in the first 200m of the water column
81 (Everett et al., 2017). The mesopelagic is still considered a “dark hole” (Robinson et al., 2010;
82 St John et al., 2016) as the gaps in sampling lead to critical gaps in knowledge regarding the
83 functioning of mesopelagic ecosystems and how they are controlled by the organic matter
84 fluxing from the euphotic zone. Local to regional field studies reported that the abundance of
85 mesozooplankton decreases exponentially with depth, in parallel with substantial changes in
86 species diversity and genus composition that remain poorly resolved (Bode et al., 2018;

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

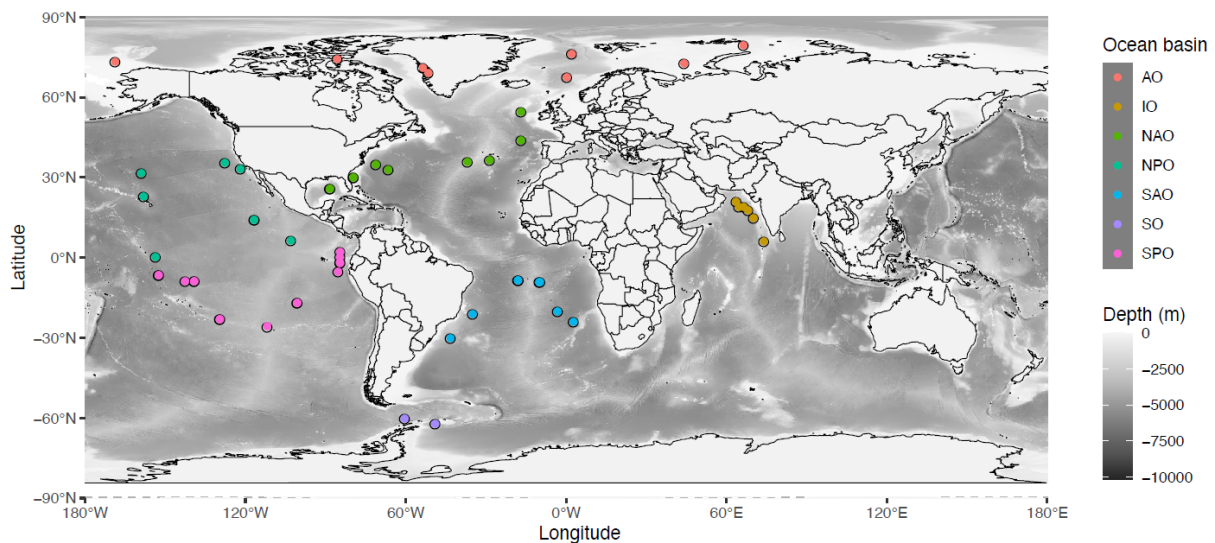
107 Here, a homogeneous dataset of community-level zooplankton images generated from
108 the TARA Oceans expeditions is explored together with associated measurements of their
109 contextual environmental conditions to: (i) test whether zooplankton communities present
110 consistent vertical variations in abundance and composition across the oceans and in different
111 latitudinal bands, and (ii) investigate the main drivers of such vertical gradients and how they
112 are coupled to the surface phytoplankton and estimates of particle flux. The TARA Oceans
113 expedition collected over 35000 samples encompassing the whole plankton community (i.e.,
114 from viruses to jellyfish) across the global ocean from 2009 to 2013 (Karsenti et al., 2011).
115 Previous studies that analysed the TARA Oceans imaging dataset explored the global latitudinal
116 gradients in richness and composition for the whole plankton community focusing on surface
117 waters (Ibarbalz et al., 2019; Brandao et al., in press). Here, we aim to describe the community
118 composition of mesozooplankton down to 1000m depth on a global scale. As the imaging
119 techniques used here cannot achieve a species-level identification of the zooplankton

120 community composition, our approach is rather oriented towards larger taxonomic and /or
121 functional groups that may be associated with broad ecological and biogeochemical functions.

122 [Materials and methods](#)

123 **Sampling sites and environmental variables**

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



128
129 **Fig. 1:** Location of the 57 stations sampled with the Multinet, grouped by ocean basin: AO=Arctic
130 Ocean, IO=Indian Ocean, NAO=North Atlantic Ocean, NPO=North Pacific Ocean, SAO=South
131 Atlantic Ocean, SO=Southern Ocean or Austral Ocean, SPO=South Pacific Ocean.

132
133 A CTD rosette equipped with optical sensors was deployed to measure the physico-
134 chemical parameters within the water column. Temperature and conductivity were measured
135 from the surface to a maximum of 1300 m depth using a Seabird 911 CTD mounted on a Sea-
136 Bird Carousel sampler with 10 Niskin bottles. The following additional sensors were mounted
137 to measure optical properties related to relevant biogeochemical variables: fluorometer (Wetlab
138 ECO-AFL/FL model), dissolved oxygen sensor (model SBE 43), nitrate sensor (ISUS with a
139 maximum rating depth of 1000m Satlantic SA), a 25 cm transmissometer for particles 0.5–20
140 μm (WETLabs), a one-wavelength backscatter meter for particles 0.5–10 μm (WETLabs), and
141 an Underwater Vision Profiler 5 (UVP5) for particles >150 μm and zooplankton >600 μm

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

157 **Zooplankton sampling, digitization, biomass estimates**

158 A Hydrobios Multinet (with a $300\mu\text{m}$ mesh and an aperture of 0.25m^2) was used to
159 sample zooplankton (Roullier et al., 2014; Pesant et al., 2015) in five distinct water layers
160 ranging from the surface to occasionally 1300 m depth. The five depth layers were locally
161 defined as a function of the vertical structure of the water column according to the profiles of
162 temperature, salinity, fluorescence, nutrients, oxygen, and particulate matter (Pesant et al.,
163 2015). The Multinet was equipped with a flowmeter to measure the volume of seawater filtered
164 by each net tow (Pesant et al., 2015). Day and night net tows were conducted at ten stations.
165 Sampling at the other stations occurred at day or night, depending on cruise schedule and
166 operational constraints. Once collected, the samples were preserved in a solution of buffered
167 formaldehyde-Borax solution (4%). In the laboratory, the samples were rinsed and split with a
168 Motoda box (MOTODA, 1959). The final split was analysed with the Zooscan imaging system
169 (Gorsky et al., 2010) which allowed a rapid and semi-automatic analysis of zooplankton
170 samples. In total, the samples comprised nearly 400,000 images of living zooplankton and
171 detritus. These images were imported into Ecotaxa, an online platform which allows an
172 automatic prediction of the taxonomic classification of each single image followed by a manual
173 validation/correction. The organisms were then identified manually down to the order,
174 sometimes to the family and rarely down to the genus level. All copepods were sorted at the

175 family level apart from the smallest copepods that cannot be recognised at the family level from
176 the image. They were all grouped into one category called Other-copepoda or other-Calanoidea
177 if their morphological features allowed classifying them as Calanoidea. This initial sorting
178 allowed classifying zooplankton into 119 taxa. As many taxa showed a very small contribution
179 to total zooplankton abundance, the 119 taxa were grouped into 19 taxonomic groups (Table
180 1). Those include all the major zooplankton groups that are frequently observed in the oceans.
181 To investigate vertical patterns in mesozooplankton abundance, these 19 groups were further
182 aggregated into eight groups representing a combination of taxonomic and functional
183 classification (Table 1).

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

$$190 \quad \text{Body Weight}(\mu\text{C}) = aS^b \quad (1)$$

191 where S is body area in mm^2 . Taxon-specific area-to-dry mass conversion factors
192 (Lehette and Hernandez-Leon, 2009) and dry mass to carbon (C) conversion factors (Kjørboe,
193 2013) were used to calculate the biomass and C content of each zooplankton organism scanned.
194 Taxonomic units and biomass conversion factors used are listed in Table 2. For large protists
195 the conversion factor was adjusted to 0.08 mgC mm^{-3} (Biard et al., 2016).

196 Shannon diversity index (H') was calculated based on the relative abundances of the
197 119 taxa for each sample as follows:

$$198 \quad H' = -\sum_i^n p_i \log p_i \quad (2)$$

199 where p_i is relative abundance of each taxa in one sample and log is the natural
200 logarithm.

201

202 **Analyzing zooplankton and particles vertical distributions**

203 Vertical attenuation rates of zooplankton (abundance and biomass) and estimated
204 particle fluxes were estimated, from the five sampled layers for zooplankton and from the 5
205 meter resolution profile of estimated vertical flux using a linear regression of the log-log (i.e.
206 natural logarithm) with the following equation :

$$207 \quad X = X_0(Z/Z_0)^b \quad (3)$$

208 where X represents the zooplankton abundance, the zooplankton biomass or the
209 particle vertical flux at the depth level Z , X_0 the zooplankton biomass or abundance and vertical
210 particle flux at the depth Z_0 (chosen as median depth of the surface net) and b the slope taken
211 as a proxy of the attenuation rate of zooplankton biomass zooplankton abundance or particle
212 flux. In the rest of the manuscript, A_{zoo} represents the slope b of vertical profile for
213 zooplankton abundance, B_{zoo} the slope b of vertical profile for zooplankton biomass, A_{flux}
214 the slope b of vertical profile for particle flux, and P_{flux1} , P_{flux2} and P_{flux3} the particle
215 flux in respectively the epipelagic, upper and lower mesopelagic. To analyse latitudinal patterns
216 in attenuation rates, the slope values were separated into three latitudinal bands based on the
217 latitudinal position of their corresponding sampling stations: intertropical (0° - 30°), temperate
218 (30° - 60°) and polar (60° - 90°). The intertropical stations gathered both OMZ and non-OMZ
219 stations, which allowed us to analyse the effect of oxygen depletion on zooplankton and
220 particles. Non-parametric variance analyses (Kruskal and Wallis tests) were performed to test
221 for differences in slope values (i.e. zooplankton and particles attenuation rates) between
222 latitudinal bands.

223 **Multivariate analysis of community composition**

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

236 To estimate the strength of the Diel Vertical Migration (DVM) at 10 stations, pairwise
237 Wilcoxon tests were performed to compare in each layers the abundance and biomass of each
238 taxa between day and night. For those 10 same pairs of stations, we used an analysis of
239 similarities (ANOSIM) to test for significant variations in community composition between day
240 and night samples. The ANOSIM tested whether the inter-groups difference (day and night

241 groups) was higher than the intra-groups difference, by providing an R coefficient. An R
242 coefficient close to one suggests dissimilarity between groups, while R value close to zero
243 suggests an even distribution of high and low ranks within and between groups. An R value
244 below zero suggests that dissimilarities are greater within groups than between groups (Clarke
245 and Gorley, 2001). ANOSIM tests were performed within each layer using log-transformed
246 (where log is the natural logarithm) abundances and Bray-Curtis distance among stations.

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

264 Data manipulation and statistical analyses were performed with Matlab 2018b
265 (MATLAB 9.5) for the vertical profiles of abundance and biomass and statistical test (Wilcoxon
266 test, Kruskal-wallis test), R environment v3.5.1 (using the following packages: vegan version
267 2.5-5, ggplot2 version 3.1.1, ggrepel version 0.8.0 and ggfortify version 0.4.7) for the
268 redundancy analysis and PRIMER6 (Version 6.1.12) and PERMANOVA+ (Version 1.0.2) for
269 the ANOSIM test.

270 Results

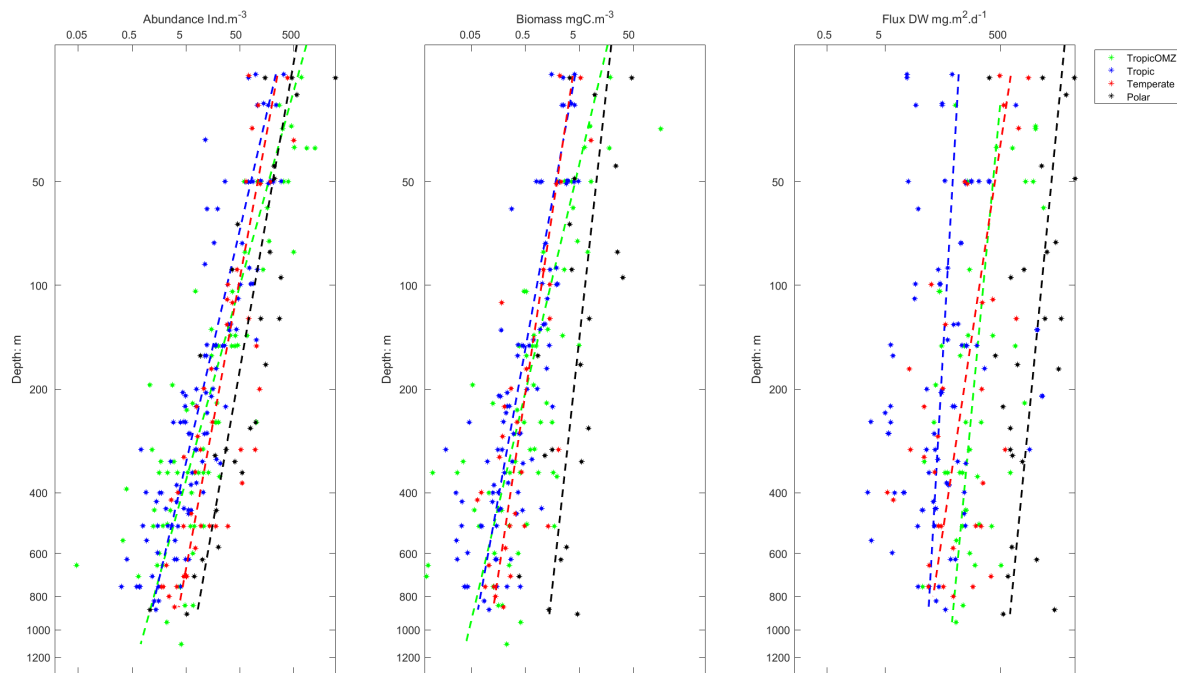
271 Day night variability

272 In each layer, the comparison between day/night of the taxonomic groups indicated that
273 only a few groups (Euphausiidae, Metridinidae, Corycaeidae and Cnidaria for abundance;
274 Eumalacostraca and Ostracoda for biomass) showed significant differences in either the surface
275 layer or the upper mesopelagic layer (Table S1). Nonetheless, the ANOSIM found no
276 significant differences in the community composition between the day and night samples at the
277 community-level ($R_{0-200m} = -0.039$; $R_{200-500m} = -0.008$; $R_{500-1100m} = -0.006$). The same
278 analyses based on biomass also indicated no significant differences ($R_{0-200m} = 0.018$; R_{200-}
279 $500m = -0.051$; $R_{500-1100m} = 0.087$). As a consequence, all further analyses were carried out
280 without making any distinctions between day and night samples.

281 Vertical patterns in zooplankton total abundance and biomass and particle flux

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

294

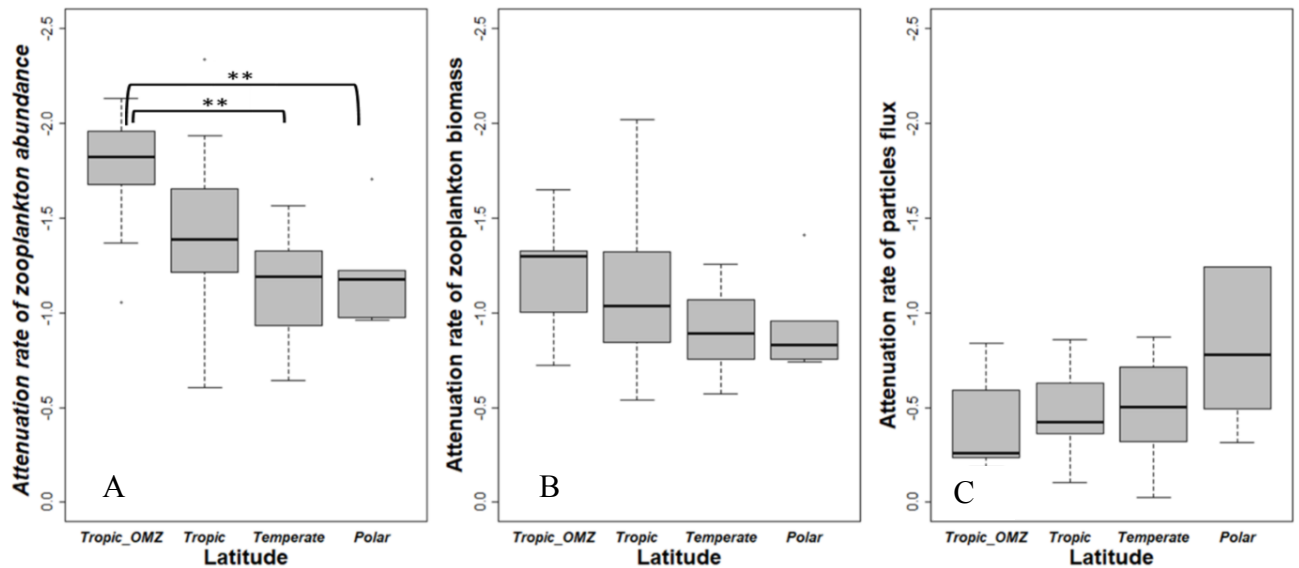


295

296 Fig. 2: Vertical distribution of zooplankton biomass, abundance and particle flux in different latitudinal
297 bands. Dotted lines represent the fitted linear regression for each latitudinal band (equation 3). The linear
298 fits to the data point are given in table 4.

299

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



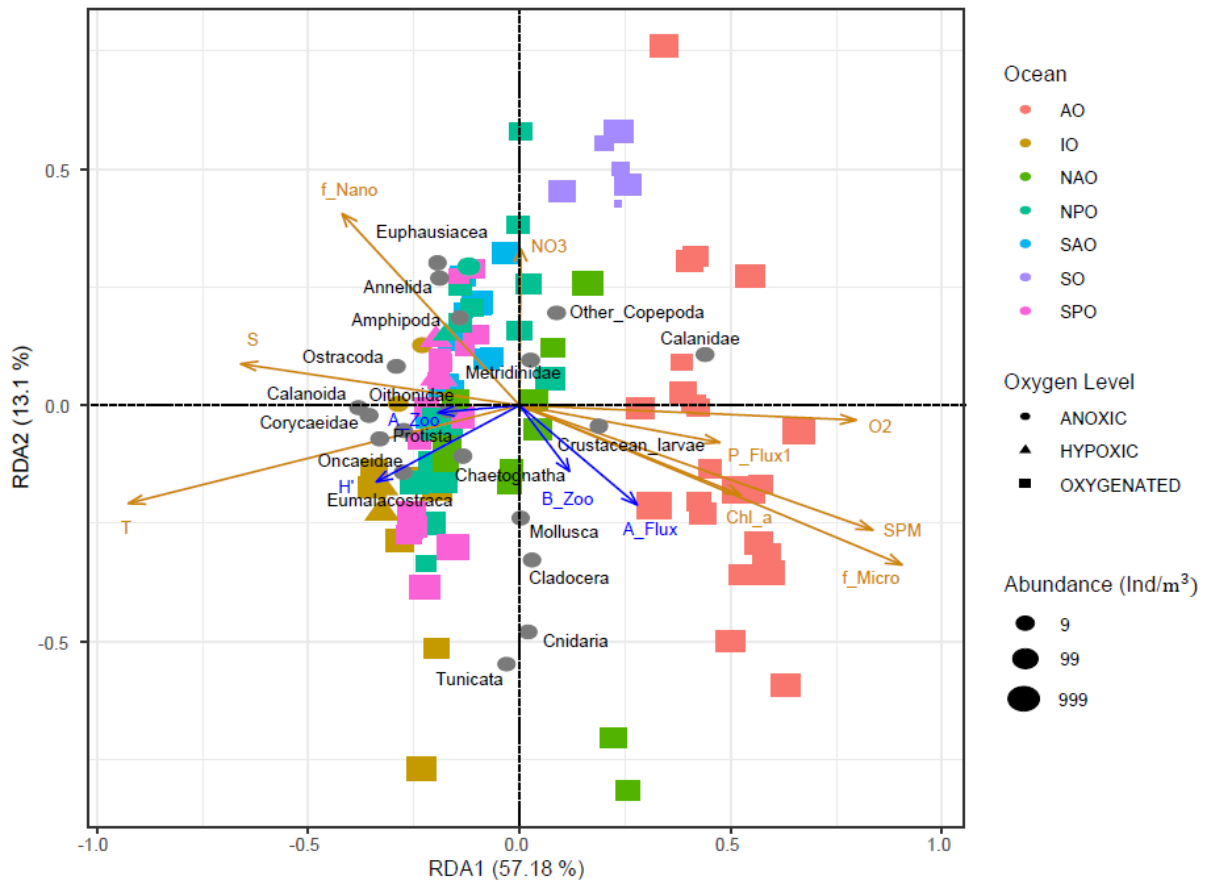
312
313 Fig. 3: Distributions of attenuation rates at each station per latitudinal bands (Tropical, Tropical
314 OMZ, Temperate, and Polar). A: Attenuation rate of zooplankton abundance (A_zoo). B: Attenuation
315 rate of zooplankton biomass (B_zoo). C: Attenuation rate of particle flux (A_flux). (***) means
316 significant Kruskal-Wallis test with $p < 0.01$ (Table 5).

317

318 Structuring of the epipelagic community composition.

319 In the epipelagic layer (0 – 200 m depth), the environmental variables explained 32.71%
320 of the total variance in mesozooplankton groups' abundances. The first RDA axis (RDA1, 57.18
321 % of constrained variance) opposed the samples from polar waters, and especially those from
322 the Arctic dominated by Calanidae and crustacean larvae (RDA1 > 0), to the tropical samples
323 presenting more even contributions from most of the remaining groups: Protista,
324 Eumalacostraca, Annelida, Amphipoda, Corycaeidae, Chaetognatha, Euphausiacea,
325 Oithonidae, Ostracoda, Oncaeidae, Calanoida (RDA1 < 0). RDA1 was negatively scored by
326 temperature and salinity and positively scored by vertical particle flux, microphytoplankton
327 contribution, suspended particle concentration, dissolved oxygen concentration and chlorophyll
328 *a* concentration. Among the supplementary variables, the attenuations of the particle flux and
329 of the zooplankton biomass were positively correlated with RDA1, while the attenuation of the
330 zooplankton abundance and the Shannon index were negatively correlated to RDA1. RDA2
331 (13.1% of constrained variance) opposed the samples from the Indian Ocean and North Atlantic
332 Ocean that present higher abundances of Cnidaria, Mollusca, Tunicata and Cladocera (RDA2
333 < 0) to those samples from the Southern Ocean presenting higher abundances of Annelida,
334 Euphausiacea, Amphipoda and Other Copepoda (RDA2 > 0). RDA2 was positively scored by

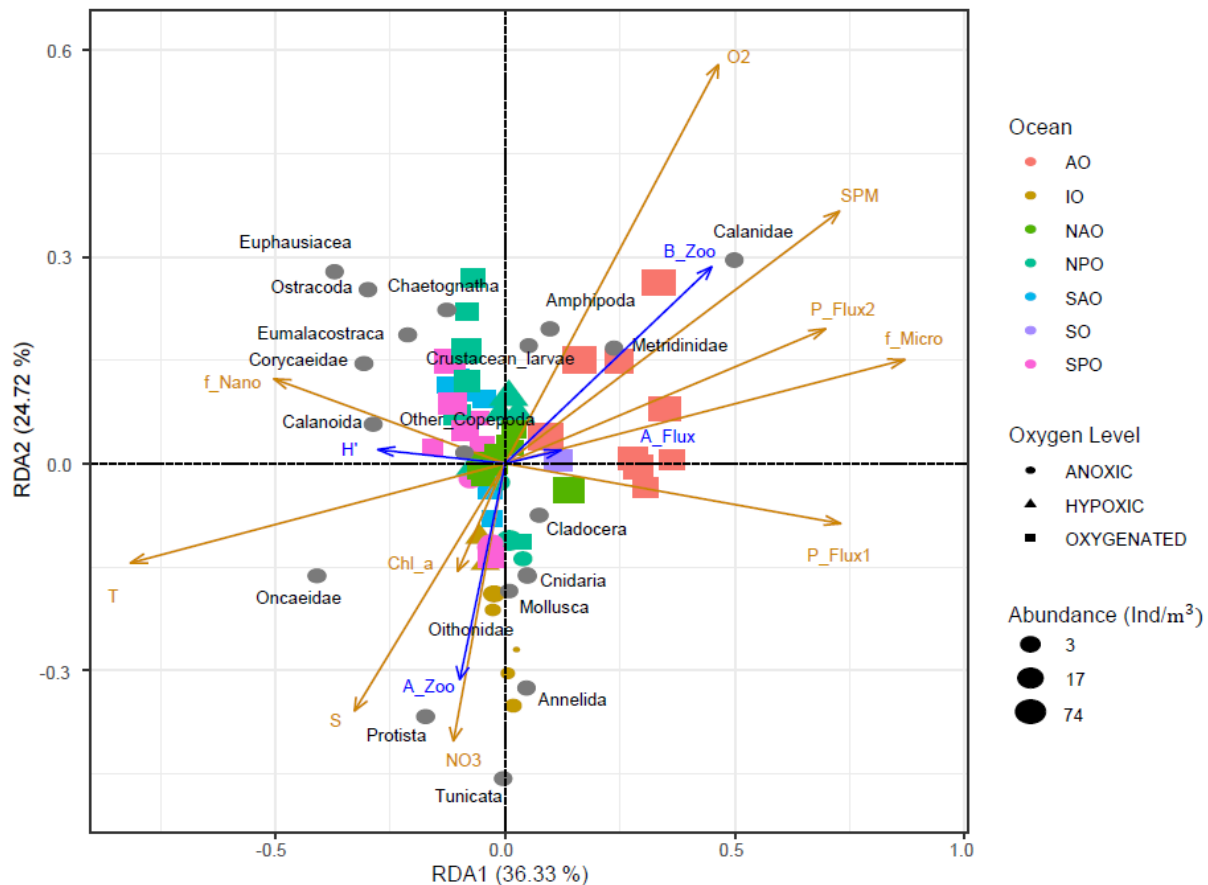
335 nitrate concentrations and the relative contribution of nanophytoplankton. It was negatively
 336 scored by the concentration of suspended particles and the relative contribution of
 337 microphytoplankton. All supplementary variables were negatively correlated with RDA2.



338
 339 Fig. 4: RDA on the epipelagic communities. Each dot corresponds to a sample, i.e., one net at one depth
 340 at one station. The orange arrows correspond to the quantitative environmental variables in RDA space:
 341 f_pico, f_nano and f_micro correspond to the relative contribution (%) of pico-, nano- and micro-
 342 phytoplankton to total phytoplankton biomass, O2 = dissolved oxygen concentration ($\mu\text{mol/kg}$), Chl_a
 343 = Chlorophyll a concentration (mg/m^3), SPM = suspended particles matter (m/sr), T = temperature ($^{\circ}\text{C}$),
 344 Sal = salinity, NO3 = nitrate concentration (mol/kg), Z = depth (m) and P_Flux= particulate flux
 345 ($\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$). Grey dots mark the projection of the zooplankton groups abundance ($\text{ind} \cdot \text{m}^{-3}$). Colors
 346 correspond to the ocean basin where the samples were taken: AO = Arctic Ocean, IO = Indian Ocean,
 347 NAO = North Atlantic Ocean, NPO = North Pacific Ocean, SAO = South Atlantic Ocean, SO = Southern
 348 Ocean, SPO = South Pacific Ocean. Shapes illustrate oxygen level, Anoxic: $[\text{O}_2] < 5 \mu\text{mol/kg}$; Hypoxic:
 349 $5 \mu\text{mol/kg} < [\text{O}_2] < 58.5 \mu\text{mol/kg}$ and oxygenated: $[\text{O}_2] > 58.5 \mu\text{mol/kg}$. Supplementary variables estimated
 350 for the epipelagic layer are represented with blue arrows: attenuation of particle flux (A_flux),
 351 attenuation of zooplankton abundance (A_zoo), attenuation of zooplankton biomass (B_zoo) and the
 352 Shannon index (H').

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

354 In the upper mesopelagic layer (200 to 500 m depth), the environmental variables
355 explained 29% of the total variance in mesozooplankton groups' abundances. Again, the first
356 RDA axis (RDA1, 36.33% of constrained variance) mainly opposed the polar samples
357 dominated by Calanidae copepods, and characterized by higher concentrations of suspended
358 particle, particle flux (both from surface and upper mesopelagic layer), and higher dissolved
359 oxygen concentrations (RDA1 > 0), from the samples characterized by more diverse
360 zooplankton communities (mainly Corycaeidae, small Calanoida, Oncaeidae) and correlated to
361 higher temperature, higher salinity and a higher relative contribution of the nanophytoplankton
362 (RDA1 < 0). Similarly, to what was observed for the epipelagic layer, among the supplementary
363 variables, the attenuations of the particle flux and of zooplankton biomass were positively
364 correlated with RDA1, while the attenuation of zooplankton abundance and the Shannon index
365 were negatively correlated to RDA1. RDA2 (24.72% of constrained variance) opposed the
366 anoxic samples from the Indian Ocean presenting higher abundances of Tunicata, Annelida,
367 Protista, Mollusca, Oithonidae and Cnidaria (RDA2 < 0) to the oxygenated ones displaying
368 higher abundances of Ostracoda, Eumalacostraca, crustacean larvae, other Copepoda,
369 Chaetognatha and Euphausiacea (RDA2 > 0). Samples from the Arctic Ocean were dominated
370 by large copepods from the Calanidae and Metridinidae families. Samples from the Pacific and
371 Atlantic Oceans were dominated by other Copepoda, Eumalacostraca, Ostracoda,
372 Euphausiacea, Chaetognatha and crustacean larvae. Higher attenuation rates of zooplankton
373 biomass and particle flux were found in polar samples whereas higher zooplankton attenuation
374 rates were found in warmer waters, especially at OMZ stations. Again, samples from the
375 tropical upper mesopelagic layers displayed more diverse communities. The distribution of the
376 supplementary variables along RDA2 differed from what was observed for the epipelagic layer,
377 as the supplementary variables, except the attenuation of the zooplankton abundances, were
378 positively correlated to RDA2.

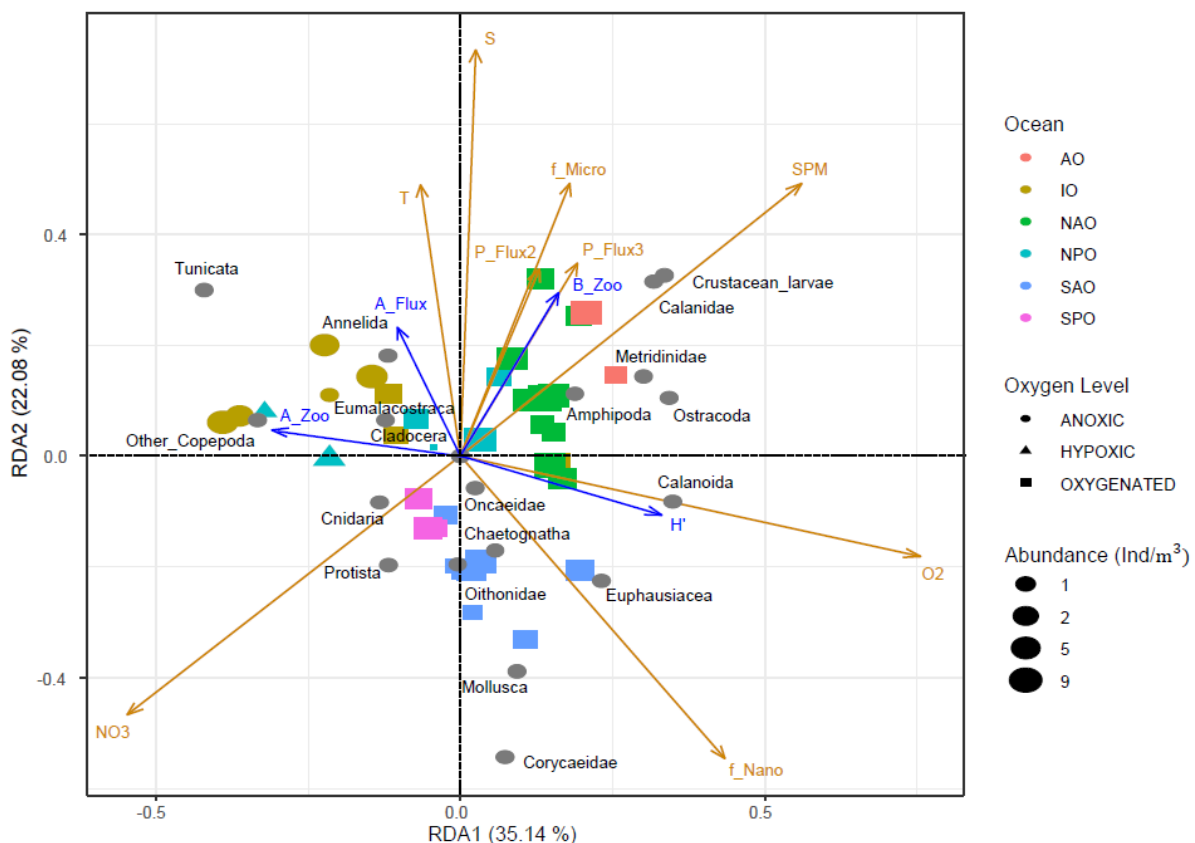


379
 380 Fig. 5: RDA performed on the upper mesopelagic abundances. Each dot corresponds to a sample, i.e.,
 381 one net at one depth at one station. The orange arrows correspond to the quantitative environmental
 382 variables (see legend of Fig. 4). Anoxic: $[O_2] < 5 \mu\text{mol/kg}$; Hypoxic: $5 \mu\text{mol/kg} < [O_2] < 58.5 \mu\text{mol/kg}$ and
 383 oxygenated: $[O_2] > 58.5 \mu\text{mol/kg}$. Supplementary variables estimated for the upper mesopelagic layer
 384 are represented with blue arrows: attenuation of particle flux (A_flux), attenuation of zooplankton
 385 abundance (A_zoo), attenuation of zooplankton biomass (B_zoo) and the Shannon index (H').

386 Structuring of the lower mesopelagic community composition

387 In the lower mesopelagic layers (500 to 1000 m depth), the environmental variables
 388 explained 29.46 % of the total variance in mesozooplankton groups' abundances. The first RDA
 389 axis (RDA1, 35.14 % of constrained variance) opposed the stations from the Arctic and North
 390 Atlantic Oceans characterized by higher dissolved oxygen concentrations, higher suspended
 391 particle concentrations (RDA1 > 0), from the anoxic and nitrate-rich stations from the Indian
 392 Ocean (RDA1 < 0). The former stations were characterized by higher abundances of Calanidae,
 393 Calanoida, Metridinidae, crustacean larvae, Ostracoda and Amphipoda, whereas the latter were
 394 characterized by higher abundances of Tunicata, Annelida, Eumalacostraca and other
 395 Copepoda. RDA2 (22.08 % of constrained variance) separated the colder and less salty stations
 396 of the Southern Atlantic Ocean (RDA2 < 0) from the warmer, saltier stations (RDA2 > 0) of

397 the North Atlantic and the Indian Oceans that are characterized by less diverse zooplankton
 398 communities. The stations that sampled the oxygenated waters of the North Atlantic and Arctic
 399 Oceans were dominated by large copepods of the Metridinidae and Calanidae families, as well
 400 as most of the small other Calanoida (i.e. those smaller copepods that could not be recognized at
 401 a more detailed taxonomic level) in addition to Ostracoda, Amphipoda, and crustacean larvae.
 402 Oxygenated stations from the South Atlantic Ocean (SAO) were characterized by higher
 403 abundances of Chaetognatha, Corycaeidae, Euphausiacea, Cnidaria, Mollusca, Oithonidae,
 404 Oncaeidae and Protista. Samples taken in the OMZ of the Indian and North Pacific Oceans
 405 displayed higher abundances of other Copepoda, Tunicata, Annelida, Eumalacostraca and
 406 Protista. Higher mesozooplankton biomass and stronger particle flux attenuation rates were
 407 found in the normoxic waters while higher zooplankton attenuation rates were observed at the
 408 stations that sampled an OMZ. The distribution of the supplementary variables showed similar
 409 association with environmental variables as in the upper mesopelagic.
 410



411
 412 Fig. 6: RDA performed on the lower mesopelagic abundances. Each dot corresponds to a sample, i.e.,
 413 one net at one depth at one station. The orange arrows correspond to the quantitative environmental
 414 variables (see legend of Fig. 4). Anoxic: $[O_2] < 5 \mu\text{mol/kg}$; Hypoxic: $5 \mu\text{mol/kg} < [O_2] < 58.5 \mu\text{mol/kg}$ and
 415 oxygenated: $[O_2] > 58.5 \mu\text{mol/kg}$. Supplementary variables estimated for the lower mesopelagic layer

416 are represented with blue arrows: attenuation of particle flux (A_{flux}), attenuation of zooplankton
417 abundance (A_{zoo}), attenuation of zooplankton biomass (B_{zoo}) and the Shannon index (H').

418

419

420 **Discussion**

421 The present global analysis of spatial patterns of the mesozooplankton community and
422 their relationship with the strength of the vertical particle flux is based on zooplankton
423 abundance and biomass estimates and vertical particles flux estimated using state-of-the-art
424 imaging techniques (Zooscan and UVP5). The rigorous quality control (see Supplementary
425 Material) allows to depict with confidence correlations between zooplankton and particle flux,
426 two important components of the biological carbon pump (BCP). Notably the study allows to
427 infer global ecological patterns in the epipelagic and mesopelagic layers, the coupling between
428 these two layers in oxygenated, hypoxic and anoxic situations.

429 **Important environmental factors for the mesozooplankton community composition in the** 430 **epipelagic layer**

431 High latitude marine ecosystems are characterised by a combination of lower species
432 diversity and shorter food webs (Laws, 1985; Stempniewicz et al., 2007) sustained by higher
433 concentrations of large microphytoplankton cells (diatoms). On the contrary, low latitude
434 ecosystems are featured by more complex and diverse food webs (Saporiti et al., 2015; Uitz et
435 al., 2006) adapted to lower production rates ensured by smaller cells (i.e. pico- and
436 nanoplankton). How the dynamics of zooplankton community composition and vertical particle
437 flux follow this scheme remains more elusive. Previous field-based studies reported peaks in
438 zooplankton species richness in the tropics (Rombouts et al., 2010; Rutherford et al., 1999;
439 Yasuhara et al., 2012), which is in line with the above-mentioned theory that the tropical food-
440 depleted regions promote more complex food-webs with higher species richness. Our RDAs
441 results result supports the view that, on a global scale, temperature and the production regime
442 of surface ecosystems are the main drivers of zooplankton community structure in the
443 epipelagic layer. Therefore, our observations fall in line with the theory described above: in the
444 epipelagic layers, less abundant and more diverse zooplankton thrive in warm, pico- and
445 nanophytoplankton-dominated waters contrary to the polar waters where zooplankton is much
446 more abundant but less diverse. Polar waters are characterised by a higher contribution of
447 microphytoplankton to total phytoplankton biomass and higher concentrations of particles. Our
448 results also indicate that the two polar communities are not completely alike, as the Arctic is
449 dominated by calanoid copepods while euphausiids and small undetermined copepods
450 dominate in the few stations sampled in the Southern Ocean. Such differentiation has been
451 previously shown by several authors who found that Arctic zooplankton were dominated by
452 *Calanus* spp. (Balazy et al., 2018; Hirche and Mumm, 1992), whereas it was shown that

453 Antarctic zooplankton were dominated by euphausiids, small calanoids, cyclopoids (i.e.
454 *Oithona* spp., *Oncaea* spp.) and salps (Park and Wormuth, 1993; Quetin et al., 1996; Ross et
455 al., 2008).

456 **Important environmental factors for the mesozooplankton community structure in the** 457 **mesopelagic layer**

458 The RDA displayed similar general patterns in both the upper and lower mesopelagic
459 layers with the stations in the Indian Ocean (with low zooplankton concentration in low oxygen)
460 and Arctic Ocean (with high zooplankton concentration in oxygenated conditions) being in all
461 layers well separated from the other stations in the remaining ocean. The highest mesopelagic
462 zooplankton concentrations were found at stations associated with high microphytoplankton
463 concentrations in the epipelagic and high particle flux, suggesting a strong impact of surface
464 production regime on the mesozooplankton in the mesopelagic (Hernández-León et al., 2020).
465 The inter-basin differences in zooplankton concentration and community composition was
466 slightly lower in the lower mesopelagic compared to the upper mesopelagic, probably due to
467 the more homogeneous habitat (Fernández de Puelles et al., 2019).

468 In general, stations associated with anoxic or hypoxic conditions at midwater depth
469 displayed lower zooplankton concentrations in the mesopelagic and different community
470 composition from oxygenated layers. The stations that sampled the tropical OMZ showed
471 higher proportions of gelatinous carnivorous zooplankton (Cnidaria), gelatinous filter feeders
472 (Tunicata), Mollusca and small omnivorous grazers (Cladocera). Anoxic or strongly hypoxic
473 conditions in the mesopelagic may have selected for those taxa adapted to low oxygen (Vaquer-
474 Sunyer and Duarte, 2008). In mesopelagic oxygenated waters, the stations of the Tropical
475 Pacific Ocean displayed a higher diversity stemming from the higher and relatively even
476 abundances of large protists (i.e. Rhizaria and Foraminifera), chaetognaths, crustaceans
477 (Ostracods, Euphausiacea, Eumalacostraca, Amphipoda), and various copepod families
478 (Corycaeidae, Oithonidae, Oncaeidae, small Calanoida). These zooplankton communities were
479 associated with oligotrophic conditions at surface (Fig. 4), lower zooplankton abundances,
480 lower concentrations of suspended matter, weaker particle fluxes and weaker attenuation rates
481 (Fig. 3B) and with stronger attenuation rates of organisms' abundances (Fig. 3A). Therefore,
482 we evidence oligotrophic regimes where the zooplankton community constitutes a network of
483 diverse taxa that is not as efficient at using the low amount of material fluxing. Our results are
484 consistent with previous studies suggesting that those oligotrophic regimes can be relatively
485 efficient at exporting the slow-sinking fraction of the little carbon that is produced in the surface

486 layers due to a low impact of zooplankton grazing on the sinking particles (Guidi et al., 2009;
487 Henson et al., 2015). This could help explain why we found the lowest particle flux attenuation
488 rates in the tropics.

489 **Global vertical patterns of zooplankton and particle flux**

490 The concentration and biomass of various zooplankton groups decreased with depth
491 (Fig. S1), confirming the general trend of decreasing zooplankton abundance and biomass from
492 the surface to 1000 m depth resolved (Fig. 2; Bode et al., 2018; Brugnano et al., 2012;
493 Hernández-León et al., 2020; Koppelman et al., 2005; Kosobokova and Hopcroft, 2010;
494 Yamaguchi et al., 2004). Among these earlier studies, two models for the attenuation of
495 zooplankton have been proposed: an exponential or a power model. Here, we used the power
496 model (equation 1) because it was widely used to model vertical flux attenuation rates (Martin
497 et al., 1987). Based on this power model, we observed rates of decrease in zooplankton
498 abundance or biomass (Fig. 3) that were in the same range as those reported in the western
499 Pacific Ocean (-1.52 to -1.41 for abundance and -1.32 to -1.10 for biomass, (Yamaguchi et al.,
500 2002). Zooplankton abundance decreased more rapidly with depth than biomass as the average
501 size of organisms increased with depth, confirming that the contribution of larger species
502 increases with depth (Homma and Yamaguchi, 2010; Yamaguchi et al., 2002). Considering a
503 larger latitudinal band than earlier studies who found weak regional or global patterns
504 (Hernández-León et al., 2020; Puelles et al., 2019), we showed that the rates of zooplankton
505 attenuation vary with latitude and to a lesser extent with oxygen concentrations (Fig. 3) and
506 also in the opposite direction of the flux attenuation.

507 Stronger surface particle fluxes and vertical attenuation rates were found at higher
508 latitudes where primary production is mainly ensured by the microphytoplankton and weaker
509 flux and attenuation was found in the low latitude dominated by picophytoplankton (Fig.4).
510 Such latitudinal pattern in particle attenuation rates results from the gradient in the production
511 regime and has been observed quasi-systematically with imaging systems on global scales
512 (Guidi et al., 2015), but also based on sediment traps (Berelson, 2001) or combining sediment
513 traps with satellite-based estimates of primary production (Henson et al., 2012). However,
514 several short-term experiments at selected sites from temperate to tropical latitudes of the
515 Pacific and Atlantic, showed an opposite pattern with stronger flux and attenuation in cold and
516 productive regions compared to inter-tropical oligotrophic (Buesseler et al., 2007; Marsay et
517 al., 2015). The inconsistency of the observations is difficult to explain although it was noted
518 that depth varying remineralisation due to varying temperature may reconcile the contrasted

519 results (Marsay et al., 2015). It is possible that some of the differences arise from the use of
520 different methodologies (instruments, time scale, global representation of the dataset) to address
521 the complexity of the processes to be measured simultaneously.

522 Such opposite pattern between A_Zoo and B_zoo in one hand and A_Flux in the other
523 hand supports the view that the abundant zooplankton community plays a crucial role in flux
524 attenuation in productive layers, by feeding and fragmenting the sinking material as suggested
525 in previous studies (Dilling and Alldredge, 2000; Lampitt et al., 1990; Sarah L. C. Giering et
526 al., 2014; Stemmann et al., 2004). However, on average and more importantly at high latitudes,
527 zooplankton attenuation rates were stronger than the vertical flux attenuation rates (Fig. 3)
528 indicating that zooplankton vertical zonation may be affected by other processes than the
529 resources provided by the flux of organic matter from the epipelagic layer. In the inter-tropical
530 OMZ regions, zooplankton vertical attenuation rates were maximum when the vertical
531 attenuation of the particle's flux was minimum. Previous studies have reported lower flux
532 attenuation rates in the OMZ of the Arabian Sea (Haake et al., 1992; Roullier et al., 2014), and
533 Eastern Tropical North Pacific (Cavan et al., 2017; Van Mooy et al., 2002). Lower zooplankton
534 activity together with reduced bacterial activity (Cram et al., 2021) would allow sinking
535 particles to transit through the OMZ core without being severely degraded (Wishner et al., 2008,
536 1995) .

537

538 **Sensitivity of plankton and vertical flux to contrasted oxygen conditions**

539 By comparing zooplankton communities from inter-tropical stations with those from
540 oxygenated mesopelagic layers to stations from OMZs, our analysis brought additional
541 evidence that change in zooplankton community composition may affect the efficiency of the
542 BCP. The zooplankton community sampled in the Indian Ocean OMZ displayed a particular
543 composition compared to the other samples, which is in line with the increasing number of
544 studies that document the profound impact of oxygen depletion on pelagic organisms (Ekau et
545 al., 2010; Hauss et al., 2016; Wishner et al., 2018). Our results underlined how the OMZ can
546 strongly reduce the abundance of several zooplankton groups (i.e. Calanoida, Euphausiacea,
547 Amphipoda, Ostracoda) that are outcompeted by more hypoxia-tolerant ones. We found that
548 tunicates (mostly Appendicularia), large protists (Collodaria and Foraminifera), polychaetes,
549 Oncaeidae, Oithinidae and to a lesser extent Cnidaria (jellyfishes) may tolerate OMZ
550 conditions, since their abundance at OMZ and at non-OMZ stations did not present significant
551 differences. All of these zooplankton groups have been reported as being able to thrive or

552 endure at low oxygen concentrations in various OMZs (Ekau et al., 2010; Hauss et al., 2016;
553 Keister and Tuttle, 2013; Kiko and Hauss, 2019; Parris et al., 2014; Tutası and Escribano, 2020;
554 Werner and Buchholz, 2013; Wishner et al., 2020). Those “hypoxiphilic” or hypoxia-tolerant
555 taxa display special adaptations that enable them to remain at extremely low oxygen
556 concentrations where other zooplankton groups cannot, because they fail to meet their
557 metabolic oxygen demand (Childress and Seibel, 1998; Seibel, 2011). Jellyfish and large
558 protists benefit from their passive feeding tactics which are less oxygen-demanding than active
559 cruising and filter feeding (Kiørboe, 2011). Indeed, hypoxia-tolerant taxa can also display
560 behavioral adaptations that cut down the metabolic costs associated with active feeding or the
561 active search for mates in the water column. Copepod species belonging to the Oncaeidae and
562 Oithonidae families are known for performing ambush feeding tactics or to attach themselves
563 on large detritus (Brun et al., 2017), which allows them to capture small preys or to feed on
564 falling detritus at very low metabolic costs. Therefore, these less motile copepods frequently
565 outcompete most of their calanoid congeners in OMZs and often co-occur with Appendicularia,
566 as those discard particle-rich aggregates on which the copepods feed (Alldredge, 1972; Brun et
567 al., 2017; Kiørboe, 2011). Other possible adaptations consist in the use of lipid storages and
568 metabolic suppression (Wishner et al., 2020). Some organisms conduct a diapause in the OMZ
569 for an extended period, allowing them to avoid foraging predators and to complete their life
570 cycle (Arashkevich et al., 1996). Diapause reduces energetic costs and thus allows the
571 organisms to survive in resource-depleted conditions. Metabolic suppression goes hand in hand
572 with the diapause, but can also occur on shorter time scales, e.g. when organisms stay at OMZ
573 depth during diel vertical migrations. Diapause and metabolic suppression are associated with
574 reduced respiratory and locomotor activity. Feeding on and disruption of particles could
575 therefore be reduced at OMZ depth not only due to the exclusion of many hypoxia intolerant
576 zooplankton organisms, but also due to the reduced activity of those zooplankton organisms
577 that can cope with OMZ conditions. The zooplankton groups we found to characterize the
578 community inhabiting the hypoxic and anoxic layers are those that commonly outcompete
579 others in OMZs worldwide. They could benefit from the likely future expansion of OMZ
580 (Oschlies et al., 2018) and thus become increasingly abundant with future climate change. This
581 would probably result in enhanced vertical particle flux in those regions. However, this requires
582 further research as some of these organisms could already be living near their physiological
583 hypoxia tolerance limits (Wishner et al., 2018).

584 **Conclusions**

585 Our study combined consistent and large-scale observations of zooplankton abundance,
586 biomass and community composition with estimates of vertical particle fluxes obtained through
587 imaging system pipelines. We showed that consistent observations can be obtained at a global
588 level using in situ camera systems and precise net sampling in various ecosystems
589 representative of different ocean conditions. In future surveys, consistently combining these
590 techniques with acoustic and other bio-optical sensors will allow the measurement of the
591 vertical and horizontal distribution of organisms with greater precision. We showed that the key
592 environmental variables driving epipelagic mesozooplankton community structure at the global
593 scale are temperature, phytoplankton biomass and phytoplankton key groups. In the
594 mesopelagic layer, surface phytoplankton size classes, particle concentration, temperature and
595 oxygen availability were identified as the main drivers of mesozooplankton community
596 structure. Our work furthermore suggests that low attenuation of zooplankton abundance and
597 biomass go in hand with high particle flux attenuation and vice versa. Such information is
598 crucial for the parameterization of the next generation of marine ecosystem models that describe
599 complex zooplankton-related processes based on coarse but increasingly numerous functional
600 types. Such models suggest that surface phytoplankton biomass and size classes, the flux of
601 particles and the oxygen content in the mesopelagic layer will all be affected further by global
602 climate change. The fact that zooplankton communities are sensitive to those factors suggests
603 that future climatic changes may profoundly alter zooplankton communities worldwide, at the
604 surface but also in the deeper mesopelagic layer.

605

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632

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

Taxonomic groups	Sub groups
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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986 Table 2: Coefficient factors used for equation 1 and that were taken from observed allometric
 987 relationships between body area and individual dry mass (Lehette et al., 2009). The conversion factors
 988 to carbon are taken from Kiorboe 2013.

Zooplankton category	Biomass Exponent (b)	Biomass Multiplier (a)	DW to C
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 ⁻³	
Other (Annelids, Cladocera, Ostracoda)	1.54 ± 0.03	43.38	0.289

989 * for the protist we used a conversion factor between biovolume and biomass (Biard et al.,
 990 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 ($Ind. m^{-3}$)		Zooplankton biomass ($mgC. m^{-3}$)		Particle vertical flux	
	b	IC (95%)	b	IC (95%)	b	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.

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

1002

1003 [Supplementary material](#)

1004

1005 [Availability of the dataset](#)

1006 **Data sets for the environment are available at Pangea:**

1007 (<https://doi.org/10.1594/PANGAEA.840721>)

1008

1009 **Tables for the RDA are available**

1010 For zooplankton: Metadata_Zooplankton_Article_RDA.xls

1011

1012

1013 **Zooplankton Pangea for the tables/ecotaxa for the vignettes**

1014 <https://ecotaxa.obs->

1015 [vlfr.fr/prj/714?taxo=56693&taxochild=N&ipp=100&zoom=100&sortby=&magenab](https://ecotaxa.obs-vlfr.fr/prj/714?taxo=56693&taxochild=N&ipp=100&zoom=100&sortby=&magenab)

1016 [bled=0&popupenabled=0&statusfilter=&samples=&instrum=&sortorder=asc&disp](https://ecotaxa.obs-vlfr.fr/prj/714?taxo=56693&taxochild=N&ipp=100&zoom=100&sortby=&magenab)

1017 [field=&projid=714&pageoffset=0](https://ecotaxa.obs-vlfr.fr/prj/714?taxo=56693&taxochild=N&ipp=100&zoom=100&sortby=&magenab)

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1020 [Quality of the dataset](#)

1021 The analysis reported here is the first to apply consistent imaging techniques in order to
1022 investigate particle flux, zooplankton community composition and biomass across the global
1023 ocean. To do so, our study relies on the combined use of the Underwater Video Profiler v5
1024 (UVP5), a Multinet and the Zooscan imaging system. These results are the first combined global
1025 zooplankton and flux estimates and as such provide a baseline for future studies. Their quality
1026 needs to be discussed with regards to 1) flux assessment, 2) mesh selectivity, mass conversion
1027 and possible impact of dead zooplankton in the images, the capacity of the sampling design to
1028 capture or not 3) day night variability and 4) mesopelagic peaks of zooplankton.

1029 Vertical particle mass fluxes ($\text{mg Dry Weight m}^{-2}\text{d}^{-1}$) were calculated from the particle
1030 size spectra (150 μm -1.5 mm) detected by the UVP5 following Guidi et al., (2008). Briefly,
1031 the procedure optimized two parameters in the flux equation by comparing UVP5 derived flux
1032 and a global sediment trap flux data set (Guidi et al., 2008). Depending on the ocean basin,
1033 regional algorithms with different sets of the two parameters have been proposed (Forest et al.,
1034 2013; Kiko et al., 2017) but the shape of the allometric relationships between particle size and
1035 flux is kept as a growing monotonic power relationship. Many studies have shown that this
1036 assumption is verified when comparing extremes size of particles but they all have also shown

1037 a high variability (Guidi et al., 2008; Iversen and Lampitt, 2020) which cannot be depicted
1038 without more information on the type of particles. In addition, we used the same parametrization
1039 for each depth layer although a few observational and modelling studies (Berelson, 2002;
1040 Gehlen et al., 2006) have proposed that the sinking speed may vary with depth. Finally, the
1041 fluxes are calculated considering all particles detected in situ by the UVP5. Because particles
1042 are so abundant in the size range presently considered for flux estimation (150 μ m to 1.5mm),
1043 the impact of zooplankton in the present flux estimates is low (Guidi et al., 2015; Kiko et al.,
1044 2020). We did not perform further sensitivity analyses as the aim of this study was not to
1045 quantify absolute carbon flux but to assess correlations with zooplankton and other
1046 environmental variables. In the future, better recognition of particles on images will possibly
1047 allow to calculate different particle speed for different types of aggregates as was proposed
1048 recently (Trudnowska et al., 2021).

1049 Zooplankton abundance estimates are sensitive to the mesh of the plankton net tow used
1050 (Gallienne et al., 2001). A mesh size of 300 μ m was selected for the Multinet as a good
1051 compromise to capture both mesozooplankton and macro-zooplankton. However, the small
1052 copepod families (Oithona, Oncaeidae, Clausocalanidae, Paracalanidae) that dominate
1053 community composition in tropical/subtropical open oceans are not collected in an optimal
1054 fashion with the present mesh size, contrary to the larger Calanidae notably in the temperate
1055 and polar regions. Therefore, our abundance estimates likely underestimate the contribution of
1056 the smallest mesozooplankton groups. Nonetheless, even a net equipped with a 150 μ m mesh
1057 can still underestimate the abundance of cyclopoids and early copepod stages (Paffenhofer and
1058 Mazzocchi, 2003).

1059 Nets can also destroy fragile organisms during the sampling process (Remsen et al.,
1060 2004). For example, the very low abundance and biomass of Rhizarians reported here
1061 contrasting with recent findings based on *in situ* cameras (Biard et al., 2016). This is likely due
1062 to such sampling biases. As for the estimation of particle fluxes from particle size spectra, we
1063 assessed the carbon biomass of each individual organism's size using published allometric
1064 relationships (Lehette and Hernández-León, 2009) in which large and rare organisms
1065 contributes importantly to the total biomass bringing strong variability in the results. To account
1066 for the excessive variability in biomass estimates, we analysed our results using both abundance
1067 and biomass.

1068 Dead zooplankton, including carcasses, are increasingly recognized as being quite
1069 abundant in the mesopelagic water (Böttger-Schnack, 1996; Roe, 1988; Terazaki and Wada,
1070 1988; Wheeler Jr, 1967). It is impossible to assess whether the damages of the organisms

1071 observed on the digitized organisms were inflicted by the net tow. This is even harder to assess
1072 in the deeper nets which spent more time in the water column. Therefore, we cannot tell whether
1073 the organisms were damaged during the sampling process or dead beforehand. We attempted
1074 to separate the carcasses from the complete bodies of copepods based on grey intensity criteria
1075 or by looking at the physical integrity of the organisms, but this was not successful because of
1076 independent and continuous changes for both criteria. Nonetheless, among the 110'000
1077 vignettes of copepods, 21'117 (20%) were initially classified as possible carcasses. Their
1078 proportion was equal to 42.90% in the surface layer, 26.71% in the upper mesopelagic and
1079 30.39% in the deepest layers. The median and interquartile of abundances varied from the
1080 surface (median = 1.21 *Ind/m*³, IQR = 2.53) to the upper mesopelagic (median = 0.75, IQR =
1081 0.89) and increased towards deeper layers (median = 0.85, IQR = 0.99). Subsequent data
1082 analyses showed that aggregating them or not with the non-damaged copepods had no effect on
1083 the analysis' results because their proportion was homogeneous across sampling sites.
1084 Therefore, all copepods were ultimately pooled together for all our numerical analyses.

1085 Zooplankton and micronekton perform diel vertical migration (DVM) in all oceans
1086 (Banse, 1964). Depending on the organism's taxonomic group and size, ranges of diel migration
1087 show tremendous variability (Ohman and Romagnan, 2016; Tarling et al., 2004). In our study,
1088 significant differences in abundances between day and night samples was found for a few
1089 groups known to be diel migrators (Euphausiids, Metridinidae, Corycaeidae, Cnidaria for
1090 abundance data; and Eumalacostraca and Ostracoda for biomass data). However, at the
1091 community level (i.e., total mesozooplankton), no significant differences could be found
1092 between the day and night samples at surface. However, total zooplankton biomass was higher
1093 in night samples compared to day samples, because of the more abundant large-bodied
1094 migrators (Eumalacostraca, Euphausiacea, Table S2). For abundance, this is a rather
1095 unexpected result as a large number of zooplankton taxa perform DVM (Kjørboe et al., 2018;
1096 Ohman and Romagnan, 2016). Yet, this absence of significant changes had already been
1097 observed in previous studies using similar types of plankton nets (Wishner et al., 2018). DVM
1098 could not be detected from the ANOSIM analysis of the surface layer for different reasons.
1099 First, the weak diel differences in abundances could easily be smeared by plankton patchiness
1100 when the replicates are too low. Second, it is possible that no differences were observed because
1101 the large organisms carrying out DVM are too few in number compared to the smaller ones in
1102 the present data. Day and night differences between the slopes of the total biomass were found,
1103 probably due to the few diel migrators species. Hence, it is well known that large zooplankton
1104 (euphausiids, sergestid shrimps, amphipods, fish such as myctophids(Morrison et al., 1999))

1105 sampled with larger Multinet nets (opening $>1\text{m}^2$ and mesh size $>500\mu\text{m}$), or detected through
1106 acoustics techniques, showed stronger DVM than smaller organisms collected through smaller
1107 Multinet nets such as ours (opening of 0.25m^2 and mesh size of $300\mu\text{m}$). Furthermore,
1108 copepods contributed to nearly 80% of total zooplankton abundance in our samples, and
1109 copepod DVM may be confined most typically to populations living within the epipelagic zone
1110 (Madhupratap et al., 2004; Morrison et al., 1999; Smith et al., 1998).

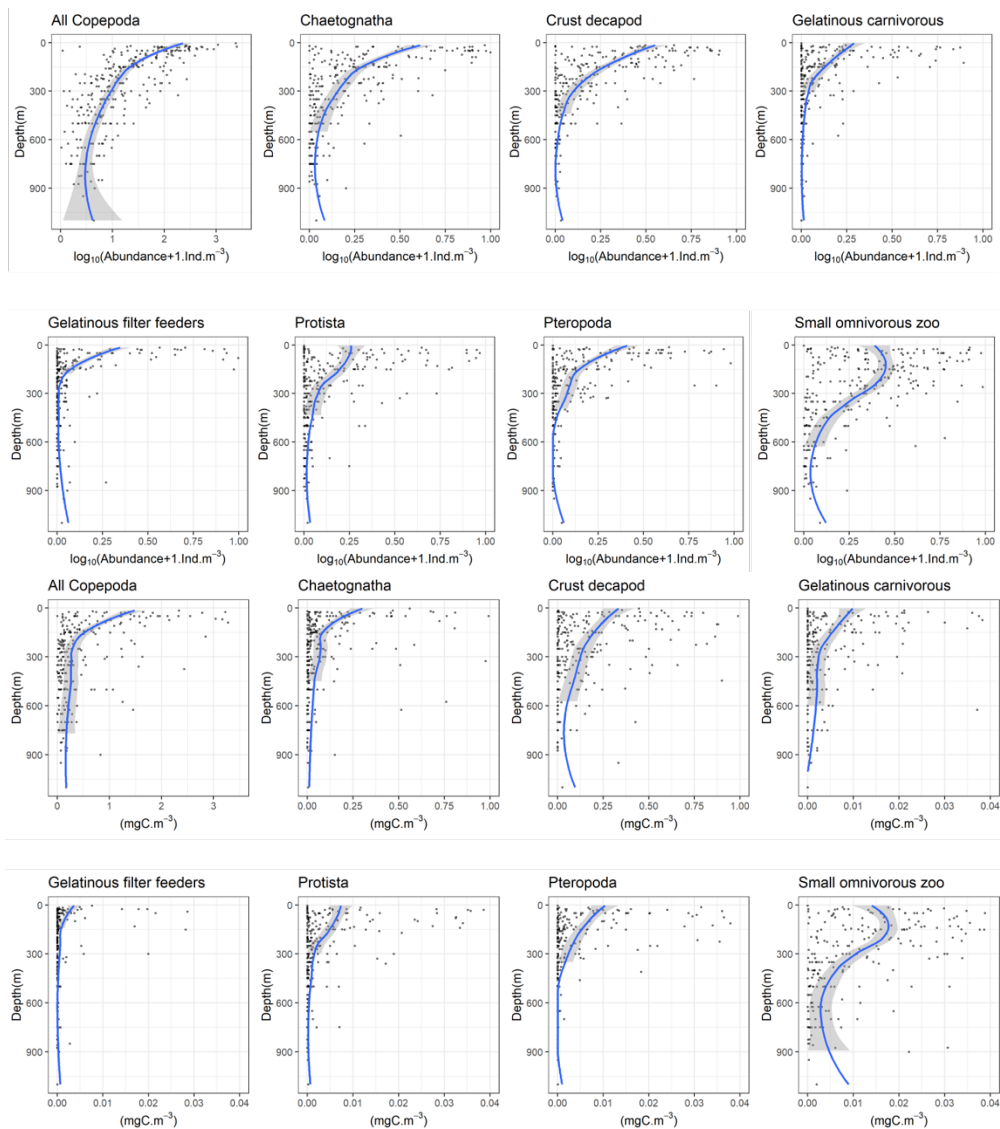
1111 Many studies have reported midwater peaks of zooplankton and nekton in 100-200 m
1112 depth layers centered around 40 to 600 m depth (Andersen et al., 1998; Irigoien et al., 2014;
1113 Koppelman et al., 2004) indicating that the use of a simple power law to describe plankton
1114 biomass may be an oversimplification of the true vertical zonation. The general lack of such
1115 peaks may be explained by the variability in methods used between studies. Midwater peaks
1116 are often reported with instruments allowing a good vertical resolution (> 10 observations in
1117 the upper kilometer) and targeting the large migrating organisms with nets having large mesh
1118 size or acoustic devices with frequencies adapted to nektonic organisms. Many studies using
1119 Multinets equipped with rather fine mesh size ($<500\mu\text{m}$) do not capture such peaks in
1120 abundance/ biomass (Homma and Yamaguchi, 2010; Yamaguchi et al., 2002). In our study, the
1121 mesopelagic layer was sampled down to 900 m depth, and only with 2 or 3 nets with a mesh
1122 size of $300\mu\text{m}$ and a small net opening (0.25m^2). Therefore, midwater peaks could have been
1123 smoothed in the few layers. Hence, the power law simplification may be a proper proxy for the
1124 smaller fraction of the mesozooplankton (mainly copepods smaller than 2 mm).

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1128 **Community vertical distribution**

1129 On a global scale, zooplankton average abundance and biomass decreased drastically
1130 with depth, with quasi similar patterns for the eight main zooplankton groups (Fig. S1). The
1131 strongest variation in abundance was observed for copepods, followed by chaetognaths, small
1132 omnivorous zooplankton and crustacean decapods (Fig. S1). The strongest variation in biomass
1133 with depth were observed for copepods followed by decapods, chaetognaths and small
1134 omnivorous zooplankton (Fig. S2).

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1139 **Fig. S1: Vertical profiles of abundance (two first lines) and biomass (two last lines) in the global ocean**
1140 **for the 8 functional mesozooplankton groups: all copepoda, chaetognatha, crustacean decapoda (crust**
1141 **decapod), gelatinous carnivorous, gelatinous filter feeders, protista, pteropoda, small omnivorous**
1142 **zooplankton. Not all abundance and biomass scales are similar to better observe the gradients. In all**

1143 cases, solid lines correspond to a smooth trends and gray ribbons to the 95% confidence intervals. These
1144 trends are drawn for illustrative purposes and were not used in down- stream analyses.

1145

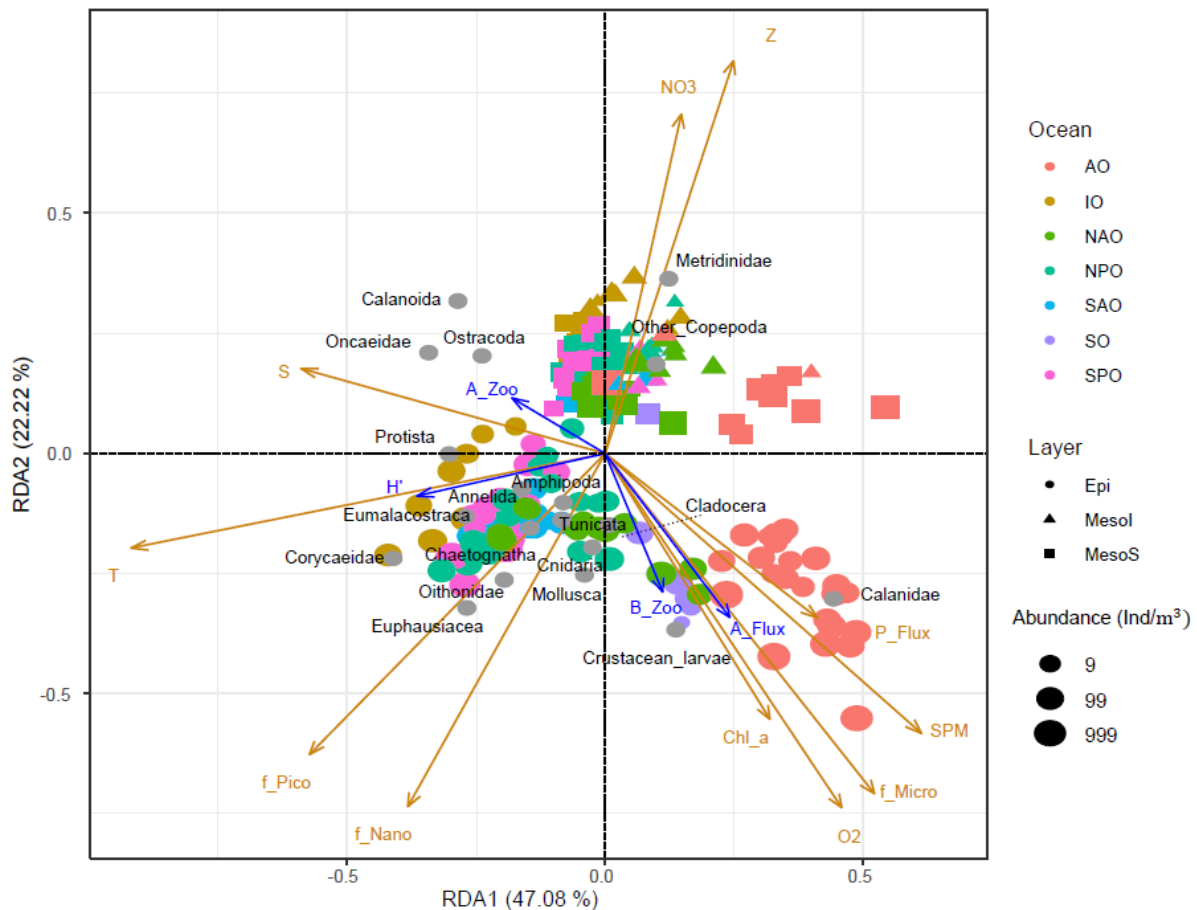
1146 **Community composition in the upper first kilometer of the ocean**

1147 When analyzing all vertical layers together, the redundant discriminant analysis (RDA)
1148 indicated that environmental variables explained 27.01% of the variance in mesozooplankton
1149 groups abundance (Fig. 4). The first RDA axis (RDA1; 47.08% of the variance constrained by
1150 the RDA) opposed the samples from polar waters (Arctic Ocean, Southern Ocean; $RDA1 > 0$)
1151 to the samples taken at lower latitudes (Indian Ocean, Northern and Southern Atlantic Ocean,
1152 Northern and Southern Pacific Ocean; $RDA1 < 0$), especially for epipelagic and upper
1153 mesopelagic samples. RDA1 was negatively scored by variables depicting a gradient of tropical
1154 to extratropical conditions: temperature, salinity, and the relative contribution of
1155 picophytoplankton and nanophytoplankton to phytoplankton community biomass. Meanwhile,
1156 RDA1 was positively scored by dissolved oxygen concentration, the intensity of the vertical
1157 particle flux and its attenuation rate, the concentration of suspended particles and the
1158 contribution of microphytoplankton to total phytoplankton biomass. The second RDA axis
1159 (22.22 % of the constrained variance) opposed the samples from the surface ($RDA2 < 0$) to the
1160 samples from mesopelagic layers ($RDA2 > 0$). This axis was positively scored by depth,
1161 salinity, and nitrate concentrations, and negatively scored by pico-, nano- and
1162 microphytoplankton concentrations, oxygen concentration, particles and chlorophyll *a*
1163 concentrations. Samples from the epipelagic layer of higher latitudes showed higher plankton
1164 abundances and were dominated by Calanidae and crustacean larvae (copepod nauplii).
1165 Samples from the epipelagic layers of lower latitudes Tropical Ocean were more diverse as they
1166 displayed more even contributions of Protista, Eumalacostraca, Annelida, Amphipoda,
1167 Tunicata, Corycaeidae, Chaetognatha, Euphausiacea, Oithonidae, Cnidaria, Mollusca and
1168 Cladocera. In the mesopelagic layer, communities were less spread in the RDA space than for
1169 the surface layer. Mesopelagic communities were dominated by Other Copepoda and
1170 Metridinidae at higher latitudes and by Calanoida, Ostracoda and Oncaeidae at lower latitudes.
1171 Polar and temperate waters displayed lower mesozooplankton diversity but higher
1172 mesozooplankton abundances/biomass, more intense vertical particle fluxes, and stronger
1173 particle attenuation rates. On the opposite, the warmer and more oligotrophic tropical waters
1174 displayed lower diversity, lower mesozooplankton biomass/ abundance, but higher attenuation
1175 rates of mesozooplankton organisms. To better disentangle the relationships between

1176 mesozooplankton composition and the environmental conditions within the different vertical
 1177 layers of the ocean, separate RDAs were then performed for each depth layer.

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1181 Figure S2: RDA performed with all layers. Each colored dot corresponds to a sample, i.e., one net at one
 1182 depth at one station. The orange arrows mark the projection of the environmental variables in RDA space:
 1183 f_{pico} , f_{nano} and f_{micro} correspond to the relative contribution (%) of pico-, nano- and micro-phytoplankton
 1184 to total phytoplankton biomass, median value of (O_2 = dissolved oxygen concentration ($\mu\text{mol/kg}$), Chl_a =
 1185 Chlorophyll a concentration (mg/m^3), SPM = suspended particles matter (m/sr), T = temperature ($^\circ\text{C}$), Sal =
 1186 salinity, NO_3 = nitrate concentration (mol/L), Z = depth (m)) and P_Flux = particulate flux ($\text{mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$).
 1187 Grey dots mark the projection of the zooplankton groups abundance ($\text{ind}\cdot\text{m}^{-3}$). Colors correspond to the ocean
 1188 basin where the samples were taken: AO = Arctic Ocean, IO = Indian Ocean, NAO = North Atlantic Ocean,
 1189 NPO = North Pacific Ocean, SAO = South Atlantic Ocean, SO = Southern Ocean, SPO = South Pacific Ocean.
 1190 Shapes illustrate the vertical layers where the samples were taken: Epi = epipelagic, MesoS = upper mesopelagic
 1191 and MesoI = lower mesopelagic.

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1195 Table S1: List of nets that were removed from the RDA analysis. AO=Arctic Ocean, IO=Indian Ocean,
 1196 NAO=North Atlantic Ocean, NPO=North Pacific Ocean, SAO=South Atlantic Ocean, SO=Southern
 1197 Ocean or Austral Ocean, SPO=South Pacific Ocean.

Ocean Bassin	Nets
IO	36_4,38_4, 39_2, 42_3
AO	163_2, 163_3, 206_2
NAO	142_4,142_4n,143_3,143_3n,147_3,147_4,150_1,150_4,151_2,151_4,152_2,152_3,155_2,158_2
NPO	131_2, 132_2,133_3,135_2,137_3,137_3n
SAO	131_2, 132_2,133_3,135_2,137_3,137_3n
SO	84_1, 85_1, 85_2
SPO	98_2, 98_3, 102_1, 106_2, 106_4,109_1,110_1,110_1n,111_1,111_1n,122_1,122_1n,125_1,125_3,127_2,127_2n

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1201 Table S2: Wilcoxon test for day and night for each taxon at level of 5% (bold values mean significant
 1202 test)

Species	Wilcoxon p-value (abundance)		Wilcoxon p-value (biomass)	
	Epipelagic	Upper Mesopelagic	Epipelagic	Upper Mesopelagic
Protista	0.50	0.13	0.8	0.06
Annelida	0.66	0.82	0.62	0.57
Chaetognatha	1	0.20	0.58	0.32
Tunicata	0.26	0.078	0.06	0.19
Cnidaria	0.90	0.037	0.58	0.009
Mollusca	0.95	0.123	0.26	0.96
Eumalacostraca	0.39	0.62	0.049	0.49
Euphausiacea	0.21	0.0098	0.0001	0.63
Amphipoda	0.07	0.91	0.39	0.83
Ostracoda	0.32	0.96	0.049	1
Crustacean_larvae	0.01	0.81	0.23	0.81
Other_Copepoda	0.76	0.46	0.95	0.41
Calanoida	0.10	0.24	0.11	0.32
Oithonidae	0.19	1	0.24	0.84
Corycaeiidae	0.01	1	0.016	0.76
Oncaeiidae	0.66	0.41	0.8	0.51
Metridinidae	0.0001	0.018	0.0001	0.006
Calanidae	0.29	0.12	0.07	1

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