



HAL
open science

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

Yawouvi Dodji Soviadan, Fabio Benedetti, Manoela Brandão,
Sakina-Dorothee Ayata, Jean-Olivier Irisson, Jean-Louis Jamet, Rainer Kiko,
Fabien Lombard, Kissao Gnandi, Lars Stemmann

► To cite this version:

Yawouvi Dodji Soviadan, Fabio Benedetti, Manoela Brandão, Sakina-Dorothee Ayata, Jean-Olivier Irisson, et al.. Patterns of mesozooplankton community composition and vertical fluxes in the global ocean. *Progress in Oceanography*, 2022, pp.102717. 10.1016/j.pocean.2021.102717 . hal-03449715

HAL Id: hal-03449715

<https://hal.science/hal-03449715v1>

Submitted on 5 Jan 2024

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

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



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 [Patterns of mesozooplankton community composition and vertical fluxes in the global](#)
2 [ocean](#)

3

4 Yawouvi Dodji Soviadan^{1,6}, Fabio Benedetti², Manoela C. Brandão^{1,3}, Sakina-Dorothee
5 Ayata^{1,7}, Jean-Olivier Irisson¹, Jean Louis Jamet⁵, Rainer Kiko¹, Fabien Lombard^{1,4}, Kissao
6 Gnandi⁶, Lars Stemmann^{1,*}

7

8 1 Sorbonne Université, CNRS, Laboratoire d'Océanographie de Villefranche, 06230
9 Villefranche-sur-mer, France.

10 2 Environmental Physics, Institute of Biogeochemistry and Pollutant Dynamics, ETH Zürich,
11 Universitätstrasse 16, 8092 Zürich, Switzerland.

12 3 Institut Français de Recherche pour l'Exploitation de la Mer, Centre Bretagne, 29280
13 Plouzané, France.

14 4 Institut Universitaire de France (IUF), Paris, France

15 5 Université de Toulon, Mediterranean Institute of Oceanology (MIO), AMU-UTLN UM110,
16 Equipe EMBIO. CS 60584, 83041 TOULON Cedex 9, FRANCE

17 6 Département de Géologie, Université de Lomé, Togo.

18 7 Sorbonne Université, CNRS, IRD, MNHN, Laboratoire d'Océanographie et du Climat:
19 Expérimentations et Approches Numériques (LOCEAN-IPSL), Paris, France

20 .

21

22 Corresponding author*

23

24

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 μ 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.

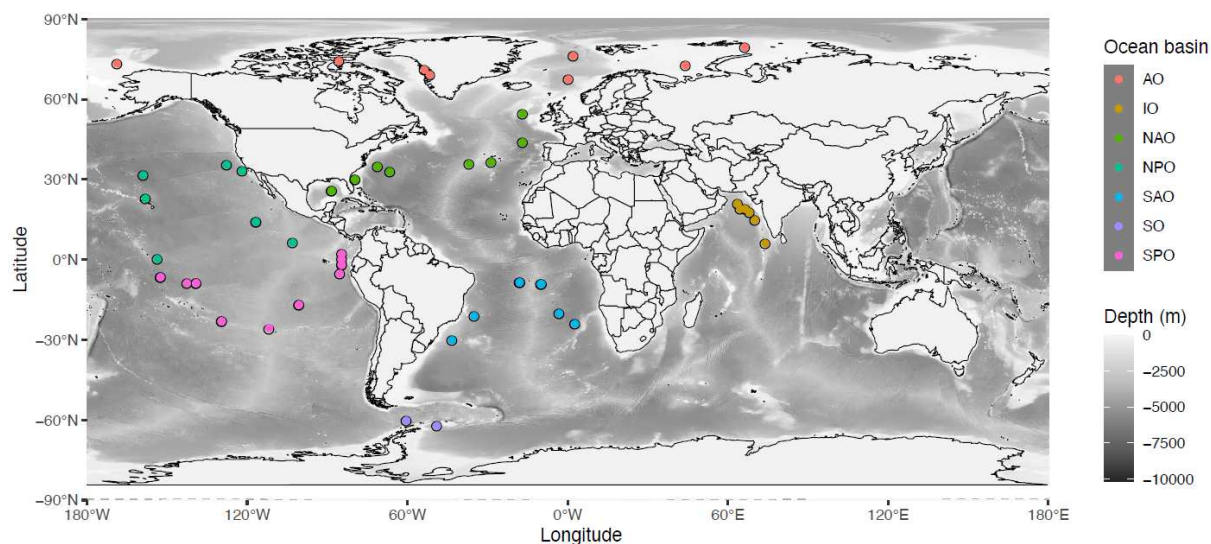
109 Here, a homogeneous dataset of community-level zooplankton images generated from
110 the TARA Oceans expeditions is explored together with associated measurements of their
111 contextual environmental conditions to: (i) test whether zooplankton communities present
112 consistent vertical variations 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 μm (WETLabs), a one-wavelength backscatter meter for particles 0.5–10 μm

143 (WETLabs), and an Underwater Vision Profiler 5 (UVP5) for particles >150 μm and
144 zooplankton >600 μm (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 μm in Equivalent Spherical Diameter), while the ones detected by
147 the UVP5 (>150 μm 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_{micro} , f_{nano} , and f_{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_{micro}
155 dominated by diatoms, f_{nano} by chromophytes, cryptophytes and nanoflagellates and f_{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 μm mesh and an aperture of 0.25 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 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 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° - 30°), temperate (30° - 60°) and polar (60° - 90°). 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

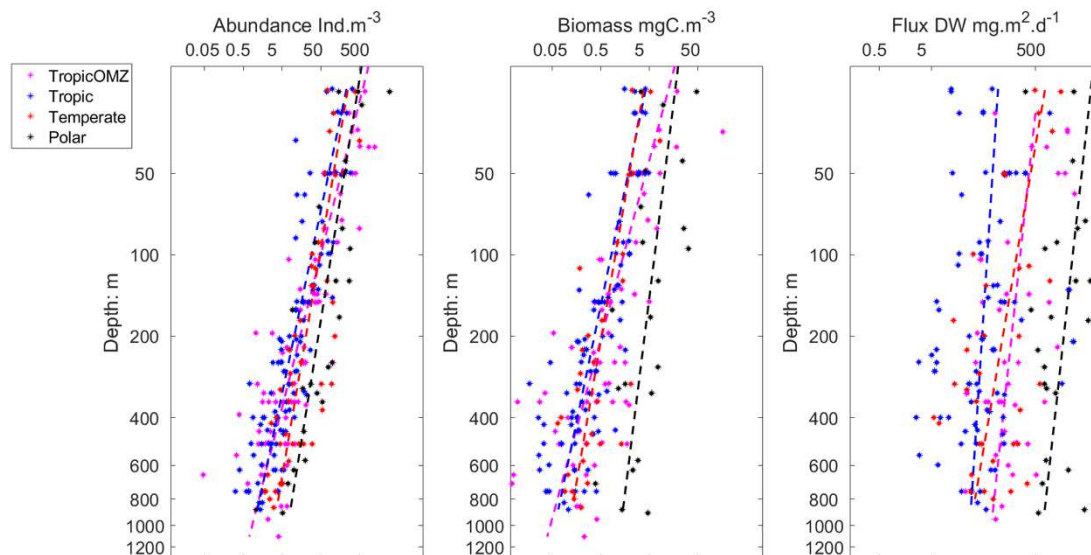
278 **Day night variability**

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

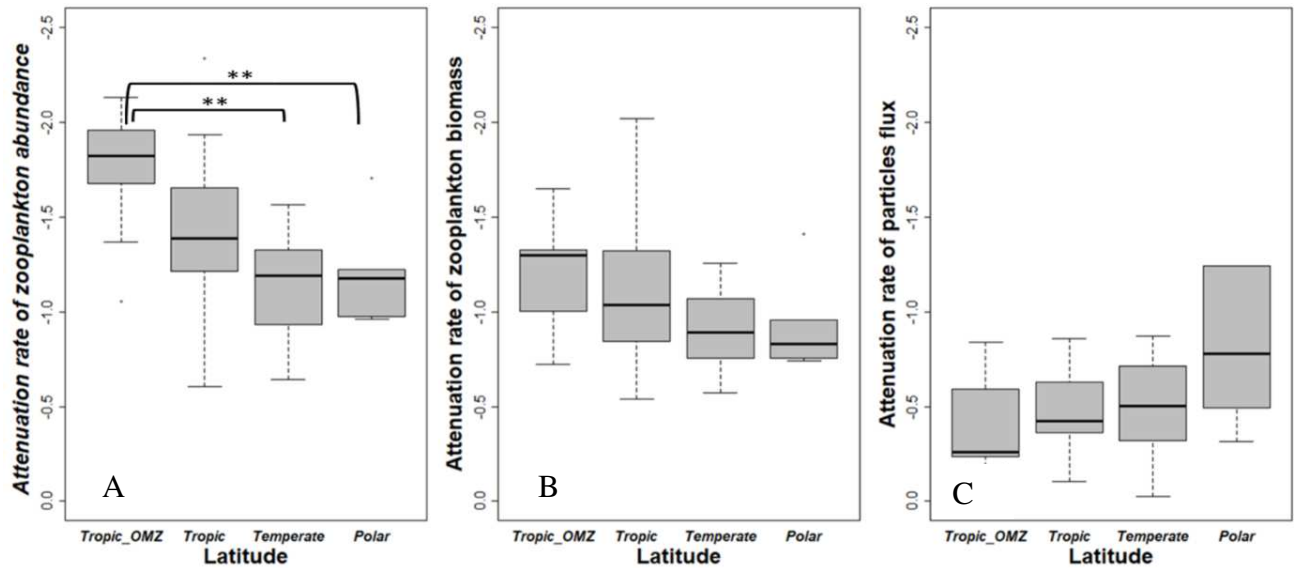


302

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).



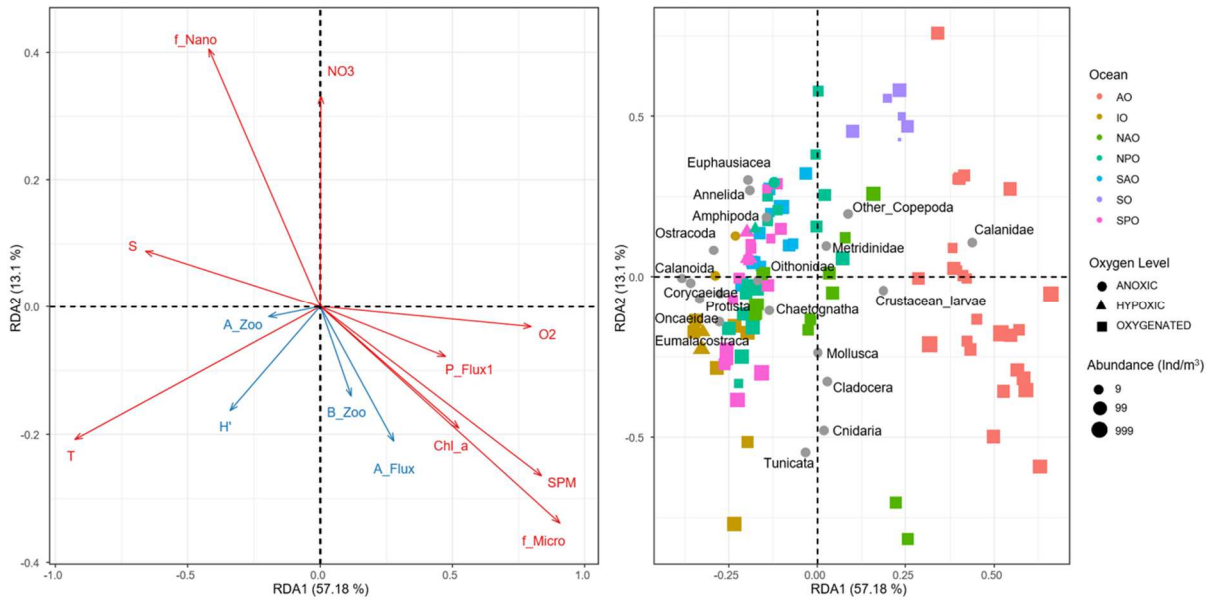
319
 320 Fig. 3: Distributions of attenuation rates per latitudinal band (Tropical, Tropical OMZ, Temperate,
 321 and Polar). A: Attenuation rate of zooplankton abundance (A_{zoo}). B: Attenuation rate of zooplankton
 322 biomass (B_{zoo}). C: Attenuation rate of particle flux (A_{flux}). (**) means 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 (mg/m^3), SPM = suspended particles
 355 matter (m^3/sr), T = temperature ($^{\circ}\text{C}$), Sal = salinity, NO3 = nitrate concentration (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: $[O_2] < 5 \mu\text{mol/kg}$;
 363 Hypoxic: $5 \mu\text{mol/kg} < [O_2] < 58.5 \mu\text{mol/kg}$ and oxygenated: $[O_2] > 58.5 \mu\text{mol/kg}$.

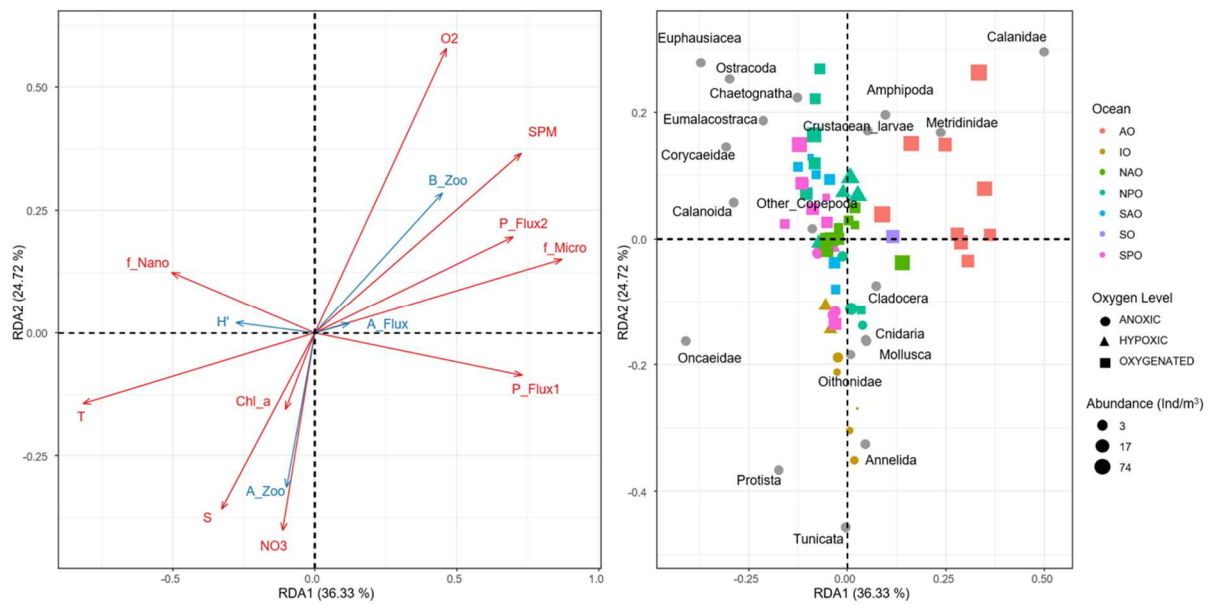
364 Structuring of the upper mesopelagic community composition.

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

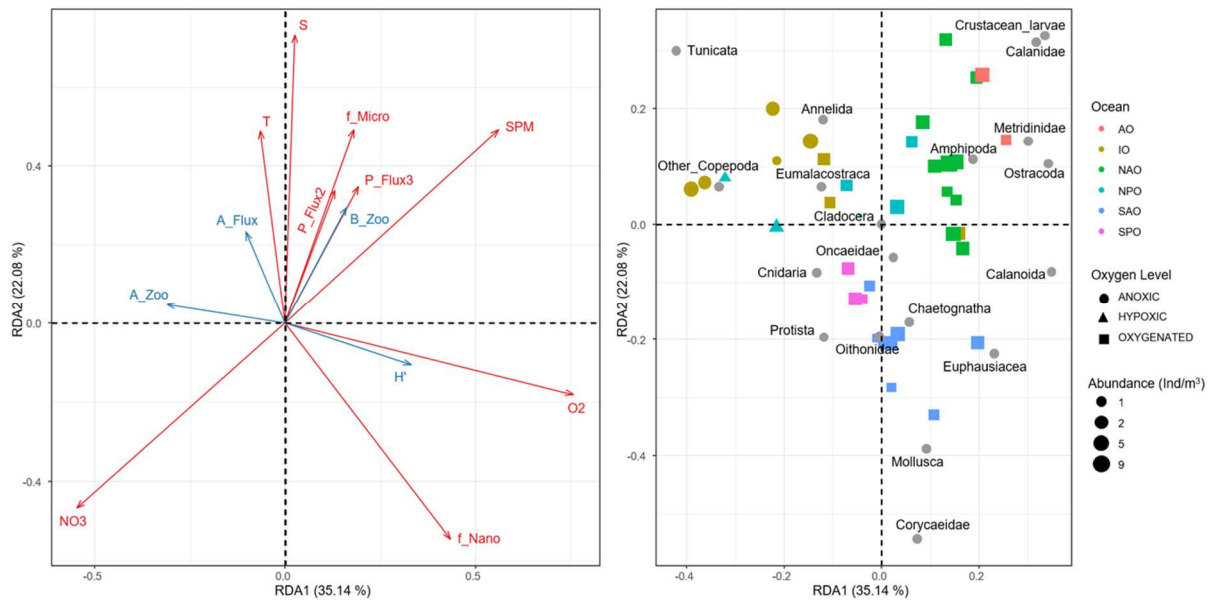


393
 394 Fig. 5: RDA performed on the upper mesopelagic abundances with the factors in the left panel and
 395 samples and taxa in the right panel. Each colored dot corresponds to a sample, i.e., one net at one
 396 depth at one station while the taxa are given as grey dots. The orange arrows correspond 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

632 **ACKNOWLEDGMENTS**

633 We thank the reviewers for their comments which help to improve the manuscript.
634 Tara Oceans (which includes both the Tara Oceans and Tara Oceans Polar Circle expeditions)
635 would not exist without the leadership of the Tara Ocean Foundation and the continuous
636 support of 23 institutes (<https://oceans.taraexpeditions.org/>). This study has received the

637 number 123. This study is part of the “Ocean Plankton, Climate and Development” project
638 funded by the French Facility for Global Environment (FFEM). Y.D.S. and M.C.B. received
639 financial support from FFEM to execute the project. R.K acknowledges support via a “Make
640 Our Planet Great Again” grant of the French National Research Agency within the
641 “Programme d’Investissements d’Avenir”; reference “ANR-19-MPGA-0012”. F.B. received
642 support from ETH Zürich. L.S. received funding from the Chair Vision at Sorbonne
643 University. This project has received funding from the European Union’s Horizon 2020
644 research and innovation programme under grant agreement No 862923. This output reflects
645 only the author’s view, and the European Union cannot be held responsible for any use that
646 may be made of the information contained therein. We further thank the commitment of the
647 following sponsors: CNRS (in particular Groupement de Recherche GDR3280 and the
648 Research Federation for the Study of Global Ocean Systems Ecology and Evolution
649 FR2022/Tara Oceans-GOSEE), the European Molecular Biology Laboratory (EMBL), the
650 French Ministry of Research, and the French Government “Investissements d’Avenir”
651 programs OCEANOMICS (ANR-11-BTBR-0008), the EMBRC-France (ANR-10-INBS-02).
652 Funding for the collection and processing of the Tara Oceans data set was provided by NASA
653 Ocean Biology and Biogeochemistry Program under grants NNX11AQ14G, NNX09AU43G,
654 NNX13AE58G, and NNX15AC08G (to the University of Maine); the Canada Excellence
655 research chair on remote sensing of Canada’s new Arctic frontier; and the Canada Foundation
656 for Innovation. We also thank Agnès b. and Etienne Bourgois, the Prince Albert II de Monaco
657 Foundation, the Veolia Foundation, Region Bretagne, Lorient Agglomeration, Serge Ferrari,
658 Worldcourier, and KAUST for support and commitment. The global sampling effort was
659 enabled by countless scientists and crew who sampled aboard the Tara from 2009–2013, and
660 we thank MERCATOR-CORIOLIS and ACRI-ST for providing daily satellite data during the
661 expeditions. We are also grateful to the countries who graciously granted sampling
662 permission.

663

665

666 Alldredge, A.L., 1972. Abandoned larvacean houses: a unique food source in pelagic
667 environment. *Science* 177, 885.

668 Andersen, V., Francois, F., Sardou, J., Picheral, M., Scotto, M., Nival, P., 1998. Vertical
669 distributions of macroplankton and micronekton in the Ligurian and Tyrrhenian Seas
670 (northwestern Mediterranean). *Oceanologica Acta* 21, 655–676.

671 Arashkevich, E., Drits, A., Timonin, A., 1996. Diapause in the life cycle of *Calanoides carinatus*
672 (Kroyer), (Copepoda, Calanoida). *Hydrobiologia* 320, 197–208.

673 Balazy, K., Trudnowska, E., Wichorowski, M., Błachowiak-Samołyk, K., 2018. Large versus
674 small zooplankton in relation to temperature in the Arctic shelf region. *Polar Research* 37,
675 1427409.

676 Banse, K., 1964. On the vertical distribution of zooplankton in the sea. *Progress in oceanography*
677 2, 53–125.

678 Beaugrand, G., Conversi, A., Atkinson, A., Cloern, J., Chiba, S., Fonda-Umani, S., Kirby, R.R.,
679 Greene, C.H., Goberville, E., Otto, S.A., Reid, P.C., Stemmann, L., Edwards, M., 2019.
680 Prediction of unprecedented biological shifts in the global ocean. *Nature Climate Change* 9,
681 237–+. <https://doi.org/10.1038/s41558-019-0420-1>

682 Berelson, W.M., 2002. Particle settling rates increase with depth in the ocean. *Deep-Sea*
683 *Research Part II-Topical Studies in Oceanography* 49, 237–251.

684 Berelson, W.M., 2001. The Flux of Particulate Organic Carbon Into the Ocean Interior: A
685 Comparison of Four U.S. JGOFS Regional Studies. *Oceanography* 14, 59–67.

686 Biard, T., Stemmann, L., Picheral, M., Mayot, N., Vandromme, P., Hauss, H., Gorsky, G., Guidi,
687 L., Kiko, R., Not, F., 2016. In situ imaging reveals the biomass of giant protists in the global
688 ocean. *Nature* 532, 504–+. <https://doi.org/10.1038/nature17652>

689 Bode, M., Hagen, W., Cornils, A., Kaiser, P., Auel, H., 2018. Copepod distribution and
690 biodiversity patterns from the surface to the deep sea along a latitudinal transect in the eastern
691 Atlantic Ocean (24°N to 21°S). *Progress in Oceanography* 161, 66–77.
692 <https://doi.org/10.1016/j.pocean.2018.01.010>

693 Böttger-Schnack, R., 1996. Vertical structure of small metazoan plankton, especially
694 noncalanoid copepods. I. Deep Arabian Sea. *Journal of Plankton Research* 18, 1073–1101.
695 <https://doi.org/10.1093/plankt/18.7.1073>

696 Brugnano, C., Granata, A., Guglielmo, L., Zagami, G., 2012. Spring diel vertical distribution of
697 copepod abundances and diversity in the open Central Tyrrhenian Sea (Western
698 Mediterranean). *Journal of Marine Systems* 105, 207–220.

699 Brun, P., Payne, M.R., Kiørboe, T., 2017. A trait database for marine copepods. *Earth System*
700 *Science Data* 9, 99–113.

701 Buesseler, K.O., Lamborg, C.H., Boyd, P.W., Lam, P.J., Trull, T.W., Bidigare, R.R., Bishop,
702 J.K.B., Casciotti, K.L., Dehairs, F., Elskens, M., Honda, M., Karl, D.M., Siegel, D.A., Silver,
703 M.W., Steinberg, D.K., Valdes, J., Van Mooy, B., Wilson, S., 2007. Revisiting Carbon Flux
704 Through the Ocean's Twilight Zone. *Science* 316, 567–570.
705 <https://doi.org/10.1126/science.1137959>

706 Cavan, E.L., Henson, S.A., Belcher, A., Sanders, R., 2017. Role of zooplankton in determining

707 the efficiency of the biological carbon pump. *Biogeosciences* 14, 177–186.

708 Childress, J.J., Seibel, B.A., 1998. Life at stable low oxygen levels: adaptations of animals to
709 oceanic oxygen minimum layers. *The Journal of experimental biology* 201, 1223–1232.

710 Chust, G., Allen, J.I., Bopp, L., Schrum, C., Holt, J., Tsiaras, K., Zavatarelli, M., Chifflet, M.,
711 Cannaby, H., Dadou, I., 2014. Biomass changes and trophic amplification of plankton in a
712 warmer ocean. *Global Change Biology* 20, 2124–2139.

713 Coma, R., Ribes, M., Serrano, E., Jiménez, E., Salat, J., Pascual, J., 2009. Global warming-
714 enhanced stratification and mass mortality events in the Mediterranean. *Proceedings of the*
715 *National Academy of Sciences* 106, 6176–6181.

716 Cram, J., Fuchsman, C., Duffy, M., Pretty, J., Lekanoff, R., Neibauer, J., Leung, S., Huebert,
717 K.B., Weber, T., Bianchi, D., 2021. Slow particle remineralization, rather than suppressed
718 disaggregation, drives efficient flux transfer through the Eastern Tropical North Pacific
719 Oxygen Deficient Zone. *Earth and Space Science Open Archive ESSOAr*.

720 Dilling, L., Alldredge, A.L., 2000. Fragmentation of marine snow by swimming
721 macrozooplankton: A new process impacting carbon cycling in the sea. *Deep-Sea Research*
722 *Part I-Oceanographic Research Papers* 47, 1227–1245.

723 Ekau, W., Auel, H., Portner, H.O., Gilbert, D., 2010. Impacts of hypoxia on the structure and
724 processes in pelagic communities (zooplankton, macro-invertebrates and fish).
725 *Biogeosciences* 7, 1669–1699. <https://doi.org/10.5194/bg-7-1669-2010>

726 Everett, J.D., Baird, M.E., Buchanan, P., Bulman, C., Davies, C., Downie, R., Griffiths, C.,
727 Heneghan, R., Kloser, R.J., Laiolo, L., 2017. Modeling what we sample and sampling what
728 we model: challenges for zooplankton model assessment. *Frontiers in Marine Science* 4, 77.

729 Fernández de Puelles, M., Gazá, M., Cabanellas-Reboredo, M., Santandreu, M., Irigoien, X.,
730 González-Gordillo, J.I., Duarte, C.M., Hernández-León, S., 2019. Zooplankton abundance
731 and diversity in the tropical and subtropical ocean. *Diversity* 11, 203.

732 Forest, A., Babin, M., Stemmann, L., Picheral, M., Sampei, M., Fortier, L., Gratton, Y.,
733 Belanger, S., Devred, E., Sahlin, J., Doxaran, D., Joux, F., Ortega-Retuerta, E., Martin, J.,
734 Jeffrey, W.H., Gasser, B., Miquel, J.C., 2013. Ecosystem function and particle flux dynamics
735 across the Mackenzie Shelf (Beaufort Sea, Arctic Ocean): an integrative analysis of spatial
736 variability and biophysical forcings. *Biogeosciences* 10, 2833–2866.
737 <https://doi.org/10.5194/bg-10-2833-2013>

738 Gaard, E., Gislason, A., Falkenhaus, T., Sjøiland, H., Musaeva, E., Vereshchaka, A., Vinogradov,
739 G., 2008. Horizontal and vertical copepod distribution and abundance on the Mid-Atlantic
740 Ridge in June 2004. *Deep Sea Research Part II: topical studies in oceanography* 55, 59–71.

741 Gallienne, C.P., Robins, D.B., Woodd-Walker, R.S., 2001. Abundance, distribution and size
742 structure of zooplankton along a 20 degrees west meridional transect of the northeast Atlantic
743 Ocean in July. *Deep-Sea Research Part II-Topical Studies in Oceanography* 48, 925–949.

744 Gehlen, M., Bopp, L., Ernprin, N., Aumont, O., Heinze, C., Raguencau, O., 2006. Reconciling
745 surface ocean productivity, export fluxes and sediment composition in a global
746 biogeochemical ocean model. *Biogeosciences* 3, 521–537.

747 Giering, S.L.C., Richard Sanders, Richard S. Lampitt, Thomas R. Anderson, Christian
748 Tamburini, Mehdi Boutrif, Mikhail V. Zubkov, Chris M. Marsay, Stephanie A. Henson,
749 Kevin Saw, Kathryn Cook, Daniel J. Mayor, 2014. Reconciliation of the carbon budget in the
750 ocean's twilight zone. *Nature* 507, 17. <https://doi.org/10.1038/nature13123>

- 751 Gorsky, G., Ohman, M.D., Picheral, M., Gasparini, S., Stemmann, L., Romagnan, J.-B.,
752 Cawood, A., Pesant, S., Garcia-Comas, C., Prejger, F., 2010. Digital zooplankton image
753 analysis using the ZooScan integrated system. *Journal of Plankton Research* 32, 285–303.
754 <https://doi.org/10.1093/plankt/fbp124>
- 755 Guidi, L., Chaffron, S., Bittner, L., Eveillard, D., Larhlimi, A., Roux, S., Darzi, Y., Audic, S.,
756 Berline, L., Brum, J.R., Coelho, L.P., Espinoza, J.C.I., Malviya, S., Sunagawa, S., Dimier, C.,
757 Kandels-Lewis, S., Picheral, M., Poulain, J., Searson, S., Stemmann, L., Not, F., Hingamp, P.,
758 Speich, S., Follows, M., Karp-Boss, L., Boss, E., Ogata, H., Pesant, S., Weissenbach, J.,
759 Wincker, P., Acinas, S.G., Bork, P., de Vargas, C., Iudicone, D., Sullivan, M.B., Raes, J.,
760 Karsenti, E., Bowler, C., Gorsky, G., Tara Oceans Consortium Coordinator, 2016. Plankton
761 networks driving carbon export in the oligotrophic ocean. *Nature* 532, 465–+.
- 762 Guidi, L., Jackson, G.A., Stemmann, L., Miquel, J.C., Picheral, M., Gorsky, G., 2008.
763 Relationship between particle size distribution and flux in the mesopelagic zone. *Deep-Sea*
764 *Research Part I-Oceanographic Research Papers* 55, 1364–1374.
- 765 Guidi, L., Legendre, L., Reygondeau, G., Uitz, J., Stemmann, L., Henson, S.A., 2015. A new
766 look at ocean carbon remineralization for estimating deepwater sequestration. *Global*
767 *Biogeochem. Cycles* 29, 1044–1059. <https://doi.org/10.1002/2014gb005063>
- 768 Guidi, L., Stemmann, L., Jackson, G.A., Ibanez, F., Claustre, H., Legendre, L., Picheral, M.,
769 Gorsky, G., 2009. Effects of phytoplankton community on production, size and export of
770 large aggregates: A world-ocean analysis. *Limnology and Oceanography* 54, 1951–1963.
771 <https://doi.org/10.4319/lo.2009.54.6.1951>
- 772 Haake, B., Ittekkot, V., Ramaswamy, V., Nair, R., Honjo, S., 1992. Fluxes of amino acids and
773 hexosamines to the deep Arabian Sea. *Marine Chemistry* 40, 291–314.
- 774 Hauss, H., Christiansen, S., Schütte, F., Kiko, R., Edvam Lima, M., Rodrigues, E., Karstensen,
775 J., Löscher, C.R., Körtzinger, A., Fiedler, B., 2016. Dead zone or oasis in the open ocean?
776 Zooplankton distribution and migration in low-oxygen modewater eddies. *Biogeosciences* 13,
777 1977–1989.
- 778 Henson, S.A., Sanders, R., Madsen, E., 2012. Global patterns in efficiency of particulate organic
779 carbon export and transfer to the deep ocean. *Global Biogeochemical Cycles* 26.
- 780 Henson, S.A., Yool, A., Sanders, R., 2015. Variability in efficiency of particulate organic carbon
781 export: A model study. *Global Biogeochemical Cycles* 29, 33–45.
- 782 Hernández-León, S., Koppelman, R., Fraile-Nuez, E., Bode, A., Mompeán, C., Irigoien, X.,
783 Olivar, M.P., Echevarría, F., de Puellas, M.F., González-Gordillo, J.I., 2020. Large deep-sea
784 zooplankton biomass mirrors primary production in the global ocean. *Nature communications*
785 11, 1–8.
- 786 Hidalgo, P., Escribano, R., Fuentes, M., Jorquera, E., Vergara, O., 2012. How coastal upwelling
787 influences spatial patterns of size-structured diversity of copepods off central-southern Chile
788 (summer 2009). *Progress in Oceanography* 92, 134–145.
- 789 Hirche, H.-J., Mumm, N., 1992. Distribution of dominant copepods in the Nansen Basin, Arctic
790 Ocean, in summer. *Deep Sea Research Part A. Oceanographic Research Papers* 39, S485–
791 S505.
- 792 Homma, T., Yamaguchi, A., 2010. Vertical changes in abundance, biomass and community
793 structure of copepods down to 3000 m in the southern Bering Sea. *Deep Sea Research Part I:*
794 *Oceanographic Research Papers* 57, 965–977.
- 795 Ibarbalz, F.M., Henry, N., Brandao, M.C., Martini, V., Busseni, G., Byrne, H., Coelho, L.P.,

796 Endo, H., Gasol, J.M., Gregory, A.C., Mahe, F., Rignonato, J., Royo-Llonch, M., Salazar, G.,
797 Sanz-Saez, I., Scalco, E., Soviadan, D., Zayed, A.A., Zingone, A., Labadie, K., Ferland, J.,
798 Marec, C., Kandels, S., Picheral, M., Dimier, C., Poulain, J., Pisarev, S., Carmichael, M.,
799 Pesant, S., Acinas, S.G., Babin, M., Bork, P., Boss, E., Bowler, C., Cochrane, G., de Vargas,
800 C., Follows, M., Gorsky, G., Grimsley, N., Guidi, L., Hingamp, P., Iudicone, D., Jaillon, O.,
801 Kandels, S., Karp-Boss, L., Karsenti, E., Not, F., Ogata, H., Pesant, S., Poulton, N., Raes, J.,
802 Sardet, C., Speich, S., Stemmann, L., Sullivan, M.B., Sunagawa, S., Wincker, P., Bopp, L.,
803 Lombard, F., Zinger, L., Tara Oceans, C., 2019. Global Trends in Marine Plankton Diversity
804 across Kingdoms of Life. *Cell* 179, 1084-+. <https://doi.org/10.1016/j.cell.2019.10.008>

805 Irigoien, X., Klevjer, T.A., Røstad, A., Martinez, U., Boyra, G., Acuña, J.L., Bode, A.,
806 Echevarria, F., Gonzalez-Gordillo, J.I., Hernandez-Leon, S., 2014. Large mesopelagic fishes
807 biomass and trophic efficiency in the open ocean. *Nature communications* 5, 1–10.

808 Iversen, M.H., Lampitt, R.S., 2020. Size does not matter after all: no evidence for a size-sinking
809 relationship for marine snow. *Progress in Oceanography* 189, 102445.

810 Karsenti, E., Acinas, S.G., Bork, P., Bowler, C., De Vargas, C., Raes, J., Sullivan, M., Arendt,
811 D., Benzoni, F., Claverie, J.M., Follows, M., Gorsky, G., Hingamp, P., Iudicone, D., Jaillon,
812 O., Kandels-Lewis, S., Krzic, U., Not, F., Ogata, H., Pesant, S., Reynaud, E.G., Sardet, C.,
813 Sieracki, M.E., Speich, S., Velayoudon, D., Weissenbach, J., Wincker, P., Tara Oceans, C.,
814 2011. A Holistic Approach to Marine Eco-Systems Biology. *Plos Biology* 9.
815 <https://doi.org/e1001177> 10.1371/journal.pbio.1001177

816 Keister, J.E., Tuttle, L.B., 2013. Effects of bottom-layer hypoxia on spatial distributions and
817 community structure of mesozooplankton in a sub-estuary of Puget Sound, Washington, USA.
818 *Limnology and Oceanography* 58, 667–680.

819 Kiko, R., Biastoch, A., Brandt, P., Cravatte, S., Hauss, H., Hummels, R., Kriest, I., Marin, F.,
820 McDonnell, A.M.P., Oschlies, A., Picheral, M., Schwarzkopf, F.U., Thurnherr, A.M.,
821 Stemmann, L., 2017. Biological and physical influences on marine snowfall at the equator.
822 *Nature Geoscience* 10, 852-+. <https://doi.org/10.1038/ngeo3042>

823 Kiko, R., Brandt, P., Christiansen, S., Faustmann, J., Kriest, I., Rodrigues, E., Schütte, F., Hauss,
824 H., 2020. Zooplankton-mediated fluxes in the eastern tropical North Atlantic. *Frontiers in*
825 *Marine Science* 1.

826 Kiko, R., Hauss, H., 2019. On the estimation of zooplankton-mediated active fluxes in oxygen
827 minimum zone regions. *Frontiers in Marine Science* 6, 741.

828 Kiørboe, T., 2013. Zooplankton body composition. *Limnology and Oceanography* 58, 1843–
829 1850.

830 Kiørboe, T., 2011. What makes pelagic copepods so successful? *Journal of Plankton Research*
831 33, 677–685.

832 Kiørboe, T., Visser, A., Andersen, K.H., Handling editor: Howard Browman, 2018. A trait-based
833 approach to ocean ecology. *ICES Journal of Marine Science*.
834 <https://doi.org/10.1093/icesjms/fsy090>

835 Koppelman, R., Weikert, H., Halsband-Lenk, C., Jennerjahn, T., 2004. Mesozooplankton
836 community respiration and its relation to particle flux in the oligotrophic eastern
837 Mediterranean. *Global Biogeochemical Cycles* 18.

838 Koppelman, R., Zimmermann-Timm, H., Weikert, H., 2005. Bacterial and zooplankton
839 distribution in deep waters of the Arabian Sea. *Deep-Sea Research Part I-Oceanographic*
840 *Research Papers* 52, 2184–2192. <https://doi.org/10.1016/j.dsr.2005.06.012>

841 Kosobokova, K.N., Hopcroft, R.R., 2010. Diversity and vertical distribution of mesozooplankton
842 in the Arctic's Canada Basin. *Deep Sea Research Part II: Topical Studies in Oceanography*
843 57, 96–110.

844 Kwiatkowski, L., Aumont, O., Bopp, L., 2019. Consistent trophic amplification of marine
845 biomass declines under climate change. *Global change biology* 25, 218–229.

846 Lampitt, R.S., Noji, T., Von Bodungen, B., 1990. What happens to zooplankton fecal pellets?
847 Implication for material flux. *Marine Biology* 104, 15–23.

848 Laws, R.M., 1985. The ecology of the Southern Ocean. *Amer. Scient.* 73, 26–40.

849 Legendre, P., Legendre, L., 1998. Numerical ecology, 2nd english. ed, *Developments in*
850 *environmental modelling* 20. Elsevier, Amsterdam.

851 Lehet, P., Hernandez-Leon, S., 2009. Zooplankton biomass estimation from digitized images: a
852 comparison between subtropical and Antarctic organisms. *Limnology and Oceanography-*
853 *Methods* 7, 304–308.

854 Madhupratap, M., Nair, K.N.V., Venugopal, P., Gauns, M., Haridas, P., Gopalakrishnan, T., Nair,
855 K.K.C., 2004. *Arabian Sea oceanography and fisheries*.

856 Marsay, C.M., Sanders, R.J., Henson, S.A., Pabortsava, K., Achterberg, E.P., Lampitt, R.S.,
857 2015. Attenuation of sinking particulate organic carbon flux through the mesopelagic ocean.
858 *Proceedings of the National Academy of Sciences* 112, 1089–1094.

859 Martin, J.H., Knauer, G.A., Karl, D.M., Broenkow, W.W., 1987. VERTEX: Carbon cycling in
860 the Northeast Pacific. *Deep-Sea Research* 34, 267–285.

861 Morrison, J.M., Codispoti, L., Smith, S.L., Wishner, K., Flagg, C., Gardner, W.D., Gaurin, S.,
862 Naqvi, S., Manghnani, V., Prosperie, L., 1999. The oxygen minimum zone in the Arabian Sea
863 during 1995. *Deep Sea Research Part II: Topical Studies in Oceanography* 46, 1903–1931.

864 MOTODA, S., 1959. Devices of simple plankton apparatus. *Memoirs of the faculty of fisheries*
865 *Hokkaido University* 7, 73–94.

866 Ohman, M.D., Romagnan, J.B., 2016. Nonlinear effects of body size and optical attenuation on
867 Diel Vertical Migration by zooplankton. *Limnology and Oceanography* 61, 765–770.
868 <https://doi.org/10.1002/lno.10251>

869 Oschlies, A., Brandt, P., Stramma, L., Schmidtko, S., 2018. Drivers and mechanisms of ocean
870 deoxygenation. *Nature Geoscience* 11, 467–473.

871 Paffenhofer, G.A., Mazzocchi, M.G., 2003. Vertical distribution of subtropical epipelagic
872 copepods. *Journal of Plankton Research* 25, 1139–1156.

873 Palomares-García, R.J., Gómez-Gutiérrez, J., Robinson, C.J., 2013. Winter and summer vertical
874 distribution of epipelagic copepods in the Gulf of California. *Journal of Plankton Research*
875 35, 1009–1026.

876 Park, C., Wormuth, J., 1993. Distribution of Antarctic zooplankton around Elephant Island
877 during the austral summers of 1988, 1989, and 1990. *Polar Biology* 13, 215–225.

878 Parris, D.J., Ganesh, S., Edgcomb, V.P., DeLong, E.F., Stewart, F.J., 2014. Microbial eukaryote
879 diversity in the marine oxygen minimum zone off northern Chile. *Frontiers in microbiology* 5,
880 543.

881 Pesant, S., Not, F., Picheral, M., Kandels-Lewis, S., Le Bescot, N., Gorsky, G., Iudicone, D.,
882 Karsenti, E., Speich, S., Trouble, R., Dimier, C., Searson, S., Tara Oceans Consortium, C.,
883 2015. Open science resources for the discovery and analysis of Tara Oceans data. *Scientific*

884 data 2, 150023–150023. <https://doi.org/10.1038/sdata.2015.23>

885 Picheral, M., Guidi, L., Stemmann, L., Karl, D.M., Iddaoud, G., Gorsky, G., 2010. The
886 Underwater Vision Profiler 5: An advanced instrument for high spatial resolution studies of
887 particle size spectra and zooplankton. *Limnology and Oceanography-Methods* 8, 462–473.
888 <https://doi.org/10.4319/lom.2010.8.462>

889 Pinkerton, M.H., Décima, M., Kitchener, J.A., Takahashi, K.T., Robinson, K.V., Stewart, R.,
890 Hosie, G.W., 2020. Zooplankton in the Southern Ocean from the continuous plankton
891 recorder: Distributions and long-term change. *Deep Sea Research Part I: Oceanographic*
892 *Research Papers* 162, 103303.

893 Quetin, L.B., Ross, R.M., Frazer, T.K., Haberman, K.L., 1996. Factors affecting distribution and
894 abundance of zooplankton, with an emphasis on Antarctic krill, *Euphausia superba*. *Antarctic*
895 *Research Series* 70, 357–371.

896 Remsen, A., Hopkins, T.L., Samson, S., 2004. What you see is not what you catch: a comparison
897 of concurrently collected net, Optical Plankton Counter, and Shadowed Image Particle
898 Profiling Evaluation Recorder data from the northeast Gulf of Mexico. *Deep-Sea Research*
899 *Part I-Oceanographic Research Papers* 51, 129–151.

900 Richardson, A.J., 2008. In hot water: zooplankton and climate change. *ICES Journal of Marine*
901 *Science* 65, 279–295. <https://doi.org/10.1093/icesjms/fsn028>

902 Robinson, C., Steinberg, D.K., Anderson, T.R., Aristegui, J., Carlson, C.A., Frost, J.R.,
903 Ghiglione, J.F., Hernandez-Leon, S., Jackson, G.A., Koppelman, R., Queguiner, B.,
904 Ragueneau, O., Rassoulzadegan, F., Robison, B.H., Tamburini, C., Tanaka, T., Wishner, K.F.,
905 Zhang, J., 2010. Mesopelagic zone ecology and biogeochemistry - a synthesis. *Deep-Sea*
906 *Research Part I-Topical Studies in Oceanography* 57, 1504–1518.
907 <https://doi.org/10.1016/j.dsr2.2010.02.018>

908 Roe, H., 1988. Midwater biomass profiles over the Madeira Abyssal Plain and the contribution
909 of copepods, in: *Biology of Copepods*. Springer, pp. 169–181.

910 Rombouts, I., Beaugrand, G., Ibanez, F., Gasparini, S., Chiba, S., Legendre, L., 2010. A
911 multivariate approach to large-scale variation in marine planktonic copepod diversity and its
912 environmental correlates. *Limnology and Oceanography* 55, 2219–2229.
913 <https://doi.org/10.4319/lo.2010.55.5.2219>

914 Ross, R.M., Quetin, L.B., Martinson, D.G., Iannuzzi, R.A., Stammerjohn, S.E., Smith, R.C.,
915 2008. Palmer LTER: Patterns of distribution of five dominant zooplankton species in the
916 epipelagic zone west of the Antarctic Peninsula, 1993–2004. *Deep Sea Research Part II:*
917 *Topical Studies in Oceanography* 55, 2086–2105.

918 Roullier, F., Berline, L., Guidi, L., De Madron, X.D., Picheral, M., Sciandra, A., Pesant, S.,
919 Stemmann, L., 2014. Particle size distribution and estimated carbon flux across the Arabian
920 Sea oxygen minimum zone. *Biogeosciences* 11, 4541–4557. [https://doi.org/10.5194/bg-11-](https://doi.org/10.5194/bg-11-4541-2014)
921 4541-2014

922 Rutherford, S., D'Hondt, S., Prell, W., 1999. Environmental controls on the geographic
923 distribution of zooplankton diversity. *Nature* 400, 749–753. <https://doi.org/10.1038/23449>

924 Saporiti, F., Bearhop, S., Vales, D.G., Silva, L., Zenteno, L., Tavares, M., Crespo, E.A.,
925 Cardona, L., 2015. Latitudinal changes in the structure of marine food webs in the
926 Southwestern Atlantic Ocean. *Marine Ecology Progress Series* 538, 23–34.

927 Schmidtko, S., Stramma, L., Visbeck, M., 2017. Decline in global oceanic oxygen content during
928 the past five decades. *Nature* 542, 335–339.

- 929 Seibel, B.A., 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen
930 minimum zones. *Journal of Experimental Biology* 214, 326–336.
- 931 Smith, S., Roman, M., Prusova, I., Wishner, K., Gowing, M., Codispoti, L.A., Barber, R., Marra,
932 J., Flagg, C., 1998. Seasonal response of zooplankton to monsoonal reversals in the Arabian
933 Sea. *Deep-Sea Research Part II* 45, 2369–2403.
- 934 St John, M.A., Borja, A., Chust, G., Heath, M., Grigorov, I., Mariani, P., Martin, A.P., Santos,
935 R.S., 2016. A dark hole in our understanding of marine ecosystems and their services:
936 perspectives from the mesopelagic community. *Frontiers in Marine Science* 3, 31.
- 937 Steinberg, D.K., Landry, M.R., 2017. Zooplankton and the ocean carbon cycle. *Annual review of*
938 *marine science* 9, 413–444.
- 939 Steinberg, D.K., Ruck, K.E., Gleiber, M.R., Garzio, L.M., Cope, J.S., Bernard, K.S.,
940 Stammerjohn, S.E., Schofield, O.M., Quetin, L.B., Ross, R.M., 2015. Long-term (1993–2013)
941 changes in macrozooplankton off the Western Antarctic Peninsula. *Deep Sea Research Part I:*
942 *Oceanographic Research Papers* 101, 54–70.
- 943 Stemmann, L., Jackson, G.A., Gorsky, G., 2004. A vertical model of particle size distributions
944 and fluxes in the midwater column that includes biological and physical processes - Part II:
945 application to a three year survey in the NW Mediterranean Sea. *Deep-Sea Research Part I-*
946 *Oceanographic Research Papers* 51, 885–908. <https://doi.org/10.1016/j.dsr.2004.03.002>
- 947 Stempniewicz, L., Błachowiak-Samołyk, K., Węślawski, J.M., 2007. Impact of climate change
948 on zooplankton communities, seabird populations and arctic terrestrial ecosystem—a
949 scenario. *Deep Sea Research Part II: Topical Studies in Oceanography* 54, 2934–2945.
- 950 Stramma, L., Schmidtko, S., Levin, L.A., Johnson, G.C., 2010. Ocean oxygen minima
951 expansions and their biological impacts. *Deep Sea Research Part I: Oceanographic Research*
952 *Papers* 57, 587–595. <https://doi.org/10.1016/j.dsr.2010.01.005>
- 953 Stukel, M.R., Ohman, M.D., Kelly, T.B., Biard, T., 2019. The roles of suspension-feeding and
954 flux-feeding zooplankton as gatekeepers of particle flux into the mesopelagic ocean in the
955 Northeast Pacific. *Frontiers in Marine Science* 6, 397.
- 956 Tarling, G.A., Shreeve, R.S., Ward, P., Atkinson, A., Hirst, A.G., 2004. Life-cycle phenotypic
957 composition and mortality of *Calanoides acutus* (Copepoda : Calanoida) in the Scotia Sea: a
958 modelling approach. *Marine Ecology-Progress Series* 272, 165–181.
- 959 Terazaki, M., Wada, M., 1988. Occurrence of large numbers of carcasses of the large, grazing
960 copepod *Calanus cristatus* from the Japan Sea. *Marine Biology* 97, 177–183.
- 961 Trudnowska, E., Lacour, L., Ardyna, M., Rogge, A., Irisson, J.O., Waite, A.M., Babin, M.,
962 Stemmann, L., 2021. Marine snow morphology illuminates the evolution of phytoplankton
963 blooms and determines their subsequent vertical export. *Nature communications* 12, 2816–
964 2816. <https://doi.org/10.1038/s41467-021-22994-4>
- 965 Tutasi, P., Escribano, R., 2020. Zooplankton diel vertical migration and downward C flux into
966 the oxygen minimum zone in the highly productive upwelling region off northern Chile.
967 *Biogeosciences* 17, 455–473.
- 968 Uitz, J., Claustre, H., Morel, A., Hooker, S.B., 2006. Vertical distribution of phytoplankton
969 communities in open ocean: An assessment based on surface chlorophyll. *Journal of*
970 *Geophysical Research. C. Oceans* 111, [doi:10.1029/2005JC003207].
- 971 Van Mooy, B.A., Keil, R.G., Devol, A.H., 2002. Impact of suboxia on sinking particulate
972 organic carbon: Enhanced carbon flux and preferential degradation of amino acids via

973 denitrification. *Geochimica et Cosmochimica Acta* 66, 457–465.

974 Vaquer-Sunyer, R., Duarte, C.M., 2008. Thresholds of hypoxia for marine biodiversity.
975 *Proceedings of the National Academy of Sciences* 105, 15452–15457.

976 Werner, T., Buchholz, F., 2013. Diel vertical migration behaviour in Euphausiids of the northern
977 Benguela current: seasonal adaptations to food availability and strong gradients of
978 temperature and oxygen. *Journal of Plankton Research* 35, 792–812.

979 Wheeler Jr, E., 1967. Copepod detritus in the deep sea. *Limnology and Oceanography* 12, 697–
980 702.

981 Wishner, K.F., Ashjian, C.J., Gelfman, C., Gowing, M.M., Kann, L., Levin, L.A., Mullineaux,
982 L.S., Saltzman, J., 1995. Pelagic and Benthic Ecology of the Lower Interface of the Eastern
983 Tropical Pacific Oxygen Minimum Zone. *Deep Sea Res.* 42, 93–115.

984 Wishner, K.F., Gelfman, C., Gowing, M.M., Outram, D.M., Rapien, M., Williams, R.L., 2008.
985 Vertical zonation and distributions of calanoid copepods through the lower oxycline of the
986 Arabian Sea oxygen minimum zone. *Prog. Oceanogr.* 78, 163–191.
987 <https://doi.org/10.1016/j.pocean.2008.03.001>

988 Wishner, K.F., Seibel, B., Outram, D., 2020. Ocean deoxygenation and copepods: coping with
989 oxygen minimum zone variability. *Biogeosciences* 17, 2315–2339.

990 Wishner, K.F., Seibel, B.A., Roman, C., Deutsch, C., Outram, D., Shaw, C.T., Birk, M.A.,
991 Mislán, K., Adams, T., Moore, D., 2018. Ocean deoxygenation and zooplankton: very small
992 oxygen differences matter. *Science advances* 4, eaau5180.

993 Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J.,
994 Ikeda, T., Mac Takahashi, M., 2004. Latitudinal differences in the planktonic biomass and
995 community structure down to the greater depths in the western North Pacific. *Journal of*
996 *Oceanography* 60, 773–787.

997 Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J.,
998 Ikeda, T., Takahashi, M., 2002. Community and trophic structures of pelagic copepods down
999 to greater depths in the western subarctic Pacific (WEST-COSMIC). *Deep Sea Research Part*
1000 *I* 49, 1007–1025.

1001 Yasuhara, M., Hunt, G., Dowsett, H.J., Robinson, M.M., Stoll, D.K., 2012. Latitudinal species
1002 diversity gradient of marine zooplankton for the last three million years. *Ecology Letters* 15,
1003 1174–1179. <https://doi.org/10.1111/j.1461-0248.2012.01828.x>

1004

1005

1006

1007

1008

1009

1010 **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

1011

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).**

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

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

1017
1018
1019

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

1020
1021
1022
1023

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 (mgDW m ⁻² d ⁻¹)	
	<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

1024
1025
1026
1027

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

1028