

1 *Title*

2 **Copepod functional traits and groups show contrasting biogeographies in the global**
3 **ocean**

4

5 *Running title*

6 Global marine copepod traits biogeography

7

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25

26 *Conflict of interest*

27 The authors declare no conflict of interests.

28

29 *Abstract*

30 **Aim:** To define global zooplankton functional groups (FGs) and to estimate their
31 environmental niche and habitat distribution. We model the spatial patterns of copepod FGs
32 habitat and identify regions sharing similar functional trait expression at the community level.

33 **Taxon:** Marine planktonic Neocopepoda.

34 **Location:** Global ocean.

35 **Methods:** Factor analysis on mixed data and hierarchical clustering were used to identify
36 copepod FGs based on five species-level functional traits. An ensemble of species distribution
37 models was used to estimate the environmental niches of the modelled species, project the
38 mean annual habitat suitability of the FGs, and to estimate the community weighted mean
39 values of the traits studied. Ocean regions were defined based on their community-level mean
40 trait expression using a principal component analysis and hierarchical clustering.

41 **Results:** Eleven global copepod FGs were identified. They displayed contrasting latitudinal
42 patterns in mean annual habitat suitability that could be explained by differences in
43 environmental niche preferences: two FGs were associated with polar conditions, one
44 followed the global temperature gradient, five were associated with tropical oligotrophic
45 gyres, and the remaining three with boundary currents and counter currents. Four main
46 regions of varying community weighted mean trait values emerged: the Southern Ocean, the
47 northern and southern high latitudes, the tropical gyres, and the boundary currents and
48 upwelling systems.

49 **Conclusions:** We build on an exhaustive species trait dataset to put forward novel FGs that
50 will improve the representation of zooplankton in global marine ecosystem models. Our
51 results contribute to our understanding of the spatial patterns and drivers of marine plankton
52 trait biogeography and will serve as a basis for studying the links between zooplankton
53 biodiversity and ecosystem functioning and how they might evolve in the context of climate
54 change.

55

56 *Keywords*

57 Planktonic copepods, Functional groups, Trait-based approach, Species Distribution
58 Modelling, Global Ocean, Community weighted mean trait

59

60 **1. Introduction**

61 Copepods are crustaceans that dominate the biomass of the mesozooplankton size class (0.2-
62 2.0 mm) and rank amongst the most abundant animals in the oceans (Turner, 2004; Kiørboe,
63 2011a). They are morphologically and functionally diverse and are adapted to almost all
64 marine ecosystems (Kiørboe, 2011a; Bron et al., 2011). Copepods play a pivotal role in the
65 food web, both as microplankton grazers and prey for small pelagic fishes and other larger
66 animals (Beaugrand, Edwards, & Legendre, 2010; Steinberg & Landry, 2017). Copepods play
67 a critical role in the marine biological carbon pump, the fixation of inorganic carbon to
68 organic matter by photosynthesis and consequent sequestration away from the surface into the
69 deep ocean. Planktonic copepods export carbon from the euphotic layer to the deep ocean in
70 several ways, such as the grazing of phytoplankton cells in the sunlit layers, followed by the
71 excretion of relatively fast-sinking fecal pellets, or by extensive vertical migration (Turner,
72 2015; Steinberg & Landry, 2017).

73 The relative contribution of planktonic copepods to the above-mentioned processes is
74 mediated by their diversity and trait expression (Barton et al., 2013). For instance, larger
75 copepods perform stronger diel vertical migration (Ohman & Romagnan, 2016) and produce
76 larger fecal pellets that sink faster and thus increase the proportion of particulate organic
77 carbon sinking to depth (Stamieszkin et al., 2015; Brun et al., 2019). The dominance of
78 certain copepod feeding modes (i.e., the mechanism through which prey is captured) impacts
79 food-web dynamics as feeding modes affect copepod grazing and mortality rates (Kenitz,
80 Visser, Mariani, & Andersen, 2017; van Someren Gréve, Almeda, & Kiørboe, 2017). Yet,
81 mechanistic ecosystem models usually represent zooplankton only through a couple of size
82 classes (Le Quéré et al., 2005), which greatly oversimplifies the contribution of species
83 diversity and functional traits to the functioning of ecosystems and biogeochemical cycles
84 (Flynn et al., 2015). Multiple modelling studies show that the number of zooplankton
85 functional groups and their grazing characteristics exerts an important control on the biomass
86 and diversity of other trophic groups, with consequences for global biogeochemical cycles in
87 these models (Prowse et al., 2012; Sailley et al., 2013; Vallina et al., 2014; Le Quéré et al.,
88 2016). Ecosystem models, however, rely strongly on parameterisations of specific traits
89 governing biological processes and food-web interactions (e.g. grazing rates or food
90 preferences) based on scarce information, as the empirical evidence included in current
91 models is often sourced from limited laboratory or field data from a narrow range of
92 culturable species (Barton et al., 2013). Consequently, investigating the potential links

93 between copepod trait distribution and ecosystem functioning contributes to improving
94 current ecosystem models (Stocker, 2014).

95 To better understand the role of planktonic copepods in marine systems, plankton ecologists
96 are increasingly adopting trait-based approaches (Litchman, Ohman, & Kiørboe, 2013;
97 Hébert, Beisner, & Maranger, 2017). Functional traits are species- or organism-level
98 characteristics (morphological, behavioral, physiological, or related to life history) that affect
99 their fitness and contribute to ecosystem functioning (Violle et al., 2007). According to
100 Litchman et al. (2013), functional traits can be classified by the main functions they
101 contribute to, namely, survival, feeding, growth, and reproduction. Organisms often cannot
102 maximize all four ecological functions at the same time since there are trade-offs between
103 these functions. For example, copepods that rely on passive feeding (i.e., copepods that
104 remain immobile and only move to capture prey) show 8.5 times lower mortality rates than
105 copepods that rely on active feeding (van Someren Gréve, Almeda, & Kiørboe, 2017). Yet,
106 adult male copepods often need to move actively to find a mate for reproduction, which
107 undermines the benefits of their feeding mode (Kiørboe, 2011b; Litchman et al., 2013).

108 Copepod functional traits can be investigated by grouping species into functional groups
109 (FGs) according to similarities in functional trait combinations (Benedetti, Gasparini, &
110 Ayata, 2016). Categorizing species according to their similarity in functional traits rather than
111 their taxonomic classification allows one to summarize highly diverse groups, and/or
112 communities, into more parsimonious categories defined by distinct ecological functions
113 (Barnett, Finlay, & Beisner, 2007; Benedetti, Vogt, Righetti, Guilhaumon, & Ayata, 2018). At
114 the regional scale, Pomerleau et al. (2015) showed that 42 zooplankton species from the North
115 East Pacific Ocean could be clustered into five groups based on their body length, feeding and
116 reproduction mode, and trophic group. Based on a similar set of traits, Benedetti, Vogt, et al.
117 (2018) grouped 106 marine copepod species that dominate Mediterranean communities into
118 seven FGs. They found that carnivorous species were associated with tropical oligotrophic
119 conditions, whereas current-feeding herbivores were associated with more productive and
120 seasonally varying conditions. Such groupings can improve the representation of zooplankton
121 in an ecosystem model since FGs increase the representation of ecological function without
122 adding taxonomic diversity and complexity. However, studies based on a regional pool of
123 species might underestimate the real range of functions ensured by zooplankton in the global
124 ocean, warranting the need for a study based on a global species pool.

125

126 The functional composition of observed plankton communities can be investigated through
127 community weighted mean (CWM) values of traits (Ricotta, 2005; Pomerleau, Sastri, &
128 Beisner, 2015; Brun et al., 2016). This is done by calculating the proportion of species in a
129 community that exhibits a particular functional trait value by accounting for their relative
130 contribution to community composition or abundance. Thereby, CWM values of functional
131 traits help to identify the relationships between the emerging expression of functional traits on
132 a community-level, the environmental conditions associated to the spatial patterns of trait
133 expression (i.e., their biogeographical patterns), and the potential trade-offs underlying trait
134 expression. Like for FGs, empirical CWM trait values of marine zooplankton have been
135 explored on local or regional levels for the northern hemisphere mostly (Pomerleau et al.,
136 2015; Pecuchet et al., 2018). They evidenced a negative impact of warming and seasonality
137 on community-level body length and offspring size. The first truly global study by Brun et al.
138 (2016) also found larger body sizes, higher proportions of myelinated species, and relatively
139 smaller offspring size in latitudes $>50^\circ$, because of gradients in temperature and seasonality in
140 phytoplankton production. To our knowledge, other qualitative traits, such as trophic groups
141 or spawning mode, have not been investigated through the CWM trait approach (McGinty et
142 al., 2018; Benedetti, Vogt et al., 2018). Therefore, their global spatial distribution remains
143 poorly documented and a more complete understanding of trade-offs between the expression
144 of these diverse traits is still needed to better characterize and map ecosystem functions
145 worldwide. If geo-referenced trait information, such as patterns of CWM values, are clustered
146 in space and time, they can be used to define ocean regions sharing common ecological
147 characteristics (Longhurst, 2010; Reygondeau et al., 2017; Hofmann Elizondo et al., 2021).
148 Such regionalization schemes have never been applied on plankton communities' functional
149 trait expressions on a global scale, although this could be more informative of large-scale
150 marine food web and ecosystem dynamics than previous regionalization schemes based on
151 environmental parameters alone.

152 In this study, we address the following questions: (i) What are the global zooplankton FGs
153 emerging from the/a clustering of the most frequently sampled copepod species according to
154 their functional traits (Benedetti et al., 2016)? (ii) Which parameters structure FGs most
155 strongly in functional trait space and environmental niche space (Benedetti, Vogt, et al.,
156 2018)? (iii) What are the habitat distribution patterns of these FGs and their community-level
157 trait expression (estimated through CWM trait values), and which regions of the global ocean
158 share similar trait expression? To do so, a new functional trait synthesis was carried out for a
159 global pool of >380 frequently observed copepod species, and five traits (body size, trophic

160 group, feeding mode, myelination, and spawning mode) were used to identify novel FGs
161 based on species' traits combinations. Occurrence-based species distribution models (SDMs)
162 were used to investigate the differences in the environmental niches and monthly habitat
163 distribution modelled for the new copepod FGs. Mean annual CWM trait values were derived
164 from the monthly SDMs-based habitat distribution maps, and hierarchical clustering was used
165 to identify regions that share similar community-level trait expression.

166

167 **2. Materials and Methods**

168 2.1. Species occurrence data

169 We used the zooplankton occurrences dataset (geo-localised and dated presences) of
170 Benedetti et al. (2021), which has been gathered to model global zooplankton species
171 biogeography, diversity and community composition. The dataset combines 165'716
172 occurrences binned into the 1° x 1° grid of the World Ocean Atlas (WOA; Boyer et al., 2013)
173 for 385 copepod species. The occurrences were initially retrieved from the Ocean
174 Biodiversity Information System (OBIS; <https://www.obis.org>), the Global Biodiversity
175 Information Facility (GBIF; <https://www.gbif.org>), as well as complementary datasets (see
176 Benedetti et al., 2021 for an exhaustive description and for the curation of species names).
177 The occurrences corresponding to benthic and parasitic taxa and those that were not fit to
178 model the habitat of copepod species in the surface open ocean were discarded as follows:
179 occurrences with missing spatial coordinates, sampling dates, sampling depth, or taxonomic
180 identification at species-level were removed. Furthermore, occurrences from drilling holes,
181 freshwater (sea surface salinity < 20 according to the WOA, grid cells within 25 km of the
182 nearest shoreline, or with a sampling depth >500 m were also discarded.

183 The copepod occurrence data displayed sampling effort biases (Appendix S1) that could
184 inflate metrics of empirical models' performance or over-represent portions of the
185 environmental space and thus hinder model predictability and interpretation (Veloz, 2009;
186 Hijmans, 2012). We addressed these potential sampling biases by further thinning the species-
187 level occurrence data (Aiello-Lammens, Boria, Radosavljevic, Vilela, & Anderson, 2015).
188 For each month and each species separately, the occurrences were thinned by applying a
189 randomization algorithm (30 randomizations per species dataset) that returned a 'thinned'
190 dataset where monthly species occurrences were at least 500 km apart (Aiello-Lammens,
191 Boria, Radosavljevic, Vilela, & Anderson, 2015). Only those species displaying at least 50
192 occurrences (n = 385) were retained and constituted the final list of species for which
193 functional traits data were searched for in the literature.

194

195 2.2. Species functional trait data

196 The five following species-level functional traits were included in our analyses, as detailed
197 below. These traits were chosen based on data availability from previous traits compilations
198 and extended literature survey (see Appendices S2 and S3):

199 Body size (quantitative continuous): mean maximum adult female body size (i.e. length of the
200 cephalothorax) in mm. Body size is considered a master functional trait as it impacts all life
201 functions and scales most physiological rates (Kiørboe & Hirst, 2014; Hébert, Beisner, &
202 Maranger, 2017) and influences predator-prey interactions (Hansen, Bjornsen, & Hansen,
203 1994).

204 Trophic group (categorical): most marine planktonic copepods are omnivorous, yet they can
205 be grouped according to their preference in food sources (Kiørboe, 2011a; Pomerleau et al.,
206 2015; Benedetti et al., 2016). Here, the following five groups were defined: Omnivore-
207 Herbivore, Omnivore-Carnivore, Omnivore-Detritivore, strict Carnivore, and Omnivore. The
208 trophic group describes the primary food source of a species and therefore its role in food-
209 web dynamics.

210 Feeding mode (categorical): copepods have developed various strategies to detect and capture
211 food items. The present feeding modes followed the definitions of Kiørboe (2011a): ambush-
212 feeding, current-feeding, cruise-feeding, particle-feeding, current-cruise feeding, and current-
213 ambush feeding (the last two referred to those mixed-feeding species that perform both
214 strategies; Kiørboe, 2011a; Litchman et al., 2013). Ambush-feeding copepods lurk stationarily
215 in the water column and detect the vibration generated by motile preys thanks to specialized
216 appendages (i.e., hydromechanical perception) and capture prey through quick jumps.
217 Copepods perform active ambush-feeding according to Kiørboe (2011a), which is considered
218 a more passive feeding mode than cruise-feeding and current-feeding (Brun et al., 2017).
219 Current-feeding describes the use of a scanning current that can detect and capture food items.
220 This strategy is believed to favor a more efficient capture of many immobile preys like
221 phytoplankton cells compared to ambush-feeding (Kiørboe, 2011a). Lastly, cruise-feeders
222 correspond to copepods that swim actively through the water column in search of their prey.

223 Myelination (binary): myelinated copepod species have a lipid-rich myelin sheath around
224 their nerves that increases the speed of nervous signals transmission and therefore enables
225 faster attack or evasive reactions (Lenz, 2012). Myelin sheaths play a key role in modulating
226 mortality and feeding rates and improving energy savings under low food conditions.

227 Spawning mode (binary): eggs are either released into the open water after fertilization (free-
228 spawning) or remain attached to the female in specialized egg-sacs until hatching (sac-
229 spawning). Sac spawning copepods display lower fecundity rates and longer hatching times
230 compared to free-spawners (Kiørboe & Sabatini, 1994).

231

232 2.3. Definition of functional groups

233 We used multivariate analysis and hierarchical clustering to identify functional groups of
234 copepod species that show similar functional trait combinations and therefore constitute
235 different functional units in marine ecosystems. Only those copepod species with a body size
236 value and no missing data for three out of five functional traits (343 out of the 385 species)
237 were retained in the analysis (Appendix S2). The species' trophic groups and feeding modes
238 were re-coded binarily to accurately represent species that belong to several feeding modes/
239 trophic groups (Appendix S2). This means that the analyses described below were performed
240 on 343 species based on ten trait dimensions instead of the initial five dimensions.

241 Since the functional traits used represented both quantitative and qualitative variables, a factor
242 analysis on mixed data (FAMD; Pagès, 2004) was used to investigate inter-species functional
243 traits variance and estimate the functional distances between species. The use of a FAMD
244 represented an improvement to the Multiple Correspondence Analysis (MCA) used in
245 Benedetti et al. (2016) as it allowed to retain body size as a quantitative continuous variable
246 instead of having to convert this trait into size classes. The FAMD reduced the dimensionality
247 of the ten traits dataset by synthesizing them through a set of principal components (PCs) that
248 described the main modes of functional trait variance. The number of retained FAMD
249 components was chosen based on a leave-one-out cross-validation method where each object
250 (i.e., species) is alternatively removed and predicted with a new FAMD model and a mean
251 square error of prediction is calculated for each n components ranging from one to ten
252 (Audigier et al., 2016). The mean square error was lowest for $n =$ four components (error =
253 0.028, whereas error $>$ 0.029 for all other values of n) and those first four FAMD components
254 explained 80.15% of the variability in inter-species trait variance. An Euclidean distance
255 matrix was calculated from these four components to represent the inter-species functional
256 distance resulting from the FAMD. To assess the quality of this dimension reduction analysis,
257 we compared this Euclidean distance to a Gower distance matrix calculated directly from the
258 trait data (10 dimensions) following the guidelines of Mouillot et al. (2021), We calculated
259 the co-ranking matrix between the two distance matrices and determined how the dimension
260 reduction distorted the initial inter-species functional distance using the area under the curve

261 (AUC) criterion, which should be > 0.7 according to Mouillot et al. (2021). We found an
262 AUC criterion of 0.81 which supports the “excellent” quality of our dimension reduction
263 analysis (Mouillot et al., 2021). We used hierarchical clustering and Ward’s agglomeration
264 link to generate the functional dendrogram. The number of clusters (i.e., FGs) was then
265 chosen by the height at which the dendrogram is “cut”.
266 We cared to investigate the sensitivity of the resulting FGs to the main parameters of our
267 clustering approach (see Appendix S4 for results not reported below): (i) the effect of
268 including species with missing values in the FAMD compared to restricting the pool to those
269 species without any missing trait value (283 instead of 343; Appendix S2), (ii) the choice of
270 the distance metric (Euclidean distance matrix based on FAMD components *versus* Gower’s
271 distance matrix based on the trait values), and the agglomeration link (Ward’s aggregation
272 link versus average link; Mouchet et al., 2008). Therefore, four combinations of distance
273 matrices and agglomeration links were considered for two subsets of the species traits data.
274 Including 60 copepod species with some missing trait values affected the structure FAMD
275 space only marginally (Fig. S4.1) and did not change the number of components to be
276 retained ($n = 4$), nor did it change their amount of explained variance (80.15%). Therefore,
277 the FAMD including 343 species was kept as the standard since it allowed for a larger pool of
278 species. To quantify the quality of the clustering procedure, four internal cluster stability
279 indices (Calinski-Harabasz index, Connectivity, Dunn’s index, and average silhouette width)
280 were calculated for each dataset, distance matrix choice, agglomeration link choice and for a
281 number of clusters ranging from three to 13 (Figs. S4.2 and S4.3). Plus, Baker’s Gamma
282 correlation coefficients (Baker, 1974) were computed between each functional dendrogram
283 stemming from the four different combinations of distance metrics and agglomeration links to
284 examine their pairwise similarity (Table S4.1). Lastly, we performed a careful expert
285 inspection of each dendrogram and resulting FGs to further evaluate their similarity and
286 ensure the ecological relevance of the final FGs (i.e., avoid few large groups that are
287 functionally heterogenous or numerous small groups that are functionally redundant).
288 Ultimately, eleven FGs were identified (Table S4.2).

289

290 2.4. Species distribution modelling

291 2.4.1. Environmental predictor selection

292 We considered 14 environmental predictors that drive the spatial ranges of copepod species in
293 the open ocean and that are commonly used to model their abiotic habitats (see Benedetti et
294 al., 2021 and references therein). A more exhaustive description of the data coverage and

295 initial resolution is given in Appendix S5. First, five predictors were retrieved from the World
296 Ocean Atlas (WOA, version 2013v2): sea surface temperature (SST, °C), dissolved oxygen at
297 175 m depth (dO_2 , $\mu\text{ml l}^{-1}$), nitrate concentration (NO_3^- , μM), phosphate concentration (PO_4^{3-} ,
298 μM), silicate concentration (SiO_2 , μM). The products N^* and Si^* were derived from the
299 monthly climatologies of the above-mentioned nutrient fields: N^* refers to the excess of NO_3^-
300 to PO_4^{3-} relative to the Redfield ratio ($\text{N}^* = [\text{NO}_3^-] - 16[\text{PO}_4^{3-}]$) and can be used as a tracer of
301 denitrification and N_2 fixation. Si^* is the excess of SiO_2 to NO_3^- ($\text{Si}^* = [\text{SiO}_2] - [\text{NO}_3^-]$) and is
302 relevant to diatom growth, as healthy diatoms take up silicate and nitrate in a one-to-one ratio
303 (Sarmiento & Gruber, 2006). Several additional variables were considered as they represent
304 complementary niche axes: surface wind speed (Wind, m s^{-1}); eddy kinetic energy (EKE, m^2
305 s^{-2}) computed according to the algorithm of Qiu and Chen (2004) as a proxy for mesoscale
306 activity; chlorophyll-a concentration (Chl, mg m^{-3}) as a proxy of surface phytoplankton
307 biomass; surface carbon dioxide partial pressure (pCO_2 , μatm); photosynthetically active
308 radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$); and mixed-layer-depth (MLD, m). Also, photosynthetically
309 available radiation (PAR) over the MLD (MLPAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) was added as an indicator of
310 available light within the mixed layer. For NO_3^- , PO_4^{3-} , SiO_2 , Chl and EKE, we added their
311 log-transformed fields to achieve distributions that are closer to a normal distribution. The
312 monthly climatologies of all predictor variables were all projected onto the $1^\circ \times 1^\circ$ cell grid of
313 the WOA and their values were matched with the monthly species occurrence data.

314 We used a two-stage procedure to select the environmental predictors of the SDMs (section
315 2.4.3 for the models set up). First, we removed collinear predictors to avoid increasing the
316 uncertainty in regression models projections through coefficients inflation (Dormann et al.,
317 2013). The collinearity of predictors at the global scale and at the FGs-level was calculated
318 for each species through pairwise Spearman's rank correlation coefficients. When a pair of
319 predictors displayed an average correlation coefficient above the widely used $|0.7|$ threshold
320 (Dormann et al., 2013), the predictor closest to a normal distribution was kept. This first step
321 narrowed down our initial 14 predictors to the following ten: SST, PAR, $\log\text{NO}_3$, MLD,
322 $\log\text{Chl}$, $\log\text{EKE}$, Si^* , N^* , Wind, and pCO_2 . Second, to avoid model overfitting the number of
323 environmental predictors included in the SDMs was restricted to five to achieve a 10:1 ratio
324 of occurrences to predictors, following Guisan et al. (2017). To choose the five most
325 influential predictors, univariate random permutation tests were performed ($n = 30$ repetitions;
326 Appendix S6). For each species and SDMs, one of the ten potential predictors was randomly
327 reshuffled while the other nine were kept as is and SDMs were trained based on this
328 reshuffled dataset. Then, a correlation coefficient was calculated between the original vector

329 of unshuffled model prediction and the vector of predictions resulting from the reshuffled
330 dataset. The higher the correlation coefficient, the lower the importance of the reshuffled
331 predictor on the final SDM prediction. We chose the top five predictors for each FG and SDM
332 separately (Appendix S6). These were then used to train the SDMs used for global habitat
333 projections. For those species that could not be assigned to a FG due to missing functional
334 traits data, the five predictors displaying the highest ranks of relative importance across all
335 species combined were used in the SDMs (Appendix S6).

336

337 2.4.2. Background data

338 Correlative SDMs such as the ones used here require both presence and absence data. Yet, the
339 occurrence data used here typically lack absence data, therefore pseudo-absence data were
340 generated (Benedetti et al., 2021). We followed the target-group approach of Phillips et al.
341 (2009) which is appropriate to model plankton species distributions based on their relatively
342 sparse data (Righetti et al., 2019; Benedetti et al., 2021). First, we investigated the spatial
343 distribution of the occurrence data of each FG separately. All FGs displayed similar patterns
344 of sampling effort except for FG2, FG4 and FG11 (Appendix S4), which had very few
345 occurrences in the Southern Ocean and the North Atlantic Ocean (Appendix S1). Therefore,
346 we chose to draw pseudo-absences from the total pool of sites (i.e., monthly 1° x 1° grid cells)
347 that displayed at least ten occurrences of all species included, except for those species
348 belonging to the three groups above. For species of FG2, FG4 and FG11, pseudo-absences
349 were only drawn from those sites where at least 10 different species of their FG were found
350 (i.e., their "target group"). The threshold of ten occurrences per site was chosen to avoid
351 relying on those sites where only a small fraction (e.g., only one or two species) of the overall
352 copepod community was detected. Once the sites were defined, the pseudo-absences of each
353 species were randomly drawn based on their occurrences in both their corresponding target
354 groups. This way, a species' background is located at the sites where its lack of presence is
355 most likely to reflect an actual absence. For each species, ten times more background data
356 than presences were generated following the guidelines of Barbet-Massin et al. (2012), and
357 presences were weighted ten times more than pseudo-absences.

358

359 2.4.3. Model configuration and habitat suitability projections

360 Following Benedetti et al. (2021), we developed an ensemble modelling approach that
361 combined three SDMs types which were configured to avoid model overfitting (Merow et al.,
362 2014): Generalized Additive Models (GAMs), Generalized Linear Models (GLMs), and

363 Artificial Neural Networks (ANNs). The GLM were run using a quadratic formula and a logit
364 link function. The GAMs were also set up to use a logit link function and a maximum of five
365 smoothing terms. ANNs were run using five cross validations with 200 iterations to optimize
366 number of unities in the hidden layer and the parameter for weight decay (Thuiller et al.,
367 2016). The SDMs were trained on 80% of the presence/pseudo-absence data chosen at
368 random and tested on the remaining 20%. For each SDM, ten random cross evaluations runs
369 were carried out. For each cross-validation run, the true skill statistic (TSS) was calculated to
370 evaluate model performance. Only species displaying a mean TSS score >0.30 were used for
371 the final species and functional trait projections.

372 The SDMs were then projected in the conditions of the global ocean as a function of all
373 monthly climatologies of the environmental predictors included in the model to obtain
374 species-level maps of habitat suitability indices (HSI). Since we used FGs-specific and SDM-
375 specific sets of predictors, the SDMs vary in number of successfully modelled species (254
376 for GAM, 244 for ANN, and 238 species for GLM). For each FG, annual mean HSI values
377 were obtained by averaging the monthly HSI maps across each species constituting the FG
378 and SDMs. These mean annual HSI estimates indicate which regions are suitable for each
379 species/FG.

380

381 2.5. Positioning FGs in environmental niche space

382 Following the approach of Benedetti, Vogt, et al. (2018), the mean univariate response curves
383 emerging from the GAMs were used to estimate the relative optimal conditions (i.e., niche
384 center) and tolerance (i.e., niche width) for each species and predictor (see Appendix S7). The
385 niche center was calculated as the weighted median and the niche width as the difference
386 between the weighted 10th and 90th percentiles. The HSI values were used as weights. For this
387 analysis, a set of eight predictors common to all species (i.e., unlike the top five FG-specific
388 predictors used for mapping, as described in section 2.4.1) had to be defined based on the
389 ranking of predictors (Appendix S6): SST, logChl, logNO₃, MLD, Si*, PAR, N* and logEKE.
390 Eight predictors were chosen to cover all top ranking predictors based on the overall rankings.
391 To investigate the inter-species and inter-FGs similarities in the above-mentioned niche
392 characteristics and test if the FGs present distinct environmental niches, a principal
393 component analysis (PCA; Legendre & Legendre, 2012) was performed on the niche centers
394 and niche widths for all 8 predictors to ordinate the species according to their niche center and
395 niche width. This space composed by the principal components (PCs) of the PCA is hereafter
396 referred to as the niche space. To explore whether FGs differ significantly in their position in

397 niche space, we averaged the PCs scores of each FG based on the scores of their constituting
398 species. Non-parametric variance analysis (Kruskal-Wallis tests) was carried out to test if FGs
399 differ in their position in niche space). Post-hoc variance analyses (Dunn's test with a p-
400 values adjustment following Bonferroni's method) were then performed to identify the pairs
401 of FGs that displayed significant variations in niche space positions.

402

403 2.6. Community weighted median (CWM) proportions of traits

404 On top of projecting the FGs-specific mean annual patterns of HSI, the CWM trait values for
405 body size, trophic group, feeding mode, myelination, and spawning mode were computed to
406 explore the biogeography of copepod traits. All qualitative traits were mapped by calculating
407 a CWM trait value based on the monthly species-specific HSI values as weights. More
408 precisely, for each grid cell and month, the CWM proportion was calculated as the sum of all
409 HSI values belonging to species exhibiting that trait over the sum of HSI values across all
410 species in that community (i.e. all the species in that grid cell). For body size (i.e., the only
411 continuous trait), we calculated the weighted median body size for each community, again
412 using monthly HSI values as weights. The CWM values were calculated according to Cormen
413 et al. (2009) using the matrixStats R package. Like for FGs, monthly CWM projections were
414 performed for every SDM type and mean annual CWM trait values were derived based on the
415 ensemble of projections (Appendices S8 and S9).

416

417 2.7. Ocean regionalization based on functional trait biogeography

418 To explore sub-global patterns of traits and FGs expression rather than reporting results for
419 broad latitudinal bands (e.g., going beyond the tropics *versus* the poles), clustering was used
420 to divide the global ocean into regions that displayed similar trait expressions (e.g., mean
421 annual projections of CWM body size, and CWM values of each trophic groups, feeding
422 modes, myelination, and spawning mode; Appendix S10). First, the spatial patterns of the
423 twelve CWM traits values were summarized through a PCA again (Appendix S10) and the
424 scores of each grid cell along the first four PCs (97.9% of total variance explained) were used
425 to derive a global Euclidean distance matrix. Second, following the same approach as in
426 section 2.3 and in Benedetti et al. (2021), various clustering approaches were explored based
427 on this distance matrix (three hierarchical clustering approaches and two widely used
428 partitioning approaches) and three internal cluster stability metrics (Dunn's index,
429 Connectivity, and the average silhouette width) were used to help us find an optimal number
430 (k) of regions (see Appendix S11). The three hierarchical approaches consisted in using three

431 alternative agglomeration linkages (average, complete and Ward's; Legendre & Legendre,
432 2012). The stability metrics enabled us to discard the two partitioning methods (kmeans and
433 partitioning around medoids; Fig. S11.1) and to narrow k down to 3 to 8 regions (Fig. S11.2).
434 Ultimately, we chose to present the CWM trait patterns obtained for $k = 4$ under Ward's
435 linkage based on the profiles of cluster stability metrics and because this linkage methods
436 minimizes intra-cluster variance. Values of $k > 4$ simply lead to smaller regions nested in
437 those obtained for $k = 4$.

438

439 **3. Results**

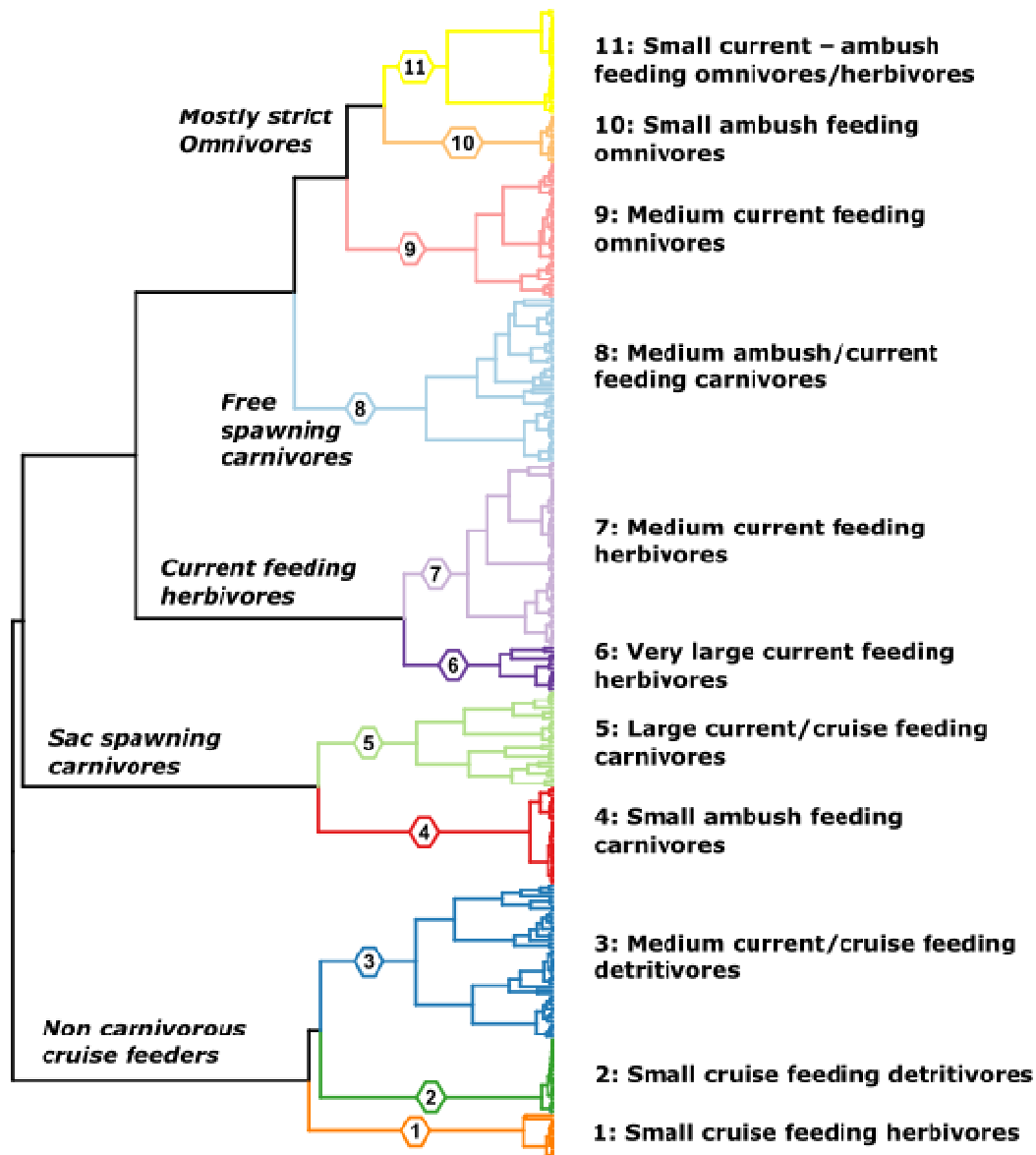
440 3.1. Copepod FGs

441 The 343 copepod species retained were clustered based on their combinations of body size,
442 feeding mode, trophic group, myelination, and spawning mode. Eleven FGs could be derived
443 from the functional dendrogram, which reflects inter-species functional similarity (Fig. 1;
444 Appendix S4). The first dichotomy in the dendrogram occurred between the small to medium-
445 sized cruise feeders (FG1, 2, 3) and other feeding modes. FG1 was composed of 14 species
446 that are small (median \pm IQR = 1.10 ± 0.52 mm) cruise-feeding herbivores. Almost all species
447 (13 out of 14) were sac-spawning and myelinated species. All but one species belonged to the
448 *Clausocalanus* genera. FG2 was defined by small (0.80 ± 0.30 mm) cruise-feeding
449 detritivores. The 22 species of this group were all amyelinated and sac-spawning. All species
450 in group 2 belonged to the Oncaeidae family. FG3 was composed of 46 medium-sized ($2.61 \pm$
451 1.70 mm) detritivores. Most species in FG3 were myelinated (74%) and free-spawning (80%).
452 Cruise- and current-feeding were the two predominant feeding modes, with *Spinocalanus*,
453 *Metridia* and *Scaphocalanus* being the dominant genera in this FG.

454 The second dichotomy in the dendrogram separated the small and large sac-spawning
455 carnivores (FG4 and 5) from the rest. FG4 consisted of 29 small (1.22 ± 0.70 mm)
456 carnivorous ambush-feeders. They were all sac-spawning and amyelinated. The 29 species
457 were part of the Corycaeidae family and thus belonged to either the *Corycaeus*, *Farranula* or
458 *Vetoria* genera. FG5 was made up of 29 species of large (4.58 ± 2.75 mm) sac-spawning
459 current- and cruise-feeding carnivores from the Sapphirinidae and Euchaetidae families.

460 The third dichotomy of the dendrogram separated the large and medium-sized current feeders
461 (FG6 and 7) from the rest. FG6 was a group of 13 very large (6.80 ± 2.15 mm) species that
462 were either current-feeding herbivores (85%) or fully omnivorous (15%). They were all
463 myelinated free-spawners. The two most represented genera were *Calanus* and *Eucalanus*.
464 FG7 was the largest FG with 55 medium-sized (1.80 ± 2.26 mm) and current-feeding

465 herbivores. Most were myelinated (95%) and free-spawning (89%). The main genera
466 contributing to the composition of FG7 were *Calanus*, *Calocalanus* and *Paracalanus*.
467 The fourth dichotomy occurred between the small and medium-sized omnivores and the
468 medium free spawning carnivores (FG8). FG8 consisted of 49 medium-sized (3.40 ± 1.7 mm)
469 omnivorous-carnivorous species which were predominantly amyelinated (86%) and free-
470 spawning (80%). This diverse group mixed current- (60%) and ambush-feeders (40%) and
471 gathered 12 genera with *Candacia*, *Haloptilus* and *Heterorhabdus* being the most dominant.
472 FG9 was composed of 40 medium-sized (2.76 ± 1.98 mm), current-feeding omnivorous
473 species. All were free-spawning and mostly amyelinated (72%). *Pleuromamma*, *Gaetanus*,
474 and *Labidocera* were the main genera.
475 Finally, the fifth and last main dichotomy separated the small and medium-sized mixed-
476 feeding omnivores (FG11) from the small ambush feeders (FG10). FG10 was also rather
477 homogeneous and contained 14 small (1.10 ± 0.52 mm), ambush-feeding, amyelinated and
478 sac-spawning omnivores. All species belonged to either the *Oithona* or the *Dioithona* genera
479 from the Oithonidae family. FG11 was a group of 32 small (1.50 ± 0.67 mm) species
480 predominantly belonging to the *Acartia* and *Centropages* genera. The species belonging to
481 *Acartia* were omnivorous-herbivorous, whereas the others were omnivorous. All species in
482 FG11 were amyelinated free-spawning current-ambush feeders.
483



484

485 *Figure 1:* Functional dendrogram representing the inter-species traits dissimilarity for 343
486 copepod species based on their functional trait combinations. The hierarchical clustering was
487 performed on a Euclidean distance matrix issued from the species coordinates ensuing from a
488 Factor Analysis of Mixed Data (FAMD). Each leaf of the functional dendrogram represents a
489 copepod species and the eleven functional groups (FGs) identified through the hierarchical
490 clustering approach are numbered and highlighted in color. The main taxonomic groups
491 representing the FGs are as follows: FG1: *Clausocalanus* spp.; FG2: Oncaeidae; FG3:
492 *Spinocalanus*, spp., *Scaphocalanus* spp. and *Metridia* spp.; FG4: Corycaeidae; FG5:
493 Sapphirinidae and Euchaetidae; FG6: Calanidae; FG7: *Paracalanus* spp., *Calocalanus* spp.,
494 and *Calanus* spp.; FG8: *Haloptilus* spp., *Heterorhabdus* spp. and *Candacia* spp.; FG9:
495 *Pleuromamma* spp., *Gaetanus* spp., and *Labidocera* spp.; FG10: Oithonidae; FG11: *Acartia*
496 spp. and *Centropages* spp.

497

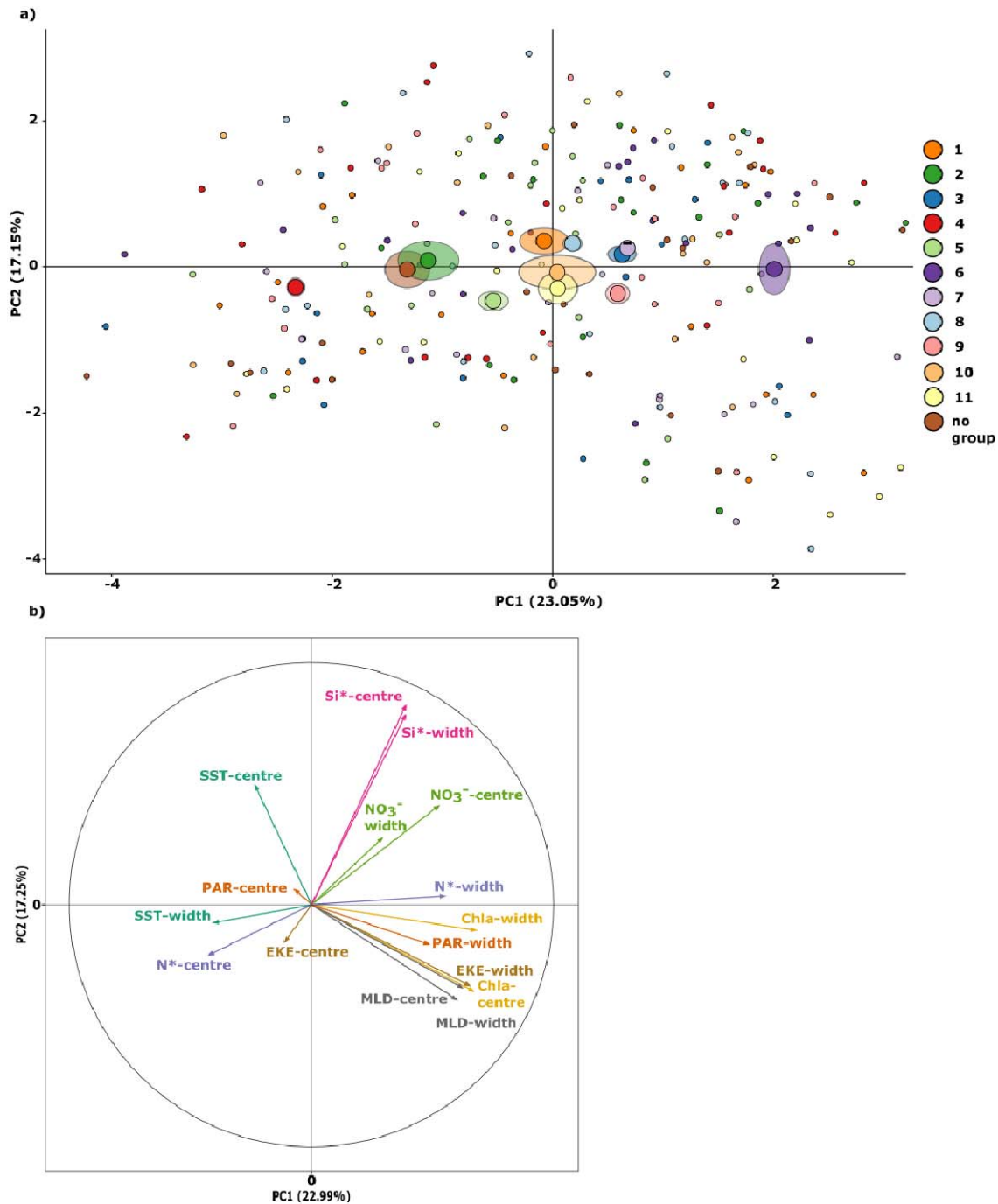
498 The functional space defined by the PCs of the FAMD (Appendix S12) served as an
499 alternative description of the reduced functional space. The first four PC of the FAMD
500 explained 79.21% of the total variance in functional traits. The largest functional distance
501 along the first component was found between FG4 and FG6. The Euclidean distance matrix
502 represented on the functional dendrogram (Fig. 1) was compared to a Gower distance matrix
503 computed from the functional traits (i.e., no dimension reduction; Appendix S4) based on the
504 AUC criterion. We found an AUC of 0.808, which indicated that the reduced FAMD space
505 results in a fairly good representation of the inter-species functional dissimilarity according to
506 Mouillot et al. (2021). Furthermore, the importance of a functional trait in scoring the
507 functional space was quantified by examining the drop in AUC score if said trait was omitted.
508 Body size was found to be the most important (-0.322 in AUC), followed by trophic group (-
509 0.265), feeding mode (-0.163), spawning mode (-0.091), and myelination (-0.063).

510

511 3.2. FGs in environmental niche space

512 The environmental niches of the copepod species were described by their univariate niche
513 centers and widths for the top eight predictors we defined as part of our core set or predictors
514 (section 2.5, Appendix S6), and these were used to examine FGs position in niche space based
515 on a PCA (Fig. 2; see Appendix S13 for PCs 3 and 4). The niche characteristics that
516 contributed the most positively to PC1 (relative contribution to PC1 given in brackets when
517 >5%) were: logChl center (12.16%), logChl width (12.51%), EKE width (11.78%), MLD
518 center (9.96%), MLD width (10.78%), N* width (7.48%), Si* width (5.64%) and Si* center
519 (5.19%). The species with negative scores on PC1 were those that are characterized by higher
520 SST width (5.65%) and N* center (4.45%). The three most important niche characteristics
521 scoring PC2 were: Si* center (30.88%), Si* width (27.90%) and SST center (11.17%). Species
522 with positive PC1 scores were those affiliated with wider niches and conditions of higher
523 concentrations of nutrients and chlorophyll-a, stronger seasonal variations, and overall higher
524 water column turbulence and mixing.

525



526

527 **Figure 2:** Position of a) functional groups (FGs, larger circles) and species (smaller circles) in
528 environmental niche space according to the first two principal components (PCs) of a
529 principal component analysis (PCA) performed on b) the species-level niche characteristics
530 derived from GAM-based univariate response curves of the chosen environmental predictors.
531 Niche centers were calculated as the weighted median value of the corresponding predictor as
532 an estimate of the species' optimum for each predictor. Niche widths were calculated as the
533 range between the weighted 10th and 90th quantiles and estimate the relative tolerance range of
534 the species to the corresponding predictor. The semi-transparent ellipses indicate two times
535 the value of the standard errors associated with the mean PC scores of the FGs.

536

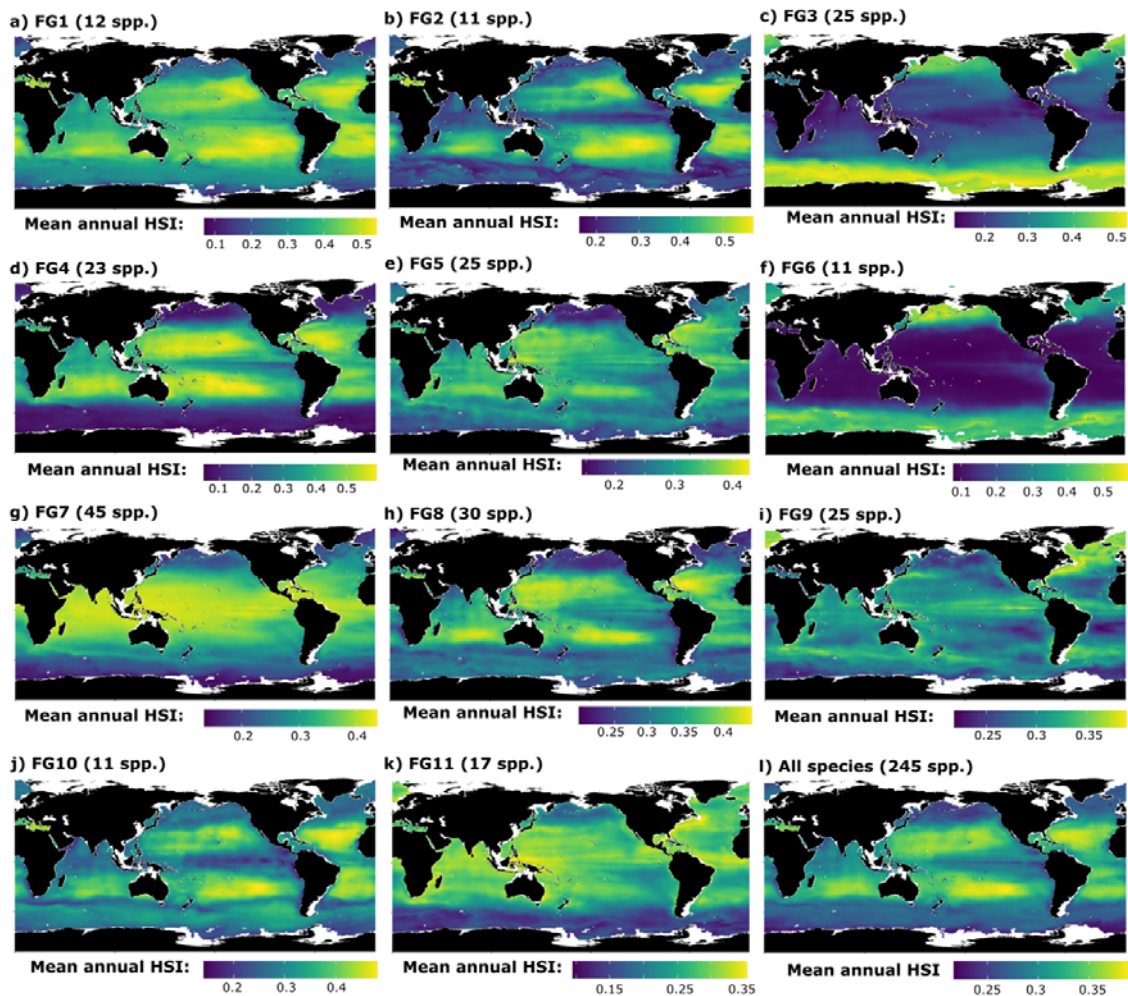
537 Post-hoc variance analyses showed significant (Dunn's tests; $p < 0.05$) inter-FGs variations in
538 niche characteristics and PC scores (see Appendix S14). The largest distance in niche space
539 (PC1) was found between FG4 and FG6 (Fig. 2a; $p = 6.5e-10$). Along PC1, FG4 also differed
540 significantly from FG1 ($p = 0.042$), FG3 ($p = 1.6e-06$), FG7 ($p = 1.3e-08$), FG8 ($p = 1.4e-4$),
541 FG9 ($p = 2.3e-06$), FG10 ($p = 0.011$) and FG11 ($p = 0.005$). Conversely, FG6 differed
542 significantly from FG2 ($p = 4.5e-4$), FG5 ($p = 0.001$) and FG8 ($p = 0.049$) along PC1. FG6
543 also differed significantly from FG2 ($p = 0.001$) and FG5 ($p = 0.002$). None of the FGs did
544 showed significant variations along PC2. Only FG3 and FG7 showed significant variations
545 along PC3 ($p = 4.2e-3$; Appendices S13 and S14). To summarize, when FGs 4 and 6 were not
546 accounted for, none of the remaining nine FGs showed significant variations in PC1 and PC2
547 scores (all $p > 0.05$). This was due to the high level of inter-FG environmental niche
548 characteristics overlap, which implies that distinct FGs display broad environmental niches
549 and can share similar abiotic habitats.

550

551 3.3. Mean annual habitat suitability indices (HSI) patterns

552 For all three SDMs and 11 FGs combined, we found SST to be the most important predictor
553 for constraining the models, followed by PAR, $\log\text{NO}_3$, MLD, $\log\text{Chl}$, $\log\text{EKE}$, Si^* , N^* ,
554 Wind, and pCO_2 (Appendix S6). SST remained the most important predictor for every FG
555 when looking at predictor importance per FG. Therefore, most FGs displayed mean annual
556 HSI patterns that were driven by the latitudinal temperature gradients at the first-order. The
557 impact of second-order predictors became clearer on a sub-global scale. Aggregating the
558 average monthly HSI projected across SDMs per FG allowed us to estimate their mean annual
559 habitat suitability patterns (Fig. 3).

560



561

562 **Figure 3:** Maps of mean annual habitat suitability index (HSI) the eleven copepod functional groups
563 (FG) identified in the present study: a) FG1 (small myelinated cruise-feeding omnivores-herbivores),
564 b) FG2 (small non myelinated cruise-feeding detritivores), c) FG3 (medium-sized myelinated mixed-
565 feeding or cruise-feeding detritivores), d) FG4 (small amyelinated ambush-feeding carnivores), e) FG5
566 (large current- or cruise-feeding carnivores), f) FG6 (very large myelinated current-feeding
567 omnivores-herbivores), g) FG7 (medium-sized myelinated current-feeding omnivores-herbivores), h)
568 FG8 (medium-sized amyelinated ambush- or current-feeding carnivores), i) FG9 (medium-sized
569 amyelinated current-feeding omnivores), j) FG10 (small amyelinated ambush-feeding omnivores), k)
570 FG11 (small amyelinated mixed-feeding omnivores) and for l) all species together. Mean annual
571 estimates were derived from the 12 monthly estimates of mean HSI obtained for each of the three
572 species distribution models (SDMs) used (generalized linear models, generalized additive models and
573 artificial neural networks). The FG were defined based on the functional traits combinations of the 245
574 copepod species described by a factorial analysis on mixed data (FAMD) whose principal components
575 were used to perform hierarchical clustering on a Euclidean distance matrix with Ward's aggregation
576 link.

577

578 The mean annual HSI of FG3 was found to be maximal towards the poles and decrease
579 progressively towards the equator. In contrast, the mean annual HSI of FG1, FG2, FG4, FG8,
580 and FG10 were found to be highest in the tropics and decreased towards higher latitudes. For
581 those five FGs, slighter decreases in HSI were modelled towards the tropical upwelling

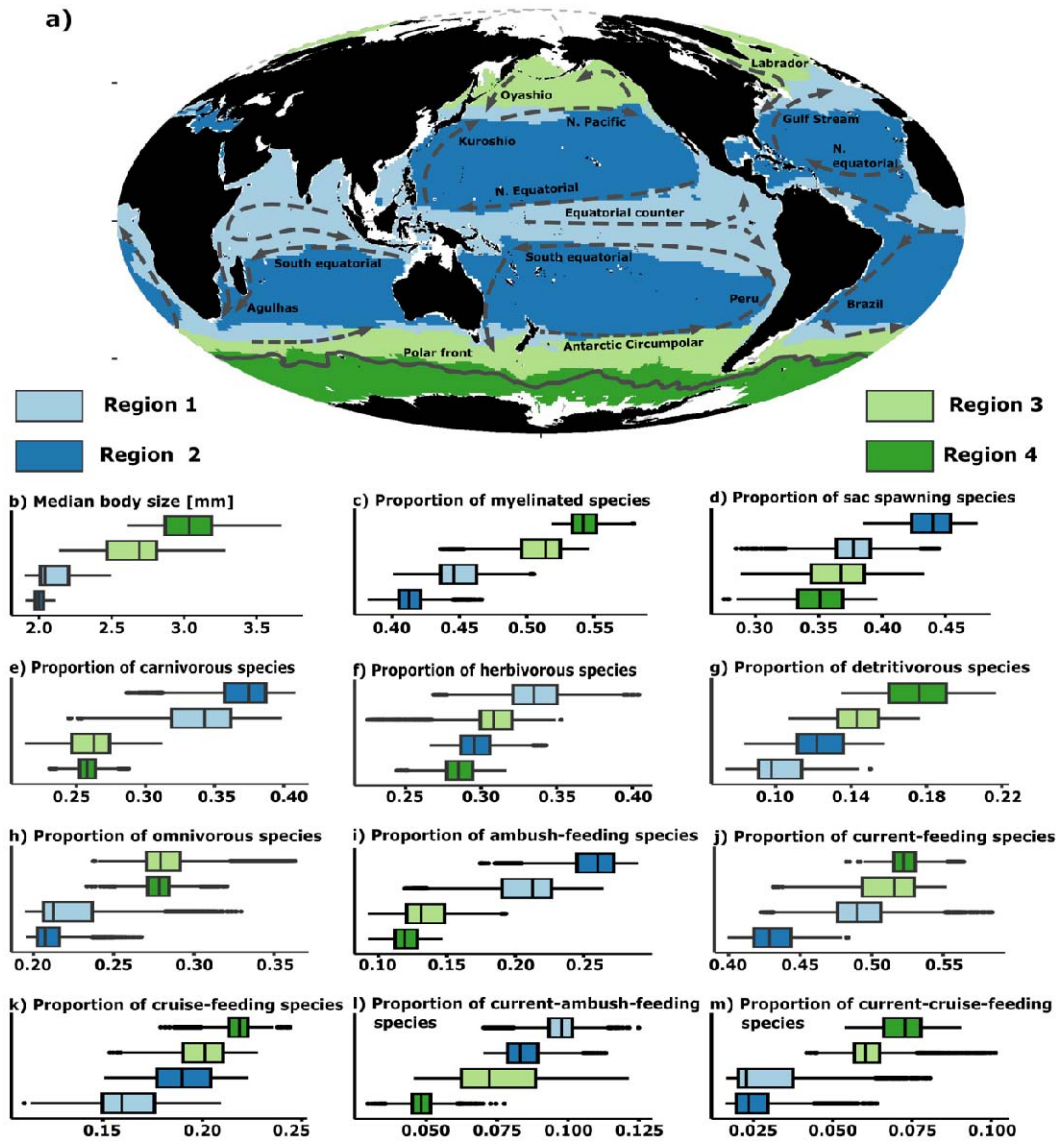
582 systems (e.g., Peru, Benguela), the northern part of the Indian Ocean and the Pacific
583 Equatorial counter current. Therefore, these five FGs reached maximal HSI in the
584 oligotrophic conditions of the tropical gyres. Meanwhile, FG5, FG9, and FG11 show less
585 marked latitudinal gradients in mean annual HSI values. No clear hotspot in HSI could be
586 found for these three FGs, but they all displayed lower HSI in higher latitudes than in the
587 tropics. Yet, the region where their mean annual HIS was lowest varied between groups: the
588 North Pacific and parts of the Southern Ocean for FG5 and FG9, the whole Southern Ocean
589 for FG11. The mean annual HSI pattern of FG7 followed the annual SST gradient very
590 closely, with maximal HSI values near the equator and progressive decrease towards the
591 poles.

592

593 3.4. Functional trait biogeography from CWM trait values and regionalization

594 We projected the CWM body size and the CWM values of trophic group, feeding mode,
595 spawning mode, and myelination for the global open ocean on a mean annual scale to
596 illustrate the biogeography of these key traits (Appendix S9). To summarize the main spatial
597 gradients of trait biogeography and assess how these could overlap with known large scale
598 oceanographic currents (i.e., currents and fronts), the global ocean was clustered based on
599 similarities in CWM values after reducing their dimensionality (see Appendices S10 and
600 S11). We identified four ocean regions that display significant contrasts in CWM trait
601 proportions (Fig. 4; Appendix S15).

602



603

604 **Figure 4:** The global ocean divided into a) four regions according to the principal components of a
 605 Principal Component Analysis (PCA) based on the CWM values of the functional traits. Major
 606 oceanographic circulation features (i.e., surface currents and fronts) are illustrated through dashed
 607 arrows to highlight their overlap between the regions' boundaries. The distribution of CWM trait
 608 values between the four regions are shown through the boxplots: b) median body size, CWM values of
 609 c) myelinated species, d) sac spawning species, e) carnivores, f) herbivores, g) detritivores, h)
 610 omnivores, i) ambush-feeders, j) current-feeders, k) cruise-feeders, l) current-ambush-feeders, and m)
 611 current-cruise-feeders. The position of the Antarctic Polar Front was taken from Orsi and Harris
 612 (2019). The positions of the main large-scale ocean currents were drawn according to Pidwirny
 613 (2006). The lower, middle, and upper boundaries of the boxplots correspond to the 25th, 50th, and
 614 75th percentiles respectively. The lower and upper whiskers extend no further than 1.5*IQR
 615 (interquartile range) from the lower and upper hinges.

616

617 Region 1 primarily fell within the equatorial band and comprised coastal upwelling regions
 618 and the main oxygen minimum zones. The copepod communities of Region 1 displayed lower

619 CWM body size (median \pm IQR = 2.043 mm \pm 0.194), higher proportions of carnivores
620 (0.342 \pm 0.040) and herbivores (0.335 \pm 0.029) but lower proportions of omnivores (0.213 \pm
621 0.030) and detritivores (0.098 \pm 0.023). The CWM values of myelinated (0.446 \pm 0.026), sac-
622 spawning (0.377 \pm 0.026), and ambush-feeding (0.212 \pm 0.036) species were lower than the
623 CWM traits values found for the communities of Region 2 and higher than those found for the
624 high latitude communities of Regions 3 and 4 (Appendix S13).

625 Region 2 comprised the tropical gyres. We found that communities in Region 2 showed the
626 lowest CW median body size (2.002 \pm 0.057 mm) but the highest CWM values of ambush-
627 feeding (0.259 \pm 0.027) carnivorous (0.372 \pm 0.028), and sac-spawning (0.440 \pm 0.030)
628 copepods. Conversely, the CWM values of myelinated (0.413 \pm 0.016) species in Region 2
629 were the lowest across all four regions.

630 Region 3 was located poleward to the previous two regions and covered the North Atlantic
631 Ocean, the North Pacific Ocean and the waters located between the Polar Front and the
632 Antarctic Circumpolar Current. The CWM body size (2.691 \pm 0.342 mm), the CWM values
633 of myelinated (0.514 \pm 0.028) and omnivorous (0.279 \pm 0.021) species were higher there than
634 in Regions 1 and 2. In contrast, the CWM values of sac-spawners (0.368 \pm 0.041), carnivores
635 (0.266 \pm 0.026), and ambush feeders (0.132 \pm 0.027) was lower.

636 Region 4 mainly corresponded to the Southern Ocean (i.e., grid cells south of the Antarctic
637 Polar Front, Fig. 4a). Region 4 displayed the highest CWM body size (3.035 \pm 0.321 mm),
638 higher CWM values of myelinated (0.541 \pm 0.018), omnivorous (0.278 \pm 0.013), and
639 detritivorous (0.176 \pm 0.030) species, and the lowest CWM values of sac-spawners (0.351 \pm
640 0.035). The CWM values of current-feeding (0.522 \pm 0.015) and cruise-feeding (0.218 \pm
641 0.009) species was higher than those of ambush-feeding (0.120 \pm 0.016).

642

643 **4. Discussion**

644 4.1. Towards meaningful global zooplankton FGs in marine ecology

645 Here, we identified eleven copepod FGs based on combinations of species-level functional
646 traits. Nine of these eleven FGs had also been found, or were nested within larger groups, in
647 previous studies based on regional species pools (Pomerleau et al., 2015; Benedetti,
648 Gasparini, & Ayata, 2016; Benedetti, Vogt, et al., 2018; Becker et al., 2021; summarized in
649 Table 1), which suggests that most of the functions performed by copepods on a global scale
650 should also be expressed at regional scales.

651

652 **Table 1:** Table summarizing the overlap between the copepod functional groups (FGs) defined in the
 653 present study and those found in previous studies based on species composition and functional trait
 654 composition.

This study	Main clade	Main traits	Pomerleau et al. (2015) - North Pacific Ocean	Benedetti et al. (2016) - Mediterranean Sea	Benedetti et al. (2018) - Mediterranean Sea	Becker et al. (2021) - South Atlantic Ocean
FG1	Clausocalanus	Small myelinated cruise-feeding omnivores-herbivores	Small current- and cruise-feeding omnivores-herbivores (Group 6)	Small cruise-feeding omnivores-herbivores (subset of Group 6)	Small cruise-feeding omnivores-herbivores (Group 7)	Small and large myelinated cruise- and current-feeding omnivores-herbivores (subset of Group B)
FG2	Oncaeidae	Small non myelinated cruise-feeding detritivores	No equivalent	Small cruise-feeding omnivores-detritivores (subset of Group 6)	Small sac-spawning detritivores (subset of Group 5)	Small amyelinated ambush- or cruise-feeding carnivores or detritivores (small subset of Group D)
FG3	Spinocalanus, Scaphocalanus, Metridia	Medium-sized myelinated mixed-feeding or cruise-feeding detritivores	No equivalent	Small cruise-feeding omnivores-detritivores (subset of Group 6)	Small sac-spawning detritivores (small subset of Group 5)	No equivalent
FG4	Corycaeidae	Small amyelinated ambush-feeding carnivores	No equivalent	Small ambush-feeding carnivores (Group 2)	Small ambush-feeding carnivores (Group 2)	Small amyelinated ambush- or cruise-feeding carnivores or detritivores (small subset of Group D)
FG5	Sapphirinidae, Euchaetidae	Large current- or cruise-feeding carnivores	No equivalent	Large cruise-feeding carnivores (Group 1)	Large cruise- or current-feeding feeding carnivores (Group 1)	Small and large myelinated cruise- and current-feeding omnivores-herbivores (subset of Group B)
FG6	Calanus, Eucalanus	Very large myelinated current-feeding omnivores-herbivores	No equivalent	No equivalent	No equivalent	No equivalent
FG7	Calanus, Paracalanus, Calocalanus	Medium-sized myelinated current-feeding omnivores-herbivores	Small and large current-feeding omnivores-herbivores (Group 5c)	Small and large current-feeding omnivores-herbivores (Group 4)	Small and large current-feeding omnivores-herbivores (Groups 3 and 4)	Large myelinated current-feeding omnivores-herbivores (subset of Group C)
FG8	Candacia, Haloptilus, Heterorhabdus	Medium-sized amyelinated ambush- or current-feeding carnivores	No equivalent	Large cruise-feeding carnivores (Group 1)	Large cruise- or current-feeding feeding carnivores (Group 1)	No equivalent
FG9	Pleuromamma, Gaetanus,	Medium-sized amyelinated	No equivalent	Small and large current-feeding	Small and large current-feeding	No equivalent

	Labidocera	current-feeding omnivores		omnivores-herbivores (subset of Group 4)	omnivores-herbivores (small subset of Group 4)	
FG10	Oithonidae	Small amyelinated ambush-feeding omnivores	No equivalent	Small ambush-feeding omnivores (Group 5)	Small ambush-feeding omnivores (Group 6)	Small amyelinated mixed- or ambush-feeding omnivores (Group A)
FG11	Acartia, Centropages	Small amyelinated mixed-feeding omnivores	Small ambush-feeding omnivores (subset of Group 4)	Small mixed-feeding omnivores (Group 3)	Small mixed-feeding omnivores (small subset of Group 4)	Small amyelinated mixed- or ambush-feeding omnivores (Group A)

655

656

657 The four FGs defined by Becker et al., (2021) based on a series of cruises in the South
 658 Atlantic Ocean were quite broad and often functionally heterogeneous (i.e., large carnivorous
 659 copepods mixed with smaller current-feeding omnivorous-herbivorous ones, or small cruise-
 660 feeding particles feeders mixed with small ambush-feeding carnivores). As a result, our FGs
 661 are often nested within, or scattered across, the groups defined by Becker et al. (2021).

662 Only the present FG3 and FG6 have no true counterparts in previous studies. These two
 663 groups find their most suitable habitats towards the poles (Fig. 3) whose zooplankton
 664 communities were not covered by the regional studies mentioned. The copepods of FG3
 665 (*Spinocalanus* spp., *Metridia* spp., or *Scaphocalanus* spp.) are known to mainly inhabit
 666 deeper ocean layers where they feed on falling particulate organic matter and zooplankton
 667 carcasses (Yamaguchi et al., 2002; Sano et al., 2013). Therefore, this group contributes to the
 668 remineralization of organic matter and marine snow at higher latitudes and/or in colder
 669 conditions. FG6 comprises the largest current-feeding omnivorous-herbivorous copepods
 670 from the Calanidae family (*Eucalanus* spp. and *Calanus* spp.). Such large copepods are not
 671 present in the warm and oligotrophic conditions of the Mediterranean Sea hence their absence
 672 in Benedetti, Gasparini, & Ayata (2016) and Benedetti, Vogt, et al. (2018). FG6 is a key
 673 group for the biological carbon pump and lipid pump (Jónasdóttir et al., 2015; Visser et al.,
 674 2017; Steinberg & Landry, 2017; Brun et al., 2019) as it represents large-bodied grazers that
 675 can actively feed on microphytoplankton, perform relatively strong vertical migrations and
 676 generate large and fast sinking pellets (Stamieszkin et al., 2015; Ohman & Romagnan 2016;
 677 Brun et al., 2019). This is confirmed by the position of FG6 in niche space (Fig. 2) as it is
 678 affiliated to turbulent and seasonally varying conditions with higher nutrient and chlorophyll-

679 a concentrations. The ecological roles and functions ensured by the other nine FGs have
680 already been detailed and discussed in those previous studies. We support the statements of
681 these authors and how they described the ecological roles of the copepod FGs. Here, we
682 found a larger range of FGs compared to previous studies due to three main reasons: (i) we
683 investigated a global and larger (hundreds of species instead of tens) pool of species, (ii) we
684 accounted for myelination as an additional trait, and (iii) we retained body size as a
685 continuous trait, contrary to Benedetti, Gasparini & Ayata (2016) and Benedetti, Vogt et al.
686 (2018) whom relied on size classes which likely smoothed out important trait variations.

687 Overall, the largest differences in niche space (Fig. 2a, Appendix S14) occurred between two
688 main sets of FGs: (i) myelinated free-spawning large-bodied, or medium-bodied, current-
689 feeding herbivores (FG3, 6, 7 and 9), and (ii) amyelinated sac-spawning small-bodied, or
690 large-bodied, cruise- and ambush-feeding detritivores and carnivores (FG2, 4 and 5). The first
691 set is associated with conditions of stronger mixing and higher nutrients and chlorophyll-a
692 concentrations (Fig. 2b). The species constituting these FGs also show larger niche widths,
693 suggesting they display broader tolerances to monthly variations in environmental conditions.
694 Therefore, these FGs are found more frequently in high latitude environments, or boundary
695 current systems, where either seasonality or horizontal and vertical mixing lead to higher
696 mean annual productivity (Sarmiento & Gruber, 2006; Roy 2018). In contrast, the FGs of the
697 second set display narrower niches and are associated with conditions typical of the warmer
698 tropical oligotrophic gyres (weaker water mixing and lower nutrients and chlorophyll-a
699 concentrations; Fig. 2b). Meanwhile, the groups that are in the center of the niche space (FG1,
700 8, 10 and 11) are those whose species are very scattered across said space, meaning these FGs
701 could not be associated to any particular environment at the scale of our study.

702 This continuum of FGs in niche space was also found in functional trait space. Indeed, the
703 FGs of sets (i) and (ii) were often found on opposite sides of the FAMD dimensions (see
704 Appendix S12). The global spatial distribution of the FGs and CWM trait values (Figs. 3 and
705 4) further support the statements above: larger myelinated free-spawning and active feeding
706 copepods occur more frequently near the poles, whereas smaller amyelinated sac-spawning
707 and passive feeding copepods tend to occur in tropical oligotrophic gyres. Similar continuums
708 of copepod functional traits and environmental niches were found at smaller scales
709 (references in Table 1) or globally (Brun et al., 2016).

710

711 Towards meaningful zooplankton FGs in marine ecosystem models

712 Our combination of analyses supports the view that planktonic copepods display a continuum
713 of functional traits with a strong latitudinal gradient (Fig. 3 and 4; Appendix S9), driven by
714 global gradients in abiotic conditions. Larger and myelinated active feeders present higher
715 metabolic rates as well as higher feeding, excretion and mortality rates (Kiørboe 2011a; Lenz
716 2012; Litchman et al., 2013; Kiørboe & Hirst, 2014; Stamieszkin et al., 2015; van Someren
717 Gréve, Almeda, & Kiørboe, 2017; Brun et al., 2019). A similar continuum can occur within a
718 trophic group: larger current-feeding phytoplankton grazers (e.g., FG6 and 7) can feed on
719 larger cells than their smaller congeners (FG1 and 11; Hansen et al., 1994), or larger active-
720 feeding predators (FG5 and 8) can exert a top-down control on smaller ambush-feeding
721 predators (FG4) or smaller zooplankton in general. Consequently, such a continuum should be
722 explicitly represented in regional and global marine ecosystem models (e.g. similar to Serra-
723 Pompei et al., 2020), which too often rely on a few size classes only (Le Quéré et al., 2005;
724 Sailley et al., 2013). However, with a few exceptions (Henson et al., 2021), global marine
725 ecosystem models do not yet routinely include >10 zooplankton FGs due to computational
726 constraints. Since these models aim to represent biomass dynamics (in units of carbon)
727 between food web components and their interactions with climate, their improvement should
728 first focus on including copepod FGs that contribute the most to community biomass, and
729 biogeochemical function (Le Quéré et al. 2005).

730 To try to rank the present FGs based on their contribution to total copepod community
731 abundance in the upper layers of the global ocean, we implemented a preliminary synthesis of
732 copepod abundance observations from various large-scale data sources (see Appendix S16).
733 When examining the relative contribution of the eleven FGs to mean annual community
734 abundance (Fig. S16b), three FGs emerge as the most abundant regardless of latitude and
735 sampling gears: FG10 (Oithonids; small ambush-feeding omnivores), FG2 (Oncaeids; small
736 cruise-feeding detritivores) and FG1 (*Clausocalanus* spp.; small cruise-feeding omnivores-
737 herbivores). FG11 (*Acartia* spp. and *Centropages* spp.; small omnivorous mixed-feeders) also
738 contributes substantially to total copepod abundance in the northern Atlantic and Pacific
739 Oceans. Consequently, we encourage modelers to represent those three FGs more explicitly in
740 future global ecosystem models. Some additional groups show a higher relative abundance on
741 a regional scale, like FG4 in the tropics, or FG7 and FG9 in the Southern Ocean, which may
742 make these groups important for regional ecosystem modeling efforts. The remaining FGs
743 (FG3, 5, 6 and 8) display very low contributions to mean annual abundance, regardless of the
744 latitude and the sampling gear. Such groups might be of a lower priority for improving the
745 representation of zooplankton in marine ecosystem models. Nonetheless, these four FGs are

746 characterized by larger body sizes than FG1, 2 or 10 (Table S4.2) so their actual contribution
747 to biomass production could be substantially higher, especially FG6 which gathers the largest
748 filter-feeding Calanidae that are several millimeters longer than the species in FG1, FG2 or
749 FG10. Future work will help model the contribution of the present copepod FGs to
750 zooplankton biomass, and to clarify their relative priorities for inclusion in marine ecosystem
751 models.

752

753 4.2. Why do copepod functional traits show contrasting biogeographic patterns in the ocean?

754 We defined four main ocean regions according to their similarity in community-level
755 functional trait expression (Fig. 4a, Appendices S9 and S15). The first-order pattern
756 corresponded to the separation between those regions poleward to $\sim 45^\circ$ latitude (regions 3
757 and 4) and those equatorward to $\sim 45^\circ$ latitude (regions 1 and 2; Appendix S10). Then, two
758 key second-order patterns emerged: the regions south of the Antarctic Polar Front (region 4)
759 showed a community trait composition distinct than those of the other high latitudes (e.g., the
760 Arctic Ocean or the North Pacific Ocean), and the oligotrophic tropical gyres (region 2) were
761 separated from the boundary upwelling and the equatorial current systems (region 1). The
762 largest dissimilarity in community trait expression was found between regions 2 and 4 (Fig.
763 4b-m) and was driven by differences in CWM body size, myelination, carnivory and ambush-
764 feeding vs. current-feeding (Appendices S9, S10 and S15). These trait patterns emerge from
765 environment-based distribution models, so they reflect combinations of environmental
766 conditions, but they also reflect biological processes that lead to the selection of trade-offs
767 between traits through abiotic and/or biotic filtering. In other words, certain trait combinations
768 are more competitive than others under varying conditions of temperature or food availability
769 because of physiological constraints or because they lead to lower mortality rates (Litchman
770 et al., 2013; Barton et al., 2013; van Someren Gréve et al., 2017; McGinty et al., 2021).

771 Median copepod body size decreased from the poles to the equator with a slight increase in
772 upwelling systems. Such a pattern has been documented by other studies and is primarily
773 driven by the strong negative relationship between the body size of marine ectotherms and
774 temperature, according to Bergmann's rule (Brun et al., 2016; McGinty et al., 2018; Evans et
775 al., 2020; Brandão et al., 2021; Campbell et al., 2021). The precise processes underlying
776 Bergmann's rule remain debated, but it is likely that warmer temperatures (or a factor
777 confounded with temperature) decrease growth efficiency and/or promote the maturation of
778 adults at smaller body sizes (Atkinson 1994; Isla et al., 2008). Dissolved oxygen
779 concentration could also limit maximal body size in marine ectotherms under the "oxygen

780 hypothesis” (Audzijonyte et al., 2019), but so far temperature outperformed oxygen in
781 explaining variations in body size structure (Campbell et al., 2021).

782 Bergmann’s rule occurs at the intraspecific level and at the interspecific level, meaning that
783 warming-induced decreases in median body size can emerge if smaller clades replace larger
784 ones along a latitudinal gradient. Such a turnover in size classes has been observed as well
785 (Evans et al., 2020; Brandão et al., 2021) and is supported by our SDM projections. Indeed,
786 functional traits that represent shifts in clade composition (i.e., those that show strong
787 taxonomic clustering) such as myelination, spawning strategy, carnivory or feeding modes
788 displayed latitudinal gradients that are positively, or negatively, collinear with the body size
789 gradient (Appendices S9 and S10). The latitudinal patterns of these functional traits likely
790 result from changes in food availability, quality, and predation pressure that are known to
791 vary greatly from polar regions to tropical gyres (Brun et al., 2016; Horne et al., 2016; van
792 Someren Gréve et al., 2017; Roy, 2018).

793 Lipid-rich myelin sheaths enable a faster conduction of nerve responses. This promotes faster
794 reaction times and thus more efficient feeding or escape behaviors (Lenz, 2012). Myelin
795 sheaths are cholesterol-rich so they require larger metabolic investments of dietary lipids
796 (Lenz, 2012), which helps explain why copepod communities show larger proportion of small
797 amyelinated taxa in tropical gyres where smaller lipid-poor phytoplankton dominate (Roy,
798 2018). Therefore, it is not surprising that the proportions of myelinated species follow the
799 same spatial pattern as body size and current-feeding (Fig. 4b,c,j,m) and peak in productive
800 environments characterized by larger and lipid-rich plankton (Roy 2018).

801 Similarly, sac-spawning is a more energy-conservative spawning strategy as it reduces egg-
802 mortality at the cost of fecundity and hatching speed. The increased proportions of sac-
803 spawners in tropical gyres (Fig. 4d) could reflect an adaptation to limited food availability
804 (Kiørboe & Sabatini, 1994; Barton et al., 2013) and higher rates of carnivory (Fig. 4e;
805 Woodd-Walker et al., 2002) and egg cannibalism among copepods (Ohman & Hirche, 2001;
806 Segers & Taborsky, 2011). Furthermore, ambush-feeding is a passive feeding mode that
807 lowers predation risk and energy costs compared to current- and cruise-feeding, but at the
808 expense of feeding efficiency (Kiørboe, 2011a; van Someren Gréve et al., 2017).
809 Consequently, the increased proportion of ambush-feeders in region 2 (Fig. 4i) should also
810 result from trade-offs in functional traits expression driven by abiotic and biotic filtering
811 (Litchman et al., 2013), as oligotrophic gyres seem to promote food-webs with increased
812 carnivorous predation (Fig. 4e) and resource competition (Wood-Walker et al., 2002; Prowe,
813 Visser, Andersen, Chiba, & Kiørboe, 2019).

814 However, our approach is based on presence data and habitat suitability indices rather than
815 abundances, which likely underestimates the contribution of very abundant ambush-feeding
816 species like *Oithona similis* at high latitudes (Gallienne & Robins, 2001; Pinkerton et al.,
817 2010; Prowe, Visser, Andersen, Chiba, & Kiørboe, 2019). As a result, we probably
818 underestimate the proportion of ambush-feeders in regions such as the Southern Ocean
819 compared to Prowe et al. (2018), although these authors discarded other ambush-feeding
820 copepods such as the Corycaeidae (Benedetti et al., 2016; Brun et al., 2017). Together, these
821 elements support the fact that our modelled zooplankton functional traits patterns emerge
822 from interactions between environmental conditions and the relative fitness (i.e., trade-offs)
823 resulting from different trait combinations.

824 The climatological conditions used to train the SDMs are influenced by large scale oceanic
825 currents as highlighted by our regionalization analysis (Fig. 4). We found the boundaries of
826 the four main regions to overlap with the trajectories of well-known boundary currents as well
827 as equatorial counter currents and fronts. Unfortunately, we cannot disentangle the effects of
828 dispersal by currents on the observed community trait expression (and their modelled spatial
829 patterns) from the effects of gradients in temperature and/or productivity, which select species
830 based on their physiological requirements. Although ocean basin connectivity is rather high at
831 the scale of our study (Jönsson & Watson, 2016), dispersal by marine currents and mesoscale
832 processes are known to impact plankton community structure (Richter et al., 2020; Sommeria-
833 Klein et al., 2021). For instance, the Antarctic Polar Front seems to be the main delimiter
834 between regions 3 and 4, which coincides with the view that it imposes a strong physical
835 barrier on passively drifting zooplankton (Murphy et al., 2021). Yet, recent evidence showed
836 that many epipelagic plankton can cross Southern Ocean fronts thanks to the very dynamic
837 meandering eddies (Murphy et al., 2021), which could explain the deviations of the region 4
838 boundaries from the Antarctic Polar Front. Therefore, the gradient in community trait
839 expression separating regions 3 and 4 may also stem from the latitudinal gradient in
840 temperature and biogeochemical conditions that select species and their traits based on
841 physiological and metabolic constraints. Similarly, the gradients in CWM traits (i.e., the
842 poleward succession of regions 2, 1 and 3) modelled in the North Pacific and North Atlantic
843 Oceans could be driven by the temperature gradient or the presence of western boundary
844 currents (e.g., the Gulf Stream and the North Pacific Current) which carry southern warm-
845 water communities eastward while they are getting mixed with northern cold-water
846 communities. Such processes could explain why the CWM trait distribution of region 1 lies in
847 between those of regions 2 and 3 (Fig. 4). This uncertainty calls for more studies combining

848 distribution models with dispersal rates and limitations (D'Amen et al., 2018; Shipley et al.,
849 2021) to study the link between zooplankton functional traits and the “seascape” (Sommeria-
850 Klein et al., 2021; Richter et al., 2020).

851

852 4.3. Caveats and future directions

853 Our results are sensitive to the three main steps of our framework: (i) the way the species
854 were positioned in a functional space and how the FGs were defined from the latter, (ii) the
855 quantity and quality of the functional trait data considered, and (iii) the SDMs chosen to
856 generate the CWM traits values. We carefully investigated the sensitivity of our FGs
857 definition to alternative choices made in our clustering approach (Appendix S4). Most of the
858 comparable studies working with functional trait spaces rely on a Gower distance matrix and
859 a principal coordinate analysis (PCoA; Legendre & Legendre, 2012) to ordinate taxa as a
860 function of their trait combinations (see the synthesis by Mouillot et al., 2021). Here, we
861 relied on an alternative dimensionality reduction analysis (i.e., the FAMD) to avoid negative
862 eigenvalues (i.e., imaginary dimensions) and the relatively low levels of explained variance
863 that are often inherent to the use of a PCoA (Legendre & Legendre, 2012; Mouillot et al.,
864 2021). We assessed how using this alternative dimension reduction analysis affected the
865 quality of the functional trait space by computing the AUC criterion recommended by
866 Mouillot et al. (2021). We found an AUC value of 0.81, which is substantially higher than the
867 recommended 0.7 threshold and indicates a “high quality trait space” according to these
868 authors. In addition, the first four PCs of our FAMD explained nearly 80% of the variance in
869 species traits, which reinforces our confidence in the quality of our functional trait space.

870 Beyond the dimensionality reduction step, the choice of the distance matrix and aggregation
871 link could have been determining factors in drawing the functional dendrogram and thus
872 defining the FGs (Fig. 1). We evaluated the similarity between the functional dendrograms
873 emerging from alternative clustering approaches and found that they were all highly
874 positively correlated (mean Baker’s Gamma correlation coefficient was 0.75 ± 0.12 ;
875 Appendix S4). This indicates that all dendrograms displayed very similar structure and
876 explains how these dendrograms would have led to similar FGs composition. Ultimately, the
877 approach that combined the FAMD, an Euclidean distance matrix, and Ward’s aggregation
878 linkage was chosen as our standard approach, since it provided ecologically meaningful FGs
879 (i.e., groups that are neither too large and functionally heterogeneous nor too numerous and
880 functionally redundant).

881 The quantity and the quality of the species-level functional trait information considered for
882 our study largely determined the FGs and their ecological meaning. The traits chosen for this
883 study only cover a fraction of the traits mentioned in the literature (Litchman et al., 2013;
884 Brun et al., 2017; Appendix S3). Therefore, our study is likely underestimating the true
885 diversity of copepod functions and FGs present in the ocean. However, it could also be that
886 the present functional groups are quite representative of natural copepod communities and
887 that adding further traits would only subdivide those FGs into smaller and functionally
888 homogeneous ones. The trait compilation of Brun et al. (2017) included the following
889 additional functional traits: growth rate, clearance rate, ingestion rate, egg diameter and
890 production, or the production of resting eggs and diapausing stages throughout the life cycle.
891 Yet, the availability and the coverage of those traits remained too poor for the wide pool of
892 species studied here (Appendix S3), reflecting the historic measurement biases that largely
893 focused on larger Calanoida species such as *Calanus* spp. Since a broad range of metabolic
894 and physiological traits scale allometrically with body size (Kiørboe & Hirst, 2014),
895 additional traits could be inferred based on body size measurements and phylogenetic
896 distances (Molina-Veigas et al., 2018). It also implies that the present FGs characterized by
897 larger body sizes (e.g., FG5 and 6) should display larger metabolic rates. Further lab-based
898 and observation-based are needed to uncover the functional trait expression for a larger range
899 of copepod species and families.

900 Differences between model projections are the main source of uncertainty in species
901 community composition and diversity under a SDMs ensemble approach (Benedetti,
902 Guilhaumon, Adloff, & Ayata, 2018; Diniz-Filho et al., 2009). We found some regional
903 differences between the mean annual HSI projections of the SDMs. When considering all
904 copepod species together, the GLM estimated higher mean HSI than the two other model
905 types for the Southern Ocean (Appendix S8). Such variability could arise from how the
906 various SDMs cope with limited predictors and species occurrence availability in winter
907 conditions at the very high latitudes. Indeed, the copepod occurrence data (Appendix S1) and
908 the climatological satellite observations (e.g., PAR and logChl) have poor coverage at
909 latitudes $>60^\circ$ in winter. The sampling effort in the Southern Ocean is slightly lower than the
910 global average between April and October and is extremely low between May and September
911 (Appendix S1), and satellite-based PAR and chlorophyll-a measurements are not available for
912 winter months due to the low light levels at high latitudes. Therefore, our mean annual
913 projections for the polar oceans are likely more representative of summer conditions. Most
914 GLMs and GAMs included one or both of these satellite-based climatologies as predictors

915 (Appendix S6). Yet only GLMs showed these relatively high HSI levels in the Southern
916 Ocean. Plus, SST was found to be the most influential predictor in both SDMs types
917 (Appendix S6). This implies that this discrepancy between GLMs and GAMs was not driven
918 by predictor selection but rather by how the responses of the species to SST and logChla/PAR
919 gradients were captured by those two types of models (Merow et al., 2014). Here, the less
920 complex response curves of the GLMs lead to higher average HSI at very cold temperatures
921 compared to GAMs. The HSI patterns obtained from the GAM and ANN were closer to the
922 latitudinal diversity gradients that were previously observed and modelled for marine
923 ectotherms, which seldom show increases in richness or habitat suitability towards the poles
924 (Tittensor et al., 2010; Benedetti et al., 2021). Consequently, we have more confidence in the
925 GAM-based and ANN-based annual HSI estimates than in the GLM-based ones.

926 Interestingly, inter-SDMs variability was much lower when looking at CWM traits
927 projections rather than HSI patterns (Appendix S8). All three SDMs lead to very similar
928 spatial patterns in CWM traits and the amplitude of these CWM values differed only slightly.
929 The regions displaying higher CWM traits variability depended on the trait considered, and
930 variability remained quite low overall (but see Appendix S8). Therefore, the present CWM
931 traits patterns display relatively low uncertainty compared to the HSI patterns. The fact that
932 CWM body size and CWM myelination show very similar spatial patterns and ranges to the
933 respective estimates of Brun et al. (2016) gives us further confidence in our approach and
934 spatial projections.

935 To conclude, we recommend the inclusion of multiple functional groups of copepods in
936 marine ecosystem models, based on our functional dendrogram (Fig. 1), with a level of
937 complexity of zooplankton representation that should be modulated by the scientific question,
938 the FGs dominating community biomass at the scale of the study region(s), the traits of
939 interest, and computing efficiency constraints. Ideally, future global marine ecosystems, that
940 cannot efficiently include 10 zooplankton groups, will include a few (3-4) FGs that cover the
941 main gradients observed in trait space (Fig. 1; Appendix S12), niche space (Fig. 2),
942 geographical space (Figs. 3, 4; Appendices S9, S10) and that represent important fractions of
943 biomass (Appendix S16). This would divide copepods into a few but ecologically meaningful
944 groups with clearly distinct ecological niches and also functional trait characteristics. For
945 other ecological applications or to represent food-web interactions across trophic levels (Ward
946 et al., 2012; Serra-Pompei et al., 2020), these groups could be split into further FGs with
947 specific characteristics (e.g., size classes, high lipid content, grazing and mortality rates etc.).
948 To achieve this, future studies are required to improve the coverage of functional traits data

949 towards more taxonomic groups and more quantitative traits (Appendix S3). Ongoing
950 compilations of zooplankton groups biomass data will also help rank the importance of the
951 present FGs worldwide and across regions. Ultimately, the present results and future data
952 compilations will help us study global patterns of zooplankton functional diversity (Mouillot
953 et al., 2013), which may link more closely to ecosystem function and service provision than
954 taxonomic diversity. Marine ecosystems will experience increasingly stressful conditions in
955 the next century due to anthropogenic climate change (IPCC, 2021). This will strongly
956 restructure zooplankton community richness and composition as species migrate poleward to
957 track suitable habitats (Benedetti et al., 2021). How these changes will impact functional trait
958 expression and functional diversity at the community-level remains too poorly understood.
959 The present study is thus a key step towards our understanding of how future climate change
960 will reshape the expression of marine functional diversity worldwide.

961

962 *Data Availability Statement*

963 The copepod species occurrences data used to train the species distribution models are
964 publicly available on Zenodo (10.5281/zenodo.5101349). The newly implemented species-
965 level functional trait table is available as Table S2 and will be made available through an open
966 access repository upon publication of our study. Any computer code used to generate the
967 results of the study are freely available upon request to the authors and all R codes are
968 currently stored on the GitHub account of J.W. (<https://github.com/jonas-wydlar>).

969

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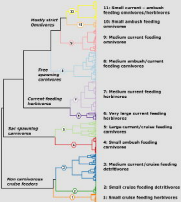
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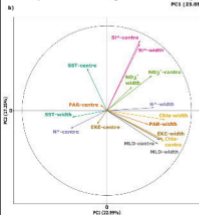
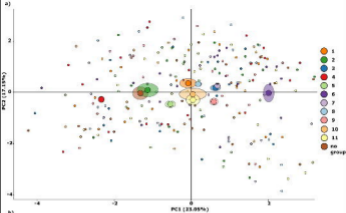
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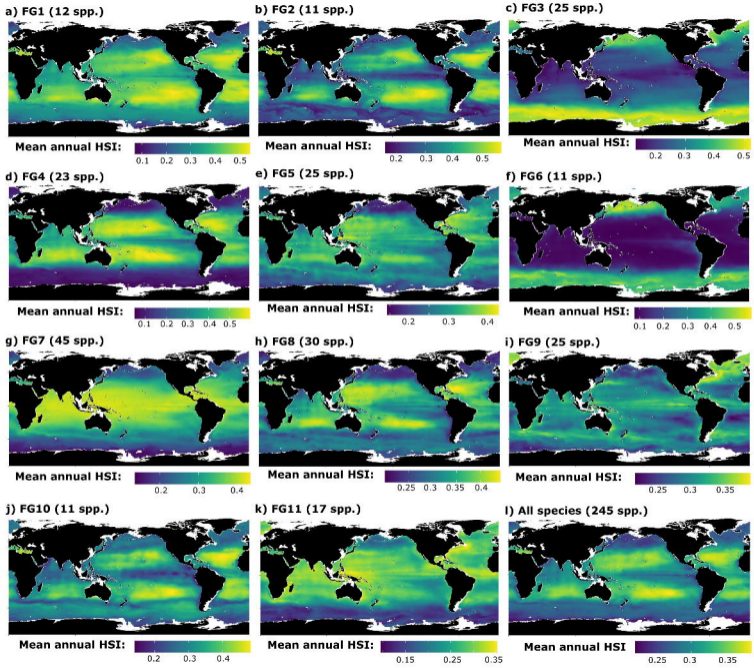
1208 *Biosketch*

1209 **Fabio Benedetti** is a postdoctoral researcher and **Meike Vogt** a senior research scientist in
1210 the Environmental Physics (UP) group of ETH Zürich. Both share broad interests in plankton
1211 biogeography and functional diversity and their links with biodiversity, ecosystem function
1212 and biogeochemical cycles in the global ocean. F.B. is a macroecologist specialized in trait-
1213 based approaches and plankton diversity modelling. M.V. is a marine ecosystem modeler
1214 specialized plankton functional types. **Jonas Wydler** has successfully completed his MSc
1215 degree in Environmental System Sciences at ETH Zürich, under the supervision of F.B. and
1216 M.V., which is the subject of this work.

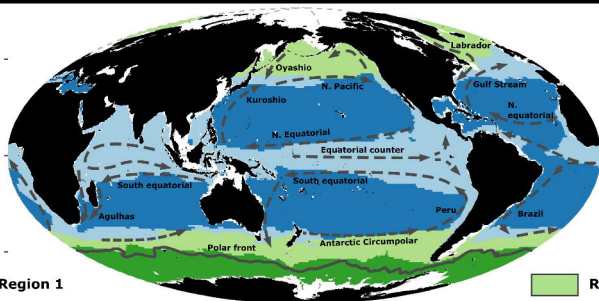
1217 F.B. and M.V. co-designed the study and F.B. collated the data used in the analyses and
1218 provided expertise with regard to every methodology used. J.W. conducted the numerical
1219 analyses and wrote the first version of the manuscript under the supervision of F.B. and M.V.
1220 F.B. wrote the final version of the manuscript with input from both M.V. and J.W.







a)



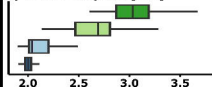
Region 1

Region 2

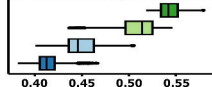
Region 3

Region 4

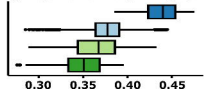
b) Median body size [mm]



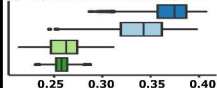
c) Proportion of myelinated species



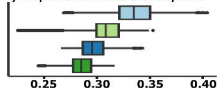
d) Proportion of sac spawning species



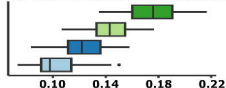
e) Proportion of carnivorous species



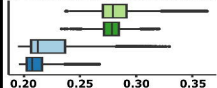
f) Proportion of herbivorous species



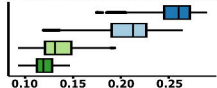
g) Proportion of detritivorous species



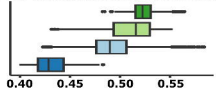
h) Proportion of omnivorous species



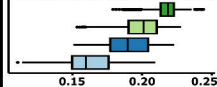
i) Proportion of ambush-feeding species



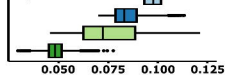
j) Proportion of current-feeding species



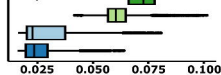
k) Proportion of cruise-feeding species



l) Proportion of current-ambush-feeding species



m) Proportion of current-cruise-feeding species



This study	Main clade	Group definition	Pomerleau et al. (2015) - North Pacific Ocean	Benedetti et al. (2016) - Mediterranean Sea	Benedetti et al. (2018) - Mediterranean Sea	Becker et al. (2021) - South Atlantic Ocean
FG1	Clausocalanus	Small myelinated cruise-feeding omnivores-herbivores	Small current- and cruise-feeding omnivore-herbivores (Group 6)	Small cruise-feeding omnivores-herbivores (subset of Group 6)	Small cruise-feeding omnivores-herbivores (Group 7)	Small and large myelinated cruise- and current-feeding omnivores-herbivores (subset of Group B)
FG2	Oncacidae	Small non myelinated cruise-feeding detritivores	No equivalent	Small cruise-feeding omnivores-detritivores (subset of Group 6)	Small sac-spawning detritivores (subset of Group 5)	Small amyelinated ambush- or cruise-feeding carnivores or detritivores (small subset of Group D)
FG3	Spinocalanus, Scaphocalanus, Metridia	Medium-sized myelinated mixed-feeding or cruise-feeding detritivores	No equivalent	Small cruise-feeding omnivores-detritivores (subset of Group 6)	Small sac-spawning detritivores (small subset of Group 5)	No equivalent
FG4	Corycaecidae	Small amyelinated ambush-feeding carnivores	No equivalent	Small ambush-feeding carnivores (Group 2)	Small ambush-feeding carnivores (Group 2)	Small amyelinated ambush- or cruise-feeding carnivores or detritivores (small subset of Group D)
FG5	Sapphirinidae, Euchaetidae	Large current- or cruise-feeding carnivores	No equivalent	Large cruise-feeding carnivores (Group 1)	Large cruise- or current-feeding feeding carnivores (Group 1)	Small and large myelinated cruise- and current-feeding omnivores-herbivores (subset of Group B)
FG6	Calanus, Eucalanus	Very large myelinated current-feeding omnivores-herbivores	No equivalent	No equivalent	No equivalent	No equivalent
FG7	Calanus, Paracalanus, Calocalanus	Medium-sized myelinated current-feeding omnivores-herbivores	Small and large current-feeding omnivores-herbivores (Group 5c)	Small and large current-feeding omnivores-herbivores (Group 4)	Small and large current-feeding omnivores-herbivores (Groups 3 and 4)	Large myelinated current-feeding omnivores-herbivores (subset of Group C)
FG8	Cardacia, Haloptilus, Heterorhabdus	Medium-sized amyelinated ambush- or current-feeding carnivores	No equivalent	Large cruise-feeding carnivores (Group 1)	Large cruise- or current-feeding feeding carnivores (Group 1)	No equivalent
FG9	Pleuromamma, Gaetanus, Labidocera	Medium-sized amyelinated current-feeding omnivores	No equivalent	Small and large current-feeding omnivores-herbivores (subset of Group 4)	Small and large current-feeding omnivores-herbivores (small subset of Group 4)	No equivalent
FG10	Oithonidae	Small amyelinated ambush-feeding omnivores	No equivalent	Small ambush-feeding omnivores (Group 5)	Small ambush-feeding omnivores (Group 6)	Small amyelinated mixed- or ambush-feeding omnivores (Group A)
FG11	Acartia, Centropages	Small amyelinated mixed-feeding omnivores	Small ambush-feeding omnivores (subset of Group 4)	Small mixed-feeding omnivores (Group 3)	Small mixed-feeding omnivores (small subset of Group 4)	Small amyelinated mixed- or ambush-feeding omnivores (Group A)