



## Trait biogeography of marine copepods - an analysis across scales

**Brun, Philipp Georg; Payne, Mark R; Kiørboe, Thomas**

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1 **Trait biogeography of marine copepods – an analysis across scales**

2 Running title (45 char): Trait biogeography of marine copepods

3 Philipp Brun<sup>1,\*</sup> Mark R. Payne<sup>1,a</sup>, and Thomas Kiørboe<sup>1,b</sup>

4 <sup>1</sup> Centre for Ocean Life, National Institute of Aquatic Resources, Technical University of  
5 Denmark, Kavalergården 6, DK-2920 Charlottenlund, Denmark

6 \* Corresponding author:

7 Email: pabr@aqu.dtu.dk

8 Phone: +45 35 88 34 80

9 Fax +45 35 88 33 33

10 a mpay@aqu.dtu.dk

11 b tk@aqu.dtu.dk

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## **Abstract**

26           Functional traits, rather than taxonomic identity, determine the fitness of individuals  
27 in their environment: traits of marine organisms are therefore expected to vary across the  
28 global ocean as a function of the environment. Here, we quantify such spatial and seasonal  
29 variations based on extensive empirical data and present the first global biogeography of key  
30 traits (body size, feeding mode, relative offspring size and myelination) for pelagic copepods,  
31 the major group of marine zooplankton. We identify strong patterns with latitude, season, and  
32 between ocean basins that are partially (approximately 50%) explained by key environmental  
33 drivers. Body size, for example, decreases with temperature, confirming the temperature-size  
34 rule, but surprisingly also with productivity, possibly driven by food-chain length and size-  
35 selective predation. Patterns unrelated to environmental predictors may originate from  
36 phylogenetic clustering. Our maps can be used as a test-bed for trait-based mechanistic  
37 models and to inspire next generation biogeochemical models.

38

## 39            **Introduction**

40            Studying the distribution and abundance of organisms is the key task in ecology  
41 (Begon *et al.* 2006). In recent decades, the growing availability of observational data and  
42 empirical models has increasingly allowed the pursuit of this task on large spatial scales. In  
43 particular the distribution patterns of individual species and their links to the physical  
44 environment have been studied intensively (Elith & Leathwick 2009). However, a major  
45 challenge for such macro-scale studies is the mechanistic linking of the observed patterns to  
46 the processes that drive them (Keith *et al.* 2012). One powerful way to identify such links is  
47 the trait-based approach, because the functional traits of an organism, rather than its  
48 taxonomic identity, determine its fitness in a given environment. The trait-based approach  
49 assumes that organism fitness is based on success in the fundamental life missions feeding,  
50 survival and reproduction, and that the outcome of each of those missions depends on a few  
51 key traits. These key traits are interrelated through trade-offs and their optimal expression is  
52 determined by the environmental conditions (Litchman *et al.* 2013).

53            The trait-based approach in biogeography is well established for primary producers  
54 but its potential for animals has rarely been exploited. The trait-based approach has a long  
55 tradition in plant ecology (e.g., Westoby *et al.* 2002) and has also been used to describe the  
56 distributions of phytoplankton (e.g., Edwards *et al.* 2013). Besides providing ecological  
57 insight, trait biogeographies have fostered a more realistic incorporation of primary producers  
58 into global vegetation and ocean circulation models and thus have advanced biogeochemistry  
59 and climate science research (Scheiter *et al.* 2013; Brix *et al.* 2015). However, trait  
60 biogeographies for animals are uncommon, although they may be equally valuable. This is  
61 particularly evident for marine zooplankton, and their dominant members, the copepods

62 (Barton *et al.* 2013b). Marine copepods are ubiquitous, typically dominate the biomass of  
63 zooplankton communities, and play a key role in pelagic food webs (Verity & Smetacek  
64 1996). For this group traits and associated trade-offs are relatively well understood (Kiørboe  
65 2011) and comparably rich observational data exists (O'Brien 2010).

66       Key traits for copepods include body size, feeding mode, relative offspring size, and  
67 myelination of the nerves, determining both their fitness and their impact on the ecosystem.  
68 Body size governs most vital rates and biotic interactions (Kiørboe & Hirst 2014) and affects  
69 marine food webs and carbon fluxes (Turner 2002; García-Comas *et al.* 2016), feeding mode  
70 determines feeding efficiency and associated predation risk (Kiørboe 2011), relative offspring  
71 size determines the success in recruitment in a given environment (Neuheimer *et al.* 2015),  
72 and myelination of the nerves is one aspect of predator defense (Lenz 2012) (Box 1).

73       The aim of this study is to establish large-scale copepod trait biogeographies,  
74 including the first ever global analyses. In addition, we tested two hypotheses: (H1) Between-  
75 community trait variation is structured in space and time, i.e., trait distributions can be largely  
76 described by assuming that they are more similar to neighboring communities than to distant  
77 communities. (H2) These spatiotemporally dependent structures form in response to key  
78 environmental drivers including food availability, temperature, water transparency, and  
79 seasonality, as suggested in Box 1. We combined information on traits for hundreds of  
80 marine pelagic copepod taxa with two of the most extensive sets of observational data for  
81 copepods, covering the North Atlantic and the global ocean. We demonstrate distinct  
82 spatiotemporal trait biogeographies for most traits that can be partly explained by  
83 environmental drivers, and partly, such as in the case of differences between ocean basins, as  
84 a result of other structuring processes.

## 85 **Methods**

### 86 **Overview**

87 The analyses consisted of two steps. Firstly, we combined copepod trait information  
88 with field observations of copepod occurrences, defined communities, and summarized those  
89 using summary statistics. We combined trait information with two observational datasets with  
90 different resolutions in space and time: the North Atlantic with seasonal resolution, and the  
91 global ocean without temporal resolution. Secondly, we used statistical models to test our  
92 hypotheses, to investigate the spatial/spatiotemporal patterns of trait distributions, and to  
93 analyze their relationship with the environment.

### 94 **Trait data**

95 Trait data originated from a collection of literature information on functional traits for  
96 marine copepods (Brun *et al.* 2016). Where multiple measurements were available per  
97 species, we took species-specific averages. We used body size measurements from adults  
98 irrespective of the life stage of the observed individuals and thus estimated an upper  
99 boundary of potential body size. In the global analysis, information on mixed feeding was not  
100 sufficient to characterize the communities, and we therefore only distinguished between  
101 active feeders and passive feeders, considering mixed feeding taxa as active feeders.

### 102 **Observational data**

#### 103 *North Atlantic*

104 Data from the Continuous Plankton Recorder (CPR) survey was used to estimate the  
105 spatiotemporal distributions of North Atlantic copepods. The CPR survey is a large-scale

106 monitoring program of North Atlantic plankton, particularly copepods, diatoms and  
107 dinoflagellates (Richardson *et al.*, 2006). The CPR is towed by ships of opportunity at  
108 approximately 7 m depth. Each CPR sample corresponds to 10 nautical miles and around 3  
109 m<sup>3</sup> of seawater filtered onto a 270 µm-sized silk gauze. We used roughly 49 000 observations  
110 of 67 copepod taxa resolved into abundance classes that have been classified by the CPR  
111 survey between 1998 and 2008 (Johns 2014, Appendix A).

112 Observations of CPR taxa were matched with taxon-specific trait estimates. Not all  
113 taxa sampled in the CPR were resolved to the species level. Traits for higher order taxa were  
114 represented by the traits of the most common species in that group, as reported in Richardson  
115 *et al.* (2006). Where no information about the most common species was available, we  
116 averaged traits of all species in the taxon that have been repeatedly observed in the study  
117 area, according to the OBIS database ([www.iobis.org](http://www.iobis.org), Appendix A). Available trait  
118 information largely covered the estimated biomass of observed taxa in the North Atlantic  
119 (Table 1).

## 120 ***Global***

121 For the global analysis we used data from the Coastal and Oceanic Plankton Ecology,  
122 Production and Observation Database (COPEPOD), which contains abundance information  
123 for various plankton groups (O'Brien 2010). This data is compiled from a global collection of  
124 cruises, projects, and institutional holdings. Data for copepods consisted of roughly one  
125 million observations distributed across the global ocean. We updated the taxonomic  
126 classification of the observations according to the most recent online taxonomy  
127 (<http://www.marinespecies.org/copepoda/>) and utilized only data with abundance information  
128 and taxonomic resolution at the genus level or higher. In a few cases, we also included pooled  
129 observations for two genera, describing their traits based on the first genus mentioned.

130 Furthermore, we filtered for observations taken in the top 200 meters of the water column and  
131 excluded parasitic taxa. While the absolute number of observations lost through the filtering  
132 was minor, observations were removed from most of the Pacific, particularly because of  
133 lacking taxonomic resolution of data from this area.

134 Observations were matched with corresponding trait information. Traits at the genus  
135 level were estimated as means of the available estimates for their species. For all traits,  
136 match-ups were possible for most of the estimated abundance (Table 1).

137 COPEPOD data were spatially binned and an expected abundance was estimated for  
138 the taxa present. Unlike the CPR data, COPEPOD observations do not have a homogeneous  
139 sampling design and no standardized catalogue of taxa was targeted. We therefore split the  
140 global ocean into roughly 5000 polygons of similar area, and estimated trait-statistics  
141 polygon-wise. For each polygon, we used geometrical means to estimate the relative  
142 abundance of each taxon present for which trait information existed.

### 143 *Summarizing community traits*

144 Community traits were summarized by mass-weighted means and, for body size, also  
145 by the Shannon size diversity index. Biomass-weighted means were estimated by using the  
146 cubed body length estimates as biomass proxies. In addition, we quantified body-size  
147 diversity in copepod communities using the Shannon size diversity index. Body-size diversity  
148 characterizes the diversity of size classes within a community, which has been related to  
149 food-web properties (García-Comas *et al.* 2016). Furthermore, it indicates whether copepod  
150 communities are affected by environmental filtering. The Shannon size diversity index ( $\mu$ ) is  
151 analogue to the Shannon diversity index but computed on the probability-density function of  
152 a continuous-random variable (Quintana *et al.* 2008). It is estimated as



153 
$$\mu = - \int_0^{+\infty} p_x(x) \log_2 p_x(x) dx$$
 1

154 where  $p_x(x)$  represents the probability density function of size  $x$ .

155 We estimated  $\mu$  non-parametrically with the Monte Carlo kernel estimation technique  
156 (Quintana *et al.* 2008). Shannon size diversity was calculated for all polygons with at least 5  
157 observed taxa. The corresponding probability density functions were estimated by weighting  
158 the body sizes with the mass fractions of the species present. The Shannon size diversity  
159 index is primarily suitable for comparisons between communities.

## 160 **Environmental data**

161 Environmental variables considered are proxies for the key factors of temperature,  
162 available amount of food, prey size, seasonality, and water transparency (Box 1). For  
163 temperature, we used the monthly sea surface temperature (SST) data HadISST1 from the  
164 Hadley Centre for Climate Prediction and Research, Meteorological Office (Rayner *et al.*  
165 2003). Available amount of food was characterized with satellite-derived monthly estimates  
166 of net primary productivity (NPP) obtained from  
167 <http://www.science.oregonstate.edu/ocean.productivity> based on the VGPM algorithm  
168 (Behrenfeld & Falkowski 1997). Median phytoplankton cell diameter (MD<sub>50</sub>) was used as  
169 proxy for prey size, prey motility, and food quality including lipid content. Flagellates of  
170 intermediate size typically have a higher motility and lipid content than large-celled diatoms  
171 or small bacterioplankton (Kleppel 1993; McManus & Woodson 2012). Although not all  
172 copepods feed solely on phytoplankton, phytoplankton cell size has a strong impact on the  
173 entire food web (Barnes *et al.* 2011). MD<sub>50</sub> was estimated based on empirical relationships  
174 with SST and chlorophyll *a* concentration (CHL) (Barnes *et al.* 2011; Boyce *et al.* 2015),  
175 where we used the monthly GlobColour CHL1 product (<http://www.globcolour.info/>) to

176 represent CHL. Seasonality manifests itself in various ways including photoperiod,  
177 temperature, and available diet. For copepods the most immediate impact of seasonality is  
178 arguably the food availability. We therefore characterized seasonality by the seasonal  
179 variation in chlorophyll *a* concentration, applying the Shannon size diversity index on the  
180 CHL data (as this index is suitable to estimate the diversity of any non-negative, continuous  
181 variable). Water-column transparency was approximated by Secchi Depth (ZSD), represented  
182 by the monthly GlobColour ZSD product. For NPP, data from the period 2003-2008 was  
183 considered; for all other predictors, the period considered was 1998-2008.

184 Environmental variables were aggregated to match the resolution of the copepod  
185 communities. For the North Atlantic analysis we produced  $1^{\circ} \times 1^{\circ}$  monthly means for each  
186 year for SST, MD<sub>50</sub>, and ZSD. Since we did not have a complete temporal coverage for NPP,  
187 we matched the observations with monthly averages based on the years 2003-2008. CHL  
188 seasonality was calculated for each year independently and matched with all months of that  
189 year. For the global models, we aggregated the predictors by the polygons used to define the  
190 copepod communities, including the entire time-span of data availability. For computational  
191 efficiency, and to avoid numerical problems, all environmental variables were discretized to  
192 200 equally-spaced steps, normalized and standardized. Note that particularly on the global  
193 scale, some of the predictors showed significant Pearson correlation coefficients (*r*) up to  
194  $r=0.86$  for SST and MD<sub>50</sub> (Appendix B). However, the analyses performed here are largely  
195 insensitive to collinearity (Dormann *et al.* 2012).

## 196 **Statistical modelling**

197 The integrated nested Laplace approximation (INLA) approach is a novel and  
198 computationally-efficient Bayesian statistical tool that is particularly powerful in handling

199 spatial and spatiotemporal correlation structures (Rue *et al.* 2009; Blangiardo & Cameletti  
200 2015). We used the INLA approach to model each trait for both observational datasets as a  
201 function of i) space (and season), ii) environmental predictors, and iii) as a combination of i)  
202 and ii). We modeled the continuous traits (body size, body-size diversity, and relative  
203 offspring size) assuming *t*- and normal-distributions for the North Atlantic and the global  
204 models, respectively. The categorical traits (feeding modes and myelination) were modeled  
205 assuming beta-binomial and binomial distributions, respectively, both of which require a  
206 number-of-trials parameter. For the North Atlantic models we defined the numbers of trials  
207 by the total counts of individuals per sample and the number of positives was estimated by  
208 the weight fraction of these counts showing the trait in question. In the global models, the  
209 number of trials was held constant at one. The fitted models were used to map the trait  
210 distributions, investigate the relationships between traits and environmental predictors, and to  
211 compare the amount of variance explained by the three model set-ups.

### 212 *Spatial and spatiotemporal models*

213 Spatial and spatiotemporal models were constructed assuming distributions of traits to  
214 have a spatially- and temporally-dependent structure. We assumed trait distributions to be  
215 isotropic, stationary Gaussian Fields which are approximated with discrete meshes in INLA  
216 (Blangiardo & Cameletti 2015). We constructed a spatial mesh for each domain and an  
217 additional seasonal mesh for the North Atlantic (Appendix C). Furthermore, we  
218 complemented the North Atlantic models with a random effect correcting for variations  
219 between the years analyzed.

### 220 *Environmental models*

221           The environmental modeling approach used is equivalent to ecological niche models,  
222 but applied to community properties rather than individual species. For each trait and both  
223 observational datasets we fitted models for all possible combinations of the candidate  
224 predictors. The predictors were fitted as smooth, non-linear effects using second-order  
225 random-walk models (Rue *et al.* 2009), an approach similar to common generalized additive  
226 models (GAMs; Wood 2006) where the non-parametric response form of each predictor is  
227 determined by the data. Based on these models we assessed the best predictor combination  
228 for each trait according to the minimum Watanabe-Akaike information criterion (WAIC), a  
229 modified version of the Akaike Information Criteria that is appropriate for use with mixed-  
230 effects models (Gelman *et al.* 2014). We further used the univariate environmental models to  
231 investigate trait-environment relationships: univariate models were chosen over multivariate  
232 models to prevent distortions due to collinear predictors (Dormann *et al.* 2012).

### 233           ***Combined models***

234           “Combined” models were created by adding spatial/spatiotemporal structures to the  
235 best environmental models (Blangiardo & Cameletti 2015).

### 236           **Evaluation of hypotheses**

237           Both of our hypotheses focused on between-community variance of traits. The  
238 existence of such variance was confirmed in a preliminary assessment (Appendix D).  
239 Hypothesis H1 (community traits are spatially structured) was then tested by quantifying the  
240 fraction of variance explained ( $R^2$ ) by spatial/spatiotemporal models, and hypothesis H2  
241 (spatial structure is explained by key environmental drivers) was evaluated by comparing the  
242  $R^2$  of the best environmental models with the  $R^2$  of the combined models.



## 244           **Results**

### 245           **Evaluation of hypotheses**

246           All traits examined showed distinct structure in space and time, both globally (no  
247 temporal resolution) and in the North Atlantic, confirming our hypothesis H1. Our spatial and  
248 spatiotemporal models could explain substantial fractions of the between-community trait  
249 variance based on the spatial dependency assumption. This was particularly true for global  
250 patterns, where  $R^2$  of spatial models ranged from 0.36 for active feeding to 0.75 for body size  
251 (Figure 1a). In the North Atlantic, the spatiotemporal models were somewhat less efficient  
252 for the more finely-resolved communities of the CPR observations and ranged from  $R^2=0.32$   
253 for body-size diversity to  $R^2=0.48$  for body size (Figure 1b).

254           Our second hypothesis, that we can explain these spatial patterns with key  
255 environmental drivers, proved partially valid. On average, environmental models (green bars  
256 in Figure 1c,d) reached approximately half of the  $R^2$  of combined models (yellow bars in  
257 Figure 1c,d), indicating that about half the patterns in the investigated traits could be  
258 explained by the environmental predictors hypothesized to be important. The ratio between  
259  $R^2$  for environmental models and  $R^2$  for combined models was somewhat higher in the global  
260 domain and peaked at 78% for the global myelination model. Similarly, body size and body-  
261 size diversity could be explained relatively well by the environment, with corresponding  
262 percentages well above the 50% in both domains. For active feeding, on the other hand,  
263 environmental models performed relatively poorly and could only explain minor fractions of  
264 the identified patterns.

### 265           **Trait distributions**

266            *Seasonal variation in trait distributions in the North Atlantic*

267            All traits examined showed seasonally-varying distribution patterns. Mean community  
268 body size varied substantially and mainly ranged between 1 and 5 mm in the North Atlantic  
269 (Figure 2a-d), corresponding to a two order-of-magnitude variation in body mass.  
270 Communities with the largest mean body size occurred from spring to autumn in the  
271 northwestern North Atlantic, in particular in the Labrador Sea (Figure 2b-d). Smallest  
272 community-averaged body size was observed in the central and eastern part of the  
273 investigated area, mainly during summer (Figure 2c). From spring to autumn, steep spatial  
274 gradients in body size existed while the distribution was mostly uniform during winter.

275            The diversity of body size in copepod communities was estimated to be highest in  
276 winter when values were evenly distributed throughout most of the investigated domain  
277 (Figure 2e). In spring and autumn, body-size diversity was similarly high in the central North  
278 Atlantic, but smaller in the coastal areas in the east and the west (Figure 2f,h). Lowest body-  
279 size diversity was found in summer in the entire investigated area, except for the  
280 northwestern North Atlantic around the Labrador Sea (Figure 2g).

281            Active feeding was estimated to be the dominant feeding mode in the North Atlantic.  
282 This was particularly true for winter and spring, where, apart from a few exceptions along the  
283 coasts, the communities consisted of at least 66% active feeders (Figure 2i,j). In the eastern  
284 part of the investigated area, including the northwestern European coasts, this dominance of  
285 active feeders was reduced during summer and autumn and often replaced by a co-dominance  
286 of mixed and active feeders (Figure 2k,l).

287            Myelinated copepods dominated the communities in the North Atlantic overall, yet  
288 there was considerable spatiotemporal variation. In winter, myelinated and amyelinated

289 fractions were roughly in balance, except for the northern central part of the investigated area,  
290 where the communities were almost exclusively amyelinated (Figure 2m). The patterns  
291 changed markedly in spring when the dominance of myelinated copepods was the greatest,  
292 foremost in the northern part of the investigated area (Figure 2n). In summer, and particularly  
293 in autumn, the fraction of amyelinated copepods increased again, mainly along the coasts and  
294 in the southern and eastern part of the investigated area (Figure 2o,p).

295 On the community level, egg-size varied on average between about 4.5% and 7.5% of  
296 the body size of adult females in the North Atlantic. Highest relative offspring size was  
297 observed during winter months in the central part of the investigated area (Figure 2q). In  
298 spring, relative offspring size was smaller, in particular in the northwestern North Atlantic,  
299 while it gradually increased toward the southeastern part of the investigated area (Figure 2r).  
300 In summer and autumn relative offspring size showed a patchy distribution with less variation  
301 (Figure 2s,t).

### 302 *Global trait distributions*

303 The traits investigated also showed clear spatial patterns on the global scale. Mean  
304 body size mainly ranged between 1.5 and 7 mm for communities observed in the global  
305 ocean (polygons in Figure 3). Largest body sizes were found at high latitudes above 50°,  
306 except for the North Atlantic where communities with intermediate body size extended  
307 somewhat further northward (Figure 3a). According to the best environmental model, the  
308 latitudes with the smallest body size were found in the subtropics while around the equator  
309 the mean body size was slightly larger. The smallest body sizes were found in the subtropical  
310 central Atlantic, 2-3 mm, whereas communities at similar latitudes in the Indian Ocean  
311 tended to have larger mean body sizes, around 3-4 mm. Myelination was distributed similarly  
312 to body size (pixel to pixel Spearman correlation coefficient,  $r_{spearman}=0.84$ ) but with more



313 small-scale variation (Figure 3b): at high latitudes myelinated copepods dominated, while at  
314 low and intermediate latitudes myelinated and amyelinated taxa were similarly abundant.  
315 Again, the central Atlantic differed from the Indian Ocean with a lower fraction of  
316 myelinated organisms. Relative offspring size was inversely proportional to body size  
317 ( $r_{spearman}=-0.69$ ) and myelination ( $r_{spearman}=-0.65$ ). In the global ocean relative egg sizes  
318 varied between about 3% and 8%, with the relatively largest eggs at low latitudes and the  
319 relatively smallest eggs at high latitudes (Figure 3c).

## 320 **Trait-environment relationships**

321 Environmental responses of most traits were comparable between the global ocean  
322 and the North Atlantic analyses (Figure 4), although they tended to be weaker in the North  
323 Atlantic. Highest body size was found at low NPP, intermediate phytoplankton cell size and  
324 low SST (Figure 4a-c). While globally only intermediate chlorophyll seasonality favored  
325 copepod communities with large body size, in the North Atlantic these communities were  
326 also found at low CHL seasonality (Figure 4d). Communities with high body-size diversity  
327 were most common in environments with low NPP, CHL seasonality and phytoplankton cell  
328 size (Figure 4e,f,h). Furthermore, high body-size diversity was found at the high and the low  
329 end of the temperature spectrum, while temperatures around 10°C were associated with the  
330 lowest diversity (Figure 4g). On the global scale, the best model for body-size diversity did  
331 not include CHL seasonality. The weight fraction of myelinated copepods was highest in  
332 environments with low NPP, and intermediate Secchi Depth (Figure 4i-k). In the global  
333 ocean the fraction of myelinated copepods increased with phytoplankton cell size, while in  
334 the North Atlantic it peaked at a median cell size of around 6  $\mu\text{m}$  and rapidly decreased with  
335 larger phytoplankton. Finally, relative offspring size was smallest for low NPP, intermediate  
336 phytoplankton cell size and relatively short Secchi Depths of 5-25 m (Figure 4l-n). The best

337 global model for relative offspring size did not include Secchi Depth. WAIC values for all  
338 model combinations of traits and environmental predictors can be seen in Appendix G.

339

340

## Discussion

341 Our analysis of copepod trait distributions revealed a wealth of strong patterns along  
342 several spatial and temporal gradients. Most of these patterns were consistent with the  
343 literature or comparable to the trait distributions of other organism groups, yet there were  
344 some surprising findings too. Several traits showed considerable latitudinal variation. For  
345 example, mean body size was clearly larger at high latitudes than at low latitudes, while it  
346 was smallest in the subtropics, and slightly larger around the equator. This pattern is  
347 equivalent to the distribution of phytoplankton cell size, and, along the Atlantic Meridional  
348 Transect, to the distribution of body size of total zooplankton (San Martin *et al.* 2006; Boyce  
349 *et al.* 2015). Relative offspring size also changed significantly with latitude and was highest  
350 in the subtropics and tropics, paralleling the distribution of seed mass in terrestrial plants  
351 (Moles & Westoby 2003). Trait distributions also showed strong seasonal dynamics. For  
352 example, body size in the North Atlantic varied considerably throughout the season with  
353 largest copepods in March and April. Similar dynamics have been found for diatoms in the  
354 same area, with the largest mean cell size between January and March (Barton *et al.* 2013a).  
355 More unexpected were the clear differences between the central Atlantic and the Indian  
356 Ocean found in all traits investigated. This difference was unrelated to the known  
357 environmental parameters and has not been found in phytoplankton trait distributions (Barnes  
358 *et al.* 2011).

359 A substantial fraction of the spatial and temporal patterns could be linked to the  
360 environmental predictors investigated. While temperature seemed to affect copepod traits  
361 directly, productivity may influence them in more complex ways. It is well established for  
362 both terrestrial and aquatic organisms that within species, body size is inversely related to

363 temperature (Forster *et al.* 2012), and this also applies to copepods (Horne *et al.* 2016). Our  
364 results demonstrate that this relationship also holds on the community level. However, body  
365 size changed relatively little with increasing temperature when compared to its steep decline  
366 with increasing productivity. A negative relationship between body size and productivity is  
367 surprising: many groups of marine fish and terrestrial mammals grow larger in areas of higher  
368 productivity (Huston & Wolverton 2011), and the same was found for copepods in laboratory  
369 experiments (Berggreen *et al.* 1988). For copepods in the field this may be different due to  
370 size-selective predation by planktivorous fish (Brucet *et al.* 2010), which are particularly  
371 abundant in productive ecosystems like upwelling regions (Cury *et al.* 2000). Furthermore, in  
372 oligotrophic open ocean areas planktonic food chains tend to be longer (Boyce *et al.* 2015).  
373 Thus, although copepods at the same trophic level may be smaller in areas with low  
374 productivity, the mean body size of the entire copepod community may be larger.

375         In contrast to body size, relative offspring size was positively correlated with NPP,  
376 possibly in response to stronger biotic interactions. Large offspring size is often seen as an  
377 adaptation to harsh environments (Segers & Taborsky 2011), and therefore a positive  
378 correlation between relative offspring size and productivity may seem surprising at first sight.  
379 However, few offspring and comparably high investments in each individual are also  
380 characteristics of K-selected species, which live in densely populated communities  
381 (MacArthur & Wilson 1967). In this case, relatively larger offspring may be better in  
382 competing for resources and avoiding predation, as has been found for fish: fish fry from  
383 large eggs are more tolerant to starvation, avoid predation risks more consequently, and have  
384 larger reaction distances to potential predators (Miller *et al.* 1988; Segers & Taborsky 2011).  
385 Similarly in terrestrial plants, seed mass is positively correlated to NPP (Moles & Westoby  
386 2003).

387 About half of the identified spatiotemporal patterns could not be explained by the  
388 environmental predictors, but arose from other structuring processes. Some of these  
389 unexplained patterns occurred on large spatial scales, where the most-pronounced and  
390 surprising differences occurred between the central Atlantic and the Indian Ocean. On these  
391 scales evolutionary history may affect trait distributions. The distribution range of copepod  
392 species is limited by their ability to maintain viable populations (Norris 2000), although, in  
393 principle, water parcels can travel between any pair of locations in the global ocean within a  
394 decade (Jönsson & Watson 2016). Patterns unexplained by the environmental predictors also  
395 occurred on smaller spatial scales in the North Atlantic. On these scales other trait-  
396 environment interactions, for example, success in overwintering, may play a role, as well as  
397 transportation by ocean currents (Melle *et al.* 2014). Finally, sampling bias may have caused  
398 some unexplained patterns, in particular in the global dataset, where sampling methods and  
399 taxonomic detail may have differed somewhat between sampling efforts in different areas.

400 Besides identifying potential drivers of trait distributions, our results, particularly the  
401 distribution of body size, also provide insight into how copepod communities affect marine  
402 ecosystems and carbon fluxes. The distribution of body size in copepod communities has  
403 implications for the fate of the primary production, and determines whether it is recycled in  
404 the upper ocean, transported to the sea floor via fecal pellets, or channeled toward higher  
405 trophic levels. Copepod fecal pellets may contribute a significant but highly variable (0-100  
406 %) fraction to the vertical material fluxes in the ocean (Turner 2002), and body size of  
407 copepods appears to be the main determinant of this fraction (Stamieszkin *et al.* 2015): small  
408 copepods produce small fecal pellets that are mainly recycled in the upper ocean, while large  
409 copepods produce large pellets that rapidly sink to the seafloor. Body-size diversity of  
410 mesozooplankton communities, which are typically dominated by copepods (Verity &

411 Smetacek 1996), is furthermore positively correlated with the transfer efficiency of primary  
412 production to higher trophic levels (García-Comas *et al.* 2016): the optimal prey size of  
413 primary consumers depends on their body size, and therefore communities of primary  
414 consumers with diverse body sizes feed efficiently on a range of prey sizes and harvest the  
415 phytoplankton communities more exhaustively. Similarly, changes in phyto- and zooplankton  
416 community body size composition have been shown to affect the spatial distribution and  
417 temporal dynamics of planktivorous fish. In upwelling areas worldwide, spatial distribution  
418 and multi-decadal fluctuations of sardine and anchovy stocks have been explained by  
419 climate-driven changes in the physical environment and their impact on plankton body size  
420 (e.g., Lindegren *et al.* 2013). Smaller-sized plankton promote filter-feeding fish species with  
421 fine gill rakes (e.g., sardine) while larger plankton support particulate-feeders with coarse gill  
422 rakes (e.g., anchovy) (van der Lingen *et al.* 2006).

423         Focusing on the large-scale spatial and temporal patterns of copepod trait distributions  
424 is necessarily crude and ignores conditions specific to certain regions, especially in data-  
425 scarce systems like the open ocean. Particularly with our global approach we defined  
426 communities in a simplistic way, included some coarse taxonomic groups, and ignored  
427 intraspecific variation in continuous traits such as body size. Our observational data were not  
428 evenly distributed in the global ocean, and, especially in the Pacific, data with the required  
429 quality were largely lacking. Furthermore, our analysis was biased toward large copepods, as  
430 it was based on traditional observational data that were mostly taken with mesh sizes of 200  
431  $\mu\text{m}$  or coarser (O'Brien 2010). These meshes may not capture one third of the copepod  
432 biomass in the small size fractions (Gallienne & Robins 2001), which is particularly rich in  
433 passive feeding taxa like *Oithona* - a potential explanation for the small fractions of passive  
434 feeders we identified in this study (Figure 2, Appendix E).

435           Some of these uncertainties could be reduced by employing approaches that measure  
436 traits directly in the field rather than indirectly via taxonomic classification and subsequent  
437 merging with trait information from the literature. *In-situ* imaging may be one way to do so  
438 (Picheral *et al.* 2010). Taking images of plankton communities with cheap, automated  
439 devices carried by commercial ships similar to the Continuous Plankton Recorder  
440 (Richardson *et al.* 2006) could greatly speed-up the sampling and improve data coverage.  
441 Imaging may be particularly suitable to measure body size compositions (García-Comas *et al.*  
442 2016), but with the rapid development of algorithm-based image recognition, it may soon be  
443 possible to also measure other traits such as sac-spawning or swimming behavior.

444           Nevertheless, our trait biogeographies showed substantial spatial and temporal  
445 structure that was consistently linked to environmental predictors for two independent  
446 observational datasets, highlighting the relevance of the trait-based approach to describe  
447 copepod biogeography. We demonstrated the value of these biogeographies to test and  
448 develop new hypotheses about the drivers of the distribution of zooplankton. Furthermore,  
449 our results may be used as a test-bed for trait-based mechanistic models. Ultimately we hope  
450 our work will contribute to the development of next generation global models of the  
451 dynamics of planktonic ecosystems and their reaction to future climate change.

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460



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653 **Tables**

654 Table 1: Trait data coverage for taxa included in observational datasets: covered  
 655 fractions of taxonomic diversity and biomass/abundance are shown for the North Atlantic and  
 656 the global ocean. Biomass fractions could be estimated for the North Atlantic using cubed  
 657 total length as mass proxies, since data on total length was available for all taxa. For the  
 658 global ocean this was not the case and we therefore report percentages of abundance (number  
 659 of individuals). North Atlantic data stems from the Continuous Plankton Recorder; global  
 660 data stems from the Coastal and Oceanic Plankton Ecology, Production and Observation  
 661 Database.

Trait	North Atlantic (67 taxa)		Global (607 taxa)	
	Diversity	Biomass	Diversity	Abundance
Body size	100%	100%	95%	99%
Feeding mode	99%	100%	78%	96%
Myelination	100%	100%	100%	100%
Relative offspring size	55%	99%	23%	70%

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## Figure captions

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Figure 1: Fraction of variance explained by INLA models for each trait based on spatial/spatiotemporal predictors (red), environmental predictors (green), and both types of predictors (yellow). Results are shown for global models (left panels) and North Atlantic models (right panels). Combined and environmental models for the North Atlantic were run on a subset of the observations used for the spatiotemporal models due to missing environmental data (satellite observations during winter months).  $R^2$  of spatiotemporal models can thus be slightly higher than corresponding  $R^2$  combined models.

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Figure 2: Seasonal succession of community traits in the North Atlantic 1998-2008. Estimated trait distributions are shown for the beginning of January, April, July, and October (columns) for body size, body-size diversity, feeding modes, myelination and relative offspring size (columns). Displayed are only pixels with a maximum distance of 400 kilometers from observations in every season. Estimates of spatial and temporal autocorrelation of trait distributions in the North Atlantic are shown in Appendix F.

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Figure 3: Global distributions of community mean traits for body size (a), myelination (b), and relative offspring size (c). Polygons on the maps represent simulated communities. Colored polygons are data-based estimates; polygons in gray scales are predictions with the best environmental models. The panels on the right show trait distributions per latitude. Median model predictions (lines) and 90% confidence intervals (polygons) are shown in grey. Data-based trait patterns are superimposed in orange, including median (circles), interquartile range (thick lines), and 90% confidence intervals (thin lines). Global maps for further traits can be seen in Appendix E. Estimates of spatial autocorrelation lengths of global trait distributions are shown in Appendix F.



686           Figure 4: Responses of trait distributions to environmental predictors of hypothetical  
687 importance based on single-predictor models. Traits include body size, body-size diversity,  
688 myelinated fraction, and relative offspring size (rows). Responses for fractional traits are  
689 shown on the logit scale. Environmental predictors are net primary production (left row),  
690 phytoplankton cell diameter (second row from left), sea surface temperature (second row  
691 from right), seasonality of chlorophyll *a* concentration (right row top), and Secchi Depth  
692 (right row bottom). Lines in dark blue represent global models, lines in cyan represent North  
693 Atlantic models. Shaded areas surrounding the lines illustrate 95% confidence intervals.  
694 Dashed lines represent predictors not included in the best environmental models of the  
695 corresponding trait and domain. Responses for active feeding are shown in Appendix H.

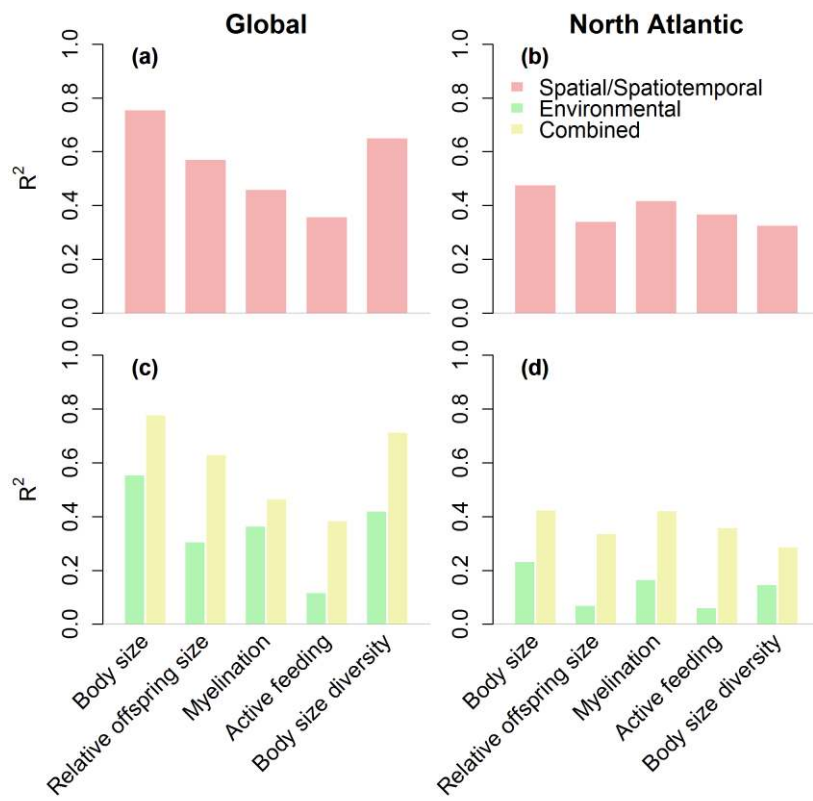
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## Figures

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Figure 1

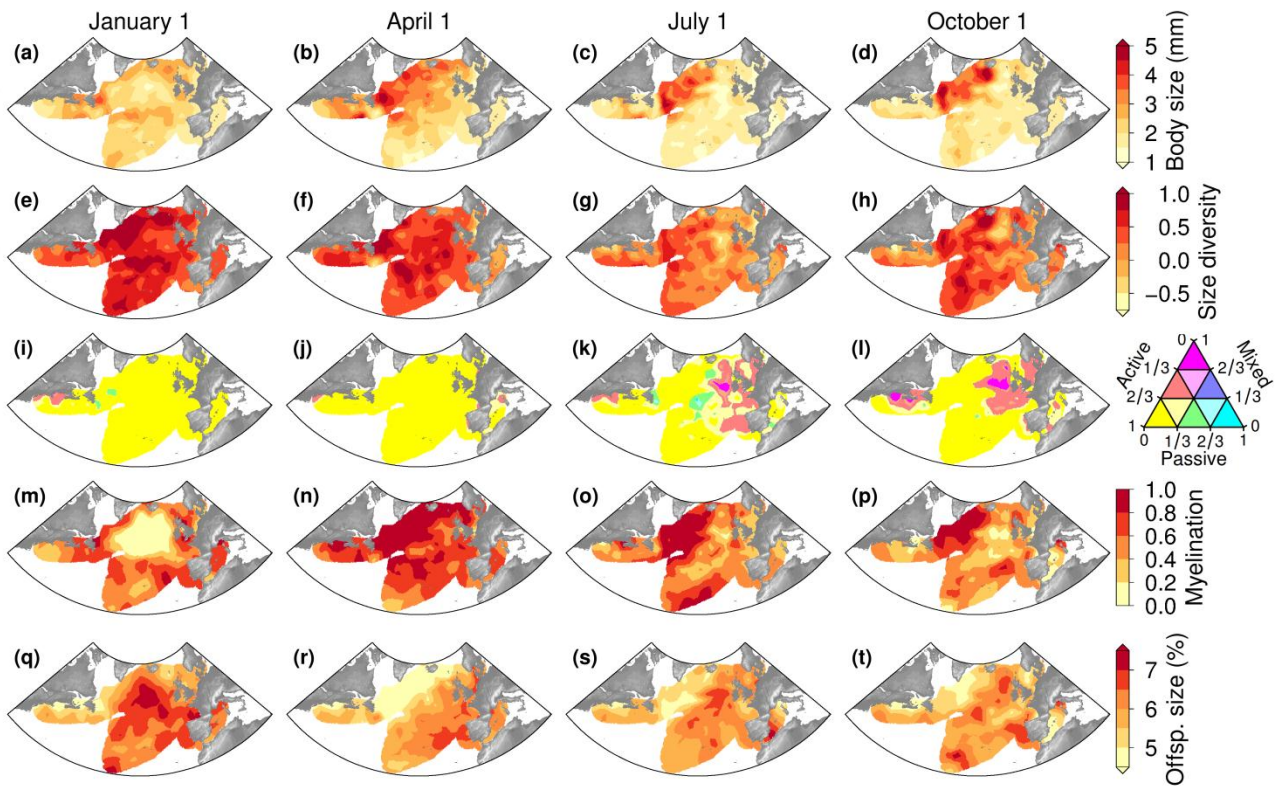


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Figure 2

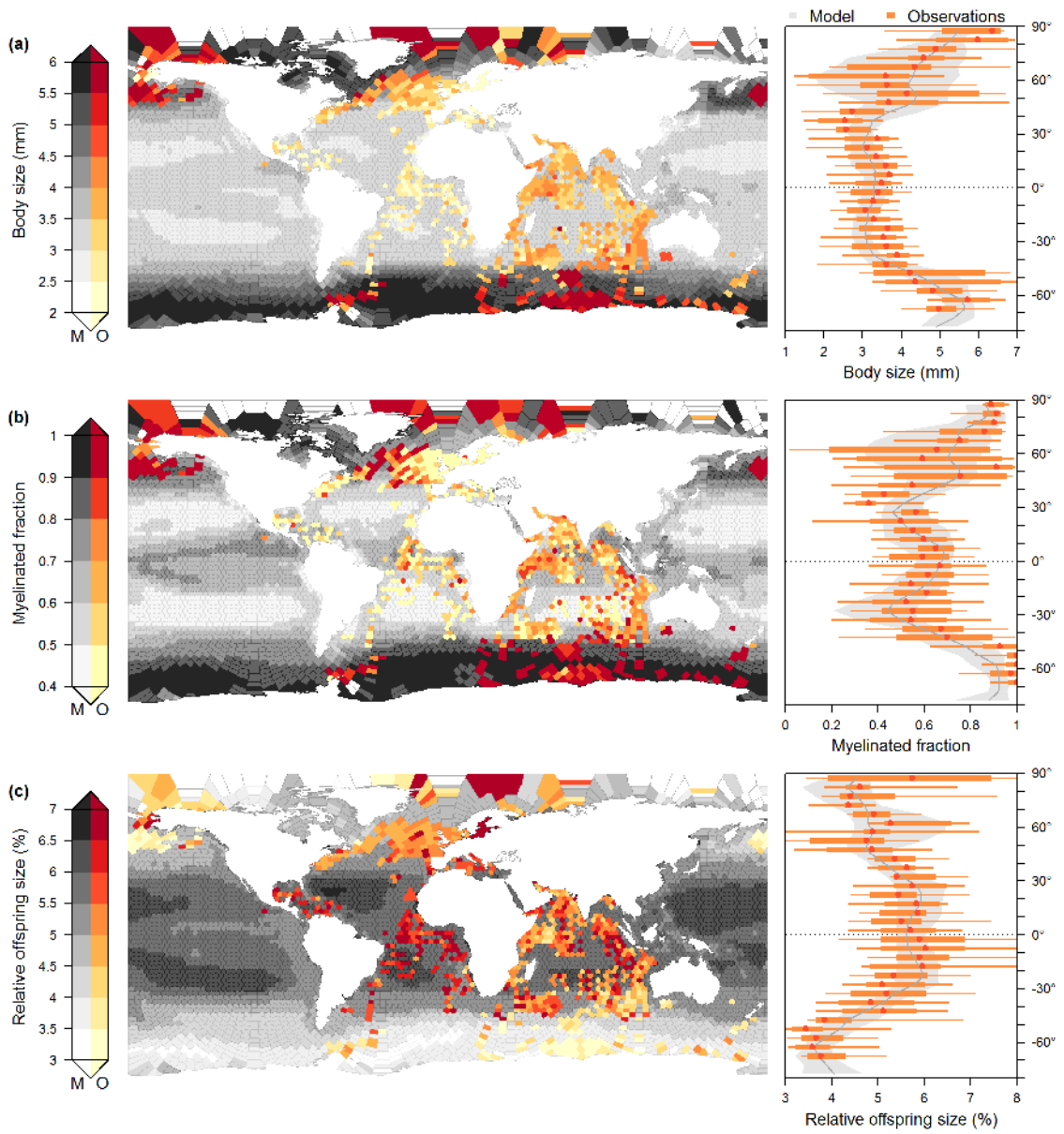


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Figure 3

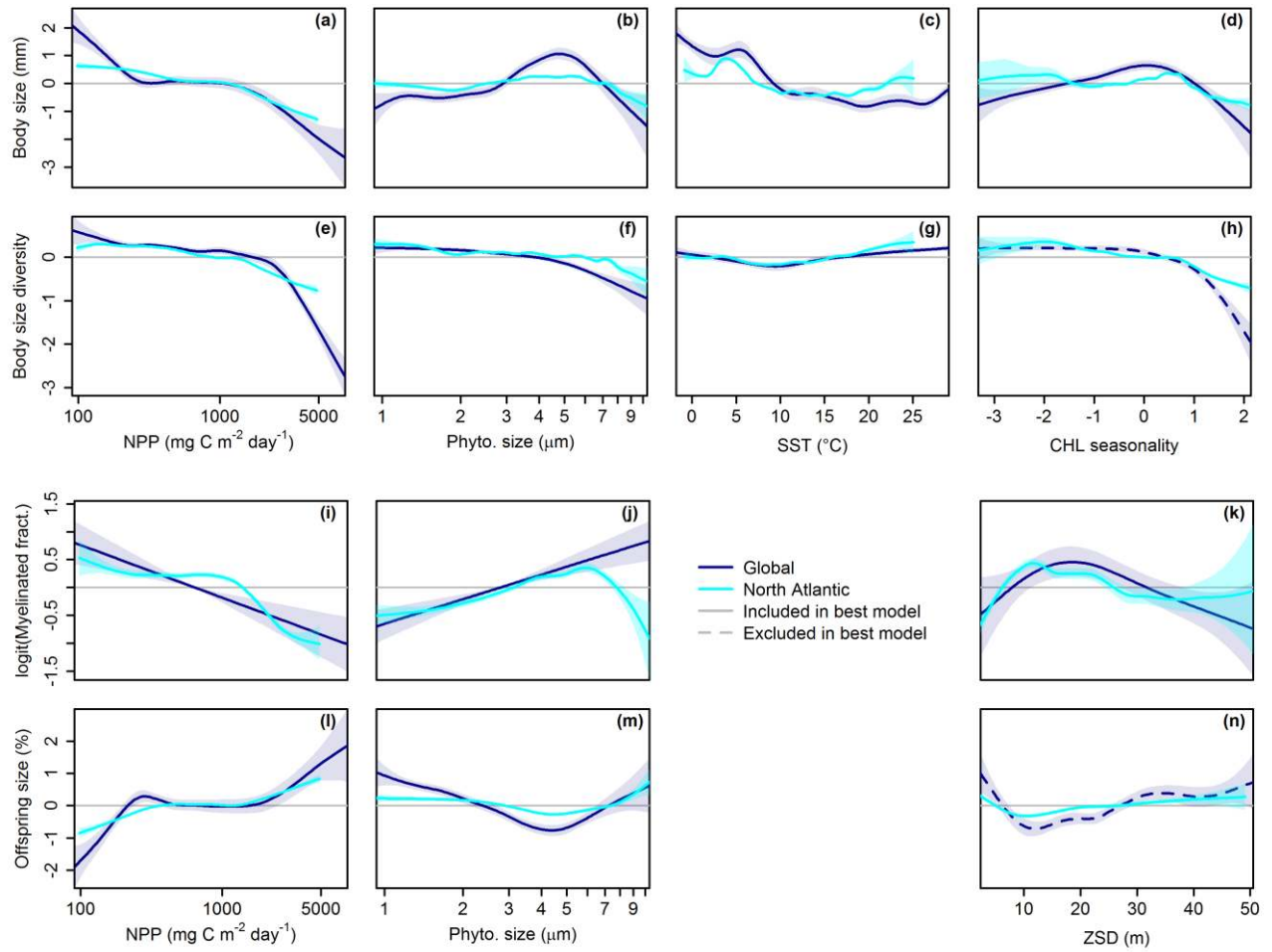


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Figure 4



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## 710 **Text boxes**

711 Box1: Traits considered and their hypothesized dependence on the environment

712 Body size

713         Body size is a master trait affecting all major life missions of an organism, i.e.,  
714 feeding, survival, and reproduction (Litchman *et al.* 2013). It can be considered a proxy for  
715 several other essential properties such as most vital rates, mobility, and prey size. Here, body  
716 size is represented by the total length of adults. We hypothesize that mean body size in  
717 copepod communities decreases with increasing temperatures. Such a relationship is known  
718 to occur within copepod species, potentially due to oxygen limitation of large organisms at  
719 warm temperatures (Forster *et al.* 2012). Furthermore, we expect copepod body size to be  
720 positively correlated to productivity, as has been shown for many animal groups (Huston &  
721 Wolverton 2011). Larger body size has also been shown to be beneficial for copepods to cope  
722 with seasonal environments (Maps *et al.* 2014), and we thus expect body size to be positively  
723 related to the intensity of the seasonal cycle. Finally, we hypothesize that copepod body size  
724 is positively related to the size of the local prey, as feeding efficiency in copepods is a  
725 function of the predator to prey size ratio (Hansen *et al.* 1994).

726 Feeding mode

727         We distinguish between three different feeding modes: passive feeding, active  
728 feeding, and mixed feeding (Kiørboe 2011). Passive feeding includes mainly ambush feeding  
729 but also particle feeding copepods. The former copepods wait for prey to pass within their  
730 perceptive range, while the latter feed on large particles of marine snow. Active strategies  
731 comprise cruise feeding and feeding current feeding, where the copepod either moves

732 through the water or generates a feeding current. Most taxa exclusively use either an active or  
733 a passive feeding behavior, but some taxa are able to alternate (called mixed feeders in this  
734 paper). Ambush feeders rely on motile prey for feeding and therefore we hypothesize that  
735 passive feeders are more common in areas with more motile phytoplankton like flagellates.  
736 Furthermore, we expect passive feeders to be less common in unproductive areas as they  
737 have lower feeding rates (Kiørboe 2013) and may struggle more with low prey  
738 concentrations. Lastly, we hypothesize mixed feeding to be a trait that is beneficial in  
739 seasonal environments with varying prey types and concentrations.

#### 740 Relative offspring size

741 Some copepod species have relatively larger (and fewer) eggs than others, suggesting  
742 differences in the investment made per offspring. We estimate these differences as relative  
743 offspring size, the ratio between egg diameter and the length of the adult female. We do not  
744 study absolute egg diameters here, as they scale positively with body size (Neuheimer *et al.*  
745 2015): according to our data the corresponding Pearson correlation coefficient is  $r=0.84$   
746 ( $n=166$ ), while  $r$  for relative offspring size versus body size is  $-0.19$  ( $n=164$ ). We expect large  
747 relative offspring size to be beneficial in harsh environments (Segers & Taborsky 2011) with  
748 low productivity, low quality of food but also low predation pressure.

#### 749 Myelination

750 Copepods can be grouped into myelinated and amyelinated taxa (Lenz 2012). Myelin  
751 is a membranous sheath that surrounds the axons of neurons and greatly enhances the speed  
752 of signal transmission. Myelinated copepods are more efficient in escaping predators and  
753 need less energy to maintain their nervous systems, but they rely on a more lipid-rich diet

754 (Lenz 2012). We hypothesize that myelination to common in areas where predation pressure  
755 is high, where productivity is low, and where food quality is high (Lenz 2012).



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**Appendix A: CPR taxa considered**

757 CPR taxa considered in the North Atlantic copepod community and species, based on

758 which traits were estimated.

CPR taxon	Species considered for trait estimate
<i>Acartia</i> spp. (unidentified) <sup>a</sup>	<i>A. clausi</i>
<i>Acartia danae</i>	<i>A. danae</i>
<i>Acartia longiremis</i>	<i>A. longiremis</i>
<i>Aetideus armatus</i>	<i>A. armatus</i>
<i>Anomalocera patersoni</i>	<i>A. patersoni</i>
<i>Calanoides carinatus</i>	<i>C. carinatus</i>
<i>Calanus finmarchicus</i>	<i>C. finmarchicus</i>
<i>Calanus glacialis</i>	<i>C. glacialis</i>
<i>Calanus helgolandicus</i>	<i>C. helgolandicus</i>
<i>Calanus hyperboreus</i>	<i>C. hyperboreus</i>
<i>Calocalanus</i> spp. <sup>b</sup>	<i>C. contractus</i> , <i>C. pavo</i> , <i>C. plumulosus</i> , <i>C. styliremis</i> , <i>C. tenuis</i>
<i>Candacia armata</i>	<i>C. armata</i>
<i>Candacia ethiopica</i>	<i>C. ethiopica</i>
<i>Candacia pachydactyla</i>	<i>C. pachydactyla</i>
<i>Paracandacia simplex</i>	<i>C. simplex</i>
<i>Centropages bradyi</i>	<i>C. bradyi</i>
<i>Centropages chierchiae</i> eyecount	<i>C. chierchiae</i>
<i>Centropages hamatus</i>	<i>C. hamatus</i>
<i>Centropages typicus</i>	<i>C. typicus</i>
<i>Centropages violaceus</i>	<i>C. violaceus</i>
<i>Clausocalanus</i> spp. <sup>b</sup>	<i>C. arcuicornis</i> , <i>C. furcatus</i> , <i>C. paululus</i> , <i>C. pergens</i>
<i>Corycaeus</i> spp. <sup>a,b</sup>	<i>C. speciosus</i> , <i>Ditrichocorycaeus anglicus</i>
<i>Ctenocalanus vanus</i>	<i>C. vanus</i>
<i>Eucalanus</i> spp. <sup>b</sup> (Unidentified)	<i>E. elongatus</i> , <i>Pareucalanus attenuatus</i>
<i>Eucalanus hyalinus</i>	<i>E. hyalinus</i>
<i>Euchaeta acuta</i>	<i>E. acuta</i>
<i>Euchaeta marina</i>	<i>E. marina</i>
<i>Euchirella rostrata</i>	<i>E. rostrata</i>
<i>Heterorhabdus norvegicus</i>	<i>H. norvegicus</i>
<i>Heterorhabdus papilliger</i>	<i>H. papilliger</i>
<i>Isias clavipes</i>	<i>I. clavipes</i>
<i>Labidocera</i> spp. <sup>b</sup> (Unidentified)	<i>L. acutifrons</i> , <i>L. aestiva</i> , <i>L. wollastoni</i>
<i>Lucicutia</i> spp. <sup>a</sup>	<i>L. flavicornis</i>
<i>Mecynocera clausi</i>	<i>M. clausi</i>
<i>Mesocalanus tenuicornis</i>	<i>M. tenuicornis</i>

<i>Metridia longa</i>	<i>M. longa</i>
<i>Metridia lucens</i>	<i>M. lucens</i>
<i>Harpacticoida</i> Total Traverse <sup>a,b</sup>	<i>Microsetella norvegica</i> , <i>Microsetella rosea</i>
<i>Nannocalanus minor</i>	<i>N. minor</i>
<i>Neocalanus gracilis</i>	<i>N. gracilis</i>
<i>Oithona</i> spp. <sup>b</sup>	<i>O. atlantica</i> , <i>O. linearis</i> , <i>O. nana</i> , <i>O. plumifera</i> , <i>O. robusta</i> , <i>O. setigera</i> , <i>O. similis</i>
<i>Oncaea</i> spp. <sup>b</sup>	<i>O. media</i> , <i>O. mediterranea</i> , <i>O. ornata</i> , <i>O. venusta</i>
<i>Para-Pseudocalanus</i> spp. <sup>b</sup>	<i>Paracalanus parvus</i> , <i>Pseudocalanus elongatus</i> , <i>Pseudocalanus minutus</i>
<i>Paracandacia bispinosa</i>	<i>P. bispinosa</i>
<i>Paraeuchaeta gracilis</i>	<i>P. gracilis</i>
<i>Paraeuchaeta hebes</i>	<i>P. hebes</i>
<i>Paraeuchaeta norvegica</i>	<i>P. norvegica</i>
<i>Parapontella brevicornis</i>	<i>P. brevicornis</i>
<i>Pleuromamma abdominalis</i>	<i>P. abdominalis</i> , <i>P. indica</i>
<i>Pleuromamma borealis</i>	<i>P. borealis</i>
<i>Pleuromamma gracilis</i>	<i>P. gracilis</i>
<i>Pleuromamma piseki</i>	<i>P. piseki</i>
<i>Pleuromamma robusta</i>	<i>P. robusta</i>
<i>Pleuromamma xiphias</i>	<i>P. xiphias</i>
<i>Pontellina plumata</i>	<i>P. plumata</i>
<i>Scolecithricella</i> spp. <sup>b</sup>	<i>P. ovata</i> , <i>S. dentata</i> , <i>S. minor</i> , <i>S. vittata</i>
<i>Rhincalanus nasutus</i>	<i>R. nasutus</i>
<i>Scolecithrix danae</i>	<i>S. danae</i>
<i>Subeucalanus crassus</i>	<i>S. crassus</i>
<i>Subeucalanus monachus</i>	<i>S. monachus</i>
<i>Temora longicornis</i>	<i>T. longicornis</i>
<i>Temora stylifera</i>	<i>T. stylifera</i>
<i>Tortanus discaudatus</i>	<i>T. discaudatus</i>
<i>Undeuchaeta major</i>	<i>U. major</i>
<i>Undeuchaeta plumosa</i>	<i>U. plumosa</i>
<i>Undinula vulgaris</i>	<i>U. vulgaris</i>
<i>Urocorycaeus</i> spp. <sup>b</sup>	<i>U. furcifer</i> , <i>U. lautus</i> , <i>U. longistylis</i>

759 <sup>a</sup>Most common species in taxon according to (Richardson *et al.* 2006) was considered for trait information.

760 <sup>b</sup>Trait estimates for genus based on arithmetic mean of species common in the North Atlantic according to

761 [www.iobis.org](http://www.iobis.org).

762

763 **Appendix B: Correlation analysis of environmental**  
 764 **variables**

765 Pearson correlation coefficients between all pairs of environmental predictors used:  
 766 values in italic indicate correlation coefficients for observations in the North Atlantic; non-  
 767 italic values indicate values on the global scale. Grey color represents variable combinations  
 768 which are never used in the models (ZSD and CHL seasonality). Fields highlighted in yellow  
 769 represent combinations used in the models with correlation coefficients higher than 0.7.

	<b>SST<sup>a</sup></b>	<b>ZSD<sup>b</sup></b>	<b>NPP<sup>c</sup></b>	<b>CHL seasonality<sup>d</sup></b>	<b>MD<sub>50</sub><sup>e</sup></b>
<b>SST</b>	1	0.47	-0.06	-0.52	-0.86
	<i>1</i>	<i>0.48</i>	<i>-0.15</i>	<i>-0.49</i>	<i>-0.58</i>
<b>ZSD</b>	0.47	1	-0.78	-0.92	-0.82
	<i>0.48</i>	<i>1</i>	<i>-0.61</i>	<i>-0.6</i>	<i>-0.79</i>
<b>NPP</b>	-0.06	-0.78	1	0.77	0.5
	<i>-0.15</i>	<i>-0.61</i>	<i>1</i>	<i>0.37</i>	<i>0.4</i>
<b>CHL seasonality</b>	-0.52	-0.92	0.77	1	0.86
	<i>-0.49</i>	<i>-0.6</i>	<i>0.37</i>	<i>1</i>	<i>0.59</i>
<b>MD<sub>50</sub></b>	-0.86	-0.82	0.5	0.86	1
	<i>-0.58</i>	<i>-0.79</i>	<i>0.42</i>	<i>0.59</i>	<i>1</i>

770 <sup>a</sup>Sea surface temperature; <sup>b</sup>Secchi Depth; <sup>c</sup>net primary productivity; <sup>d</sup>seasonality in chlorophyll *a* concentrations;  
 771 <sup>e</sup>median diameter of phytoplankton cells

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## Appendix C: Spatial and temporal meshes for INLA

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### North Atlantic

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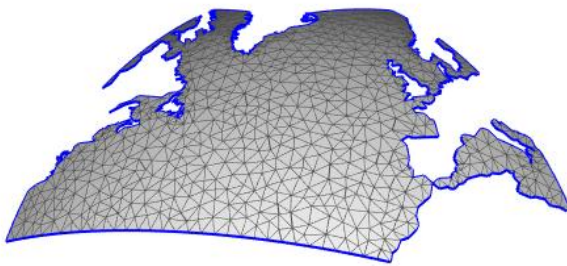
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Models for the North Atlantic were constructed including both, a spatial and a seasonal mesh. The spatial mesh covered the North Atlantic and was constrained by the coastlines (islands with an area smaller than 100 000 km<sup>2</sup> were ignored). The maximum distance between mesh points was chosen to be about 300 km (Figure C1). The seasonal mesh had nodes at the beginning of January, April, July, and October and was cyclic at its boundaries.



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Figure C1: Delaunay triangulation of the North Atlantic domain. Points (intersections) of the field are used to estimate the spatial dependencies in INLA models. We projected the coordinates onto a sphere in order to realistically represent the spatial distances.

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### Global

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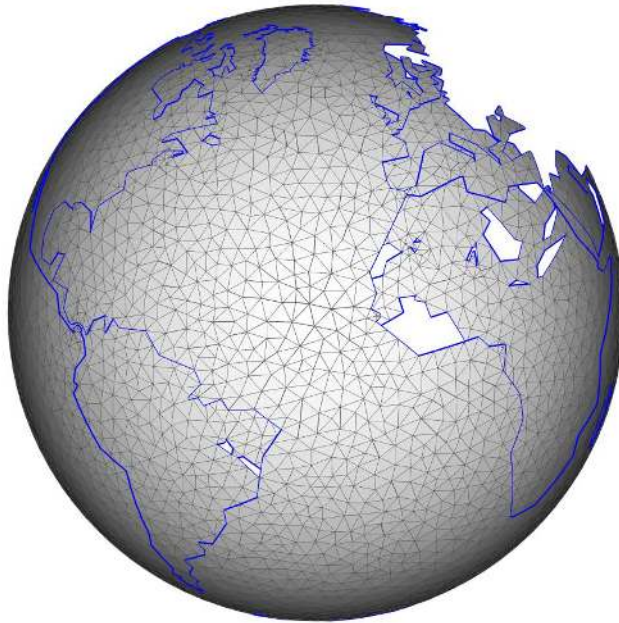
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Spatial models of global trait distributions were modeled based on a spherical, global mesh defined with a maximum distance of about 500 km between the points and constrained by coarse continental borders (again, islands with an area smaller than 100 000 km<sup>2</sup> were ignored) (Figure C2).

790



791

792           Figure C2: Delaunay triangulation of the global domain. Points (intersections) of the  
793 field are used to estimate the spatial dependencies in INLA models. We projected the  
794 coordinates onto a sphere in order to realistically represent the spatial distances.

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## Appendix D: Verification of the existence of between-

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## community trait variance

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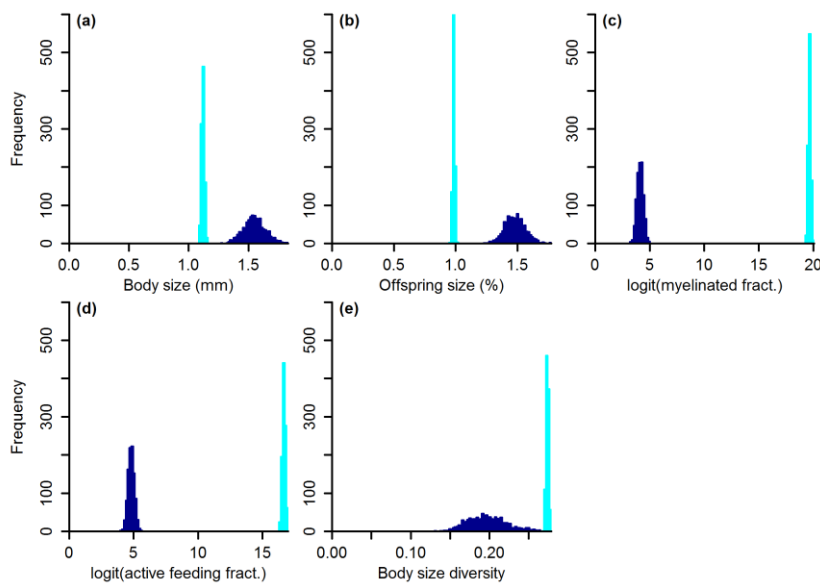
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We found clear variation between communities in all traits of both the North Atlantic and the global domain. The existence of variation was assessed using a bootstrapping approach on the variance of the summary statistics (see Methods). We tested whether the variance among communities of these summary statistics differed from zero. To this end we resampled each summary statistic in of both domains 1000 times with replacement. For each of these 1000 pseudo-samples of communities we then calculated the variance. The histograms for these variances are shown in Figure D1. For all traits and both domains we could clearly confirm our hypothesis that a significant variation of traits exists between copepod communities.



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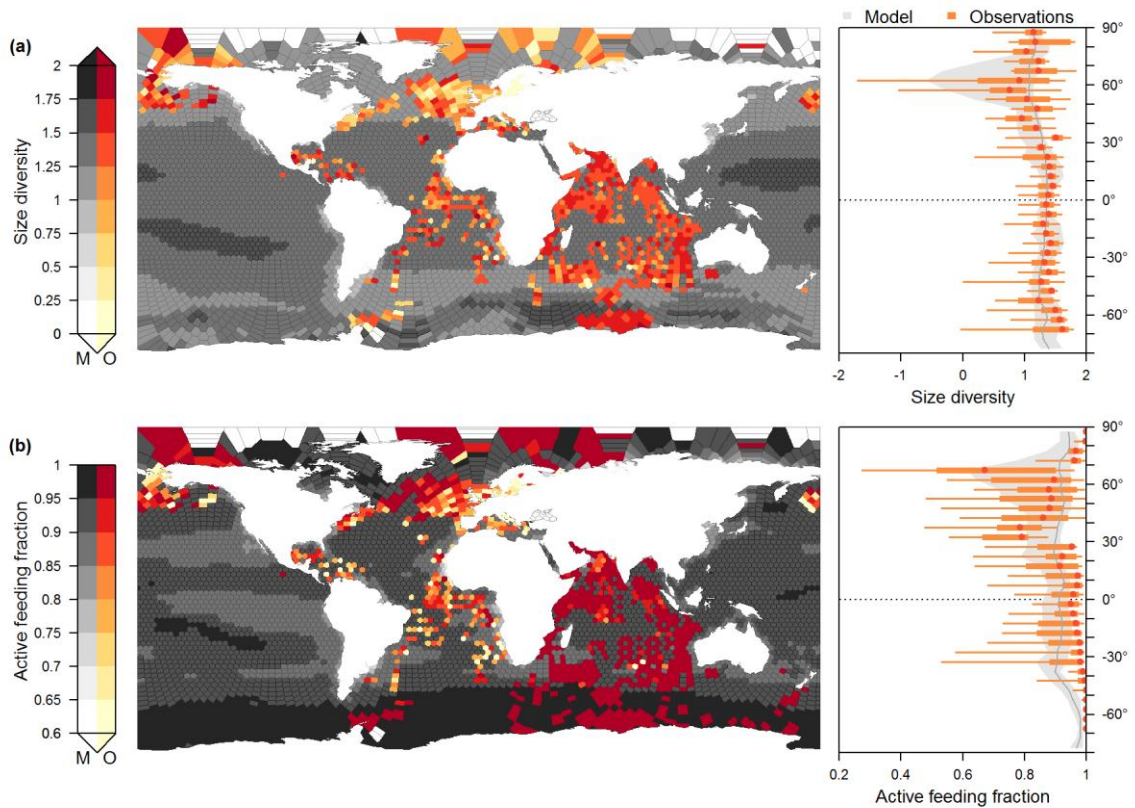
Figure D1: Histograms of standard deviations for body size (a), relative offspring size (b), the logit transformed fraction of myelinated copepods (c), the logit transformed fraction of active feeding copepods (d), and body-size diversity (e). Variance estimates for the North

812 Atlantic domain are shown in cyan and variance estimates for global domain are shown in  
813 dark blue.

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## Appendix E: Further global traits



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817 Global distributions of community mean traits for body-size diversity (a) and active  
818 feeding (b). Polygons on the maps represent simulated communities. Colored polygons are  
819 data-based estimates; polygons in gray scales are predictions with the best environmental  
820 models. The panels on the right show latitudinal trait variation. Median model predictions  
821 (lines) and 90% confidence intervals (polygons) are shown in grey. Data-based trait patterns  
822 are superimposed in orange, including median (circles), inter quartile range (thick lines), and  
823 90% confidence intervals (thin lines).

824



825 **Appendix F: Spatial and temporal correlations**

826 Table F1: Spatial and temporal autocorrelation of trait distributions in the North  
 827 Atlantic obtained from spatiotemporal models. Depicted are means and standard deviations.  
 828 Temporal autocorrelation is defined as Pearson correlation coefficients between subsequent  
 829 seasons; spatial autocorrelation length is defined as the distance at which the Pearson  
 830 correlation coefficients between points fall below about 0.13.

<b>Trait</b>	<b>Temporal autocorrelation (between seasons)</b>	<b>Spatial autocorrelation length (km)</b>
Body size	0.511 ± 0.054	810 ± 87
Relative offspring size	0.277 ± 0.082	1017 ± 85
Myelination	0.243 ± 0.073	998 ± 90
Active feeding	0.406 ± 0.069	1074 ± 127
Mixed feeding	0.522 ± 0.066	970 ± 88
Passive feeding	0.153 ± 0.085	675 ± 83
Body-size diversity	0.250 ± 0.074	634 ± 6

831  
 832 Table F2: Spatial autocorrelation length of trait distributions in the global ocean  
 833 obtained from spatial models. Depicted are means and standard deviations. Spatial  
 834 autocorrelation length is defined as the distance at which the Pearson correlation coefficients  
 835 between points fall below about 0.13.

<b>Trait</b>	<b>Spatial autocorrelation length (km)</b>
Body size	5575 ± 1286
Relative offspring size	4117 ± 787
Myelination	30 745 ± 22 955

Active feeding

2549± 5

Body-size diversity

1721 ± 316

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838 **Appendix G: Skill of environmental models with all**  
839 **predictor combinations**

840 Table G1: Model skill in terms of deviance information criterion (DIC), Wanatabe-  
841 Akaike information criterion (WAIC), and explained variance ( $R^2$ ) of global environmental  
842 models. Best models for each trait are highlighted in yellow.

<b>Response</b>	<b>Predictors</b>	<b>DIC</b>	<b>WAIC</b>	<b>R<sup>2</sup></b>	<b>Best model</b>
Feeding_mode.Active		521.80	521.01		0
Feeding_mode.Active	diverCHL	520.73	519.18	0.02	0
Feeding_mode.Active	meanNPP	507.63	505.99	0.11	0
Feeding_mode.Active	medianPhyto	523.12	521.56	0.00	0
Feeding_mode.Active	diverCHL & medianPhyto	521.52	519.13	0.03	0
Feeding_mode.Active	meanNPP & diverCHL	502.49	500.07	0.13	1
Feeding_mode.Active	meanNPP & medianPhyto	507.36	504.93	0.10	0
Feeding_mode.Active	meanNPP & diverCHL & medianPhyto	503.62	500.35	0.14	0
Myelination		1103.57	1102.82		0
Myelination	meanNPP	1088.48	1086.95	0.08	0
Myelination	meanZSD	1087.71	1084.27	0.12	0
Myelination	medianPhyto	1083.23	1081.79	0.11	0
Myelination	meanNPP & medianPhyto	1029.80	1027.42	0.31	0
Myelination	meanZSD & meanNPP	1024.59	1022.14	0.34	0
Myelination	meanZSD & medianPhyto	1048.60	1044.45	0.26	0
Myelination	meanZSD & meanNPP & medianPhyto	1019.67	1016.37	0.36	1

OffspringSize		2652.67	2655.54		0
OffspringSize	meanNPP	2575.61	2574.39	0.11	0
OffspringSize	meanZSD	2563.92	2563.02	0.12	0
OffspringSize	medianPhyto	2450.52	2452.46	0.22	0
OffspringSize	meanNPP & medianPhyto	2325.52	2328.54	0.33	1
OffspringSize	meanZSD & meanNPP	2380.24	2380.92	0.29	0
OffspringSize	meanZSD & medianPhyto	2347.13	2349.12	0.32	0
OffspringSize	meanZSD & meanNPP & medianPhyto	2331.31	2331.70	0.33	0
Size		2748.86	2749.15		0
Size	diverCHL	2663.16	2667.00	0.10	0
Size	meanNPP	2621.78	2621.75	0.15	0
Size	meanSST	2316.70	2324.12	0.41	0
Size	medianPhyto	2530.59	2533.88	0.24	0
Size	diverCHL & medianPhyto	2363.88	2367.20	0.38	0
Size	meanNPP & diverCHL	2294.15	2295.89	0.42	0
Size	meanNPP & medianPhyto	2265.79	2266.23	0.44	0
Size	meanSST & diverCHL	2197.55	2203.25	0.50	0
Size	meanSST & meanNPP	2160.57	2168.47	0.52	0
Size	meanSST & medianPhyto	2174.24	2182.39	0.51	0
Size	meanNPP & diverCHL & medianPhyto	2241.91	2242.00	0.46	0
Size	meanSST & diverCHL & medianPhyto	2134.15	2145.48	0.53	0
Size	meanSST & meanNPP & diverCHL	2147.14	2156.90	0.52	0
Size	meanSST & meanNPP & medianPhyto	2130.55	2142.20	0.54	0

Size	meanSST & meanNPP & diverCHL & medianPhyto	2089.48	2106.09	0.56	1
Size_diversity		988.22	995.21		0
Size_diversity	diverCHL	756.29	770.96	0.27	0
Size_diversity	meanNPP	624.68	631.16	0.38	0
Size_diversity	meanSST	911.16	923.45	0.11	0
Size_diversity	medianPhyto	855.45	867.05	0.16	0
Size_diversity	diverCHL & medianPhyto	751.58	761.19	0.27	0
Size_diversity	meanNPP & diverCHL	623.02	630.48	0.39	0
Size_diversity	meanNPP & medianPhyto	596.43	610.23	0.41	0
Size_diversity	meanSST & diverCHL	721.89	736.67	0.31	0
Size_diversity	meanSST & meanNPP	594.31	602.39	0.41	0
Size_diversity	meanSST & medianPhyto	721.33	732.50	0.31	0
Size_diversity	meanNPP & diverCHL & medianPhyto	588.82	599.09	0.42	0
Size_diversity	meanSST & diverCHL & medianPhyto	680.14	697.85	0.35	0
Size_diversity	meanSST & meanNPP & diverCHL	597.90	605.54	0.41	0
Size_diversity	meanSST & meanNPP & medianPhyto	581.59	595.75	0.43	1
Size_diversity	meanSST & meanNPP & diverCHL & medianPhyto	582.21	596.36	0.43	0

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844 Table G2: Model skill in terms of deviance information criterion (DIC), Wanatabe-  
845 Akaike information criterion (WAIC), and explained variance ( $R^2$ ) of North Atlantic  
846 environmental models. Best models for each trait are highlighted in yellow.

Response	Predictors	DIC	WAIC	$R^2$	Best mode I
Feeding_mode.Active		215857	215863	0.00	0
Feeding_mode.Active	Diver_CHL	210778	210784	0.01	0
Feeding_mode.Active	NPP	208409	208410	0.02	0
Feeding_mode.Active	Phyto_size	211310	211312	0.01	0
Feeding_mode.Active	Diver_CHL & Phyto_size	210529	210536	0.04	0
Feeding_mode.Active	NPP & Diver_CHL	208143	208149	0.02	0
Feeding_mode.Active	NPP & Phyto_size	207843	207845	0.04	0
Feeding_mode.Active	NPP & Diver_CHL & Phyto_size	207459	207469	0.06	1
Myelination		242754	242757	0.00	0
Myelination	NPP	241690	241692	0.07	0
Myelination	Phyto_size	242291	242294	0.01	0
Myelination	ZSD	242179	242183	0.04	0
Myelination	NPP & Phyto_size	240331	240334	0.11	0
Myelination	NPP & ZSD	241302	241306	0.08	0
Myelination	ZSD & Phyto_size	240022	240027	0.14	0
Myelination	NPP & ZSD & Phyto_size	239348	239353	0.16	1
OffspringSize		86733	86734	0.00	0
OffspringSize	NPP	85972	85972	0.03	0
OffspringSize	Phyto_size	86061	86062	0.02	0

OffspringSize	ZSD	86157	86159	0.02	0
OffspringSize	NPP & Phyto_size	84842	84841	0.06	0
OffspringSize	NPP & ZSD	85256	85257	0.05	0
OffspringSize	ZSD & Phyto_size	85196	85197	0.05	0
OffspringSize	NPP & ZSD & Phyto_size	84145	84147	0.09	1
Size		97476	97478	0.00	0
Size	Diver_CHL	92815	92823	0.04	0
Size	NPP	94444	94444	0.08	0
Size	Phyto_size	93403	93409	0.03	0
Size	SST	90243	90251	0.11	0
Size	Diver_CHL & Phyto_size	95434	95435	0.06	0
Size	NPP & Diver_CHL	92736	92735	0.12	0
Size	NPP & Phyto_size	91645	91645	0.15	0
Size	NPP & SST	89445	89444	0.21	0
Size	SST & Diver_CHL	92424	92424	0.13	0
Size	SST & Phyto_size	89597	89612	0.13	0
Size	NPP & Diver_CHL & Phyto_size	91088	91086	0.17	0
Size	NPP & SST & Diver_CHL	89219	89216	0.21	0
Size	NPP & SST & Phyto_size	84696	84736	0.23	0
Size	SST & Diver_CHL & Phyto_size	92156	92155	0.14	0
Size	NPP & SST & Diver_CHL & Phyto_size	84477	84485	0.23	1
Size_diversity		49562	49559	0.01	0
Size_diversity	Diver_CHL	48154	48157	0.05	0
Size_diversity	NPP	45518	45513	0.13	0

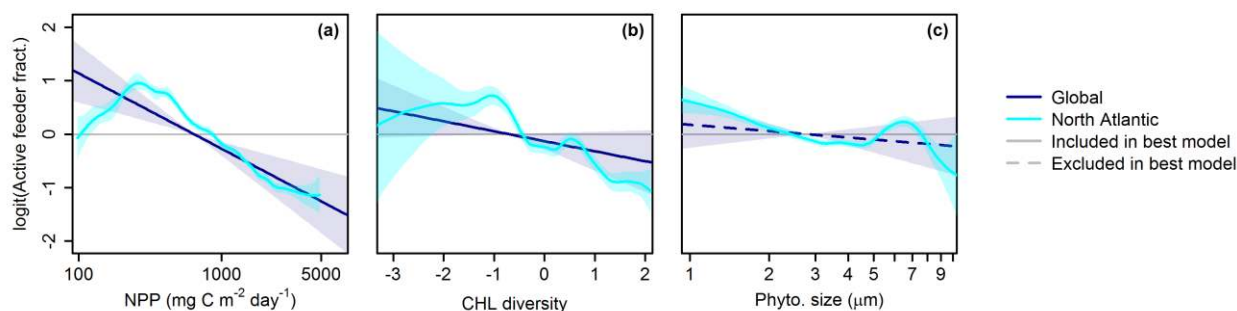
Size_diversity	Phyto_size	49191	49188	0.02	0
Size_diversity	SST	48973	48974	0.03	0
Size_diversity	Diver_CHL & Phyto_size	48086	48086	0.05	0
Size_diversity	NPP & Diver_CHL	45267	45263	0.13	0
Size_diversity	NPP & Phyto_size	45295	45291	0.13	0
Size_diversity	NPP & SST	45379	45375	0.13	0
Size_diversity	SST & Diver_CHL	47922	47921	0.06	0
Size_diversity	SST & Phyto_size	48662	48671	0.04	0
Size_diversity	NPP & Diver_CHL & Phyto_size	44943	44943	0.14	0
Size_diversity	NPP & SST & Diver_CHL	45147	45144	0.14	0
Size_diversity	NPP & SST & Phyto_size	45171	45168	0.14	0
Size_diversity	SST & Diver_CHL & Phyto_size	47851	47846	0.06	0
Size_diversity	NPP & SST & Diver_CHL & Phyto_size	44855	44857	0.15	1

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## Appendix H: Environmental responses of active feeding



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850 Responses of active feeding to environmental predictors of hypothetical importance,  
851 based on single-predictor models. Responses are shown on the logit scale. Environmental  
852 predictors are net primary production, seasonality of chlorophyll *a* concentration, and  
853 phytoplankton cell diameter (columns). Lines in dark blue represent global models, lines in  
854 cyan represent North Atlantic models. Shaded areas surrounding the lines illustrate 95%  
855 confidence intervals. Dashed lines represent predictors not included in the best models of the  
856 corresponding trait and domain.