



## 1 **A trait database for marine copepods**

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### 6 **Abstract**

7 The trait-based approach is gaining increasing popularity in marine plankton ecology but the  
8 field urgently needs more and easier accessible trait data to advance. We compiled trait  
9 information on marine pelagic copepods, a major group of zooplankton, from the published  
10 literature and from experts, and organised the data into a structured database. We collected  
11 9345 records for 14 functional traits. Particular attention was given to body size, feeding  
12 mode, egg size, spawning strategy, respiration rate and myelination (presence of nerve  
13 sheathing). Most records were reported on the species level, but some phylogenetically  
14 conserved traits, such as myelination, were reported on higher taxonomic levels, allowing the  
15 entire diversity of around 10 800 recognized marine copepod species to be covered with few  
16 records. Besides myelination, data coverage was highest for spawning strategy and body size  
17 while information was more limited for quantitative traits related to reproduction and  
18 physiology. The database may be used to investigate relationships between traits, to produce  
19 trait biogeographies, or to inform and validate trait-based marine ecosystem models. The data  
20 can be downloaded from PANGAEA, doi:10.1594/PANGAEA.862968.

### 21 **Keywords**

22 Marine copepods, zooplankton, traits, body size, egg size, feeding mode, spawning strategy,  
23 respiration rate, myelination

24



## 25 **1 Introduction**

26 The trait-based approach is an increasingly popular framework in ecology that aims to  
27 describe the structure and function of communities or ecosystems in a simple way. It seeks to  
28 identify the main characteristics of organisms that control their fitness (Litchman et al., 2013).  
29 Organisms must be successful in three main missions in order to thrive: feeding, survival and  
30 reproduction. Functional traits determine the outcome of one or several of those missions.

31 Functional traits are heritable properties of the individual that are interrelated through trade-  
32 offs and selected by the environment. They are measurable on the individual without any  
33 assisting information (Violle et al., 2007). Swimming behavior, therefore, is a functional trait  
34 of some animals, but preferred habitat is not, as it depends on the characterization of the  
35 environment in which an individual occurs.

36 The trait-based approach is well established in plant ecology (e.g., van Bodegom et al., 2014;  
37 Westoby et al., 2002) and more recently also in marine plankton ecology (Barton et al., 2013;  
38 Litchman and Klausmeier, 2008; Litchman et al., 2013). One key group of marine  
39 zooplankton, for which traits and trade-offs are relatively well understood, is copepods  
40 (Kiørboe, 2011). These ubiquitous crustaceans typically dominate the biomass of zooplankton  
41 communities (Verity and Smetacek, 1996), play a central role in marine food webs, and affect  
42 the global carbon cycle (Jónasdóttir et al., 2015).

43 We focus here on a set of 14 commonly-described functional traits for marine copepods, for  
44 which data are available (Fig. 1). The set includes one trait affecting all life missions, three  
45 feeding-related, six growth-related and three reproduction-related traits. Body size affects all  
46 life missions as it is related to several essential properties including metabolism, feeding,  
47 growth, mortality, mobility, and prey size (Litchman et al., 2013). Feeding-related traits  
48 include clearance rate, i.e., the effective volume of water cleared for prey items per unit of  
49 time, when the prey concentration is low (Kiørboe and Hirst, 2014); maximum ingestion rate -  
50 the feeding rate at non-limiting food concentration (Kiørboe and Hirst, 2014); and feeding  
51 mode (behaviour) (Kiørboe, 2011). For the latter, the following behaviours are separated:  
52 Ambush feeding copepods remain largely immobile and wait for approaching prey. Cruise  
53 feeding copepods move actively through the water in search for prey. Feeding-current feeders  
54 produce a current by beating their appendages and capture entrapped prey. Particle feeding  
55 copepods colonize large aggregates of marine snow on which they feed for extended periods,  
56 and parasites colonize larger hosts, such as fish, from which they feed. Growth related traits



57 include maximum growth rate (the maximum amount of body mass gained per unit time), and  
58 the number of generations per year. Reproductive traits include spawning strategy, which  
59 distinguishes between free-spawners that release their eggs into the water, and sac-spawners  
60 that carry their eggs until hatching, egg size, clutch size (eggs produced in one ‘spawning  
61 event’), and fecundity (the number of eggs produced over the life-time of a female). Finally,  
62 the traits related to survival are myelination (the insulation of nerve tracts with membranous  
63 tissue, which greatly enhances the speed of signal transmission and allows rapid response to  
64 predators (Lenz et al., 2000)), respiration rate, the volume of oxygen consumed per unit time,  
65 hibernation, which allows individuals to endure adverse conditions over seasonal time frames,  
66 and resting eggs, which can endure adverse conditions over several decades (Williams-  
67 Howze, 1997).

68 Here, we followed a recent call for efforts to collect trait data (Barton et al., 2013), and  
69 established a database for the 14 copepod traits introduced above. We screened the literature  
70 for information on marine copepods, mainly on pelagic taxa. Particular attention was given to  
71 the traits body size, feeding mode, egg size, spawning strategy, myelination, and respiration  
72 rate, for some of which we have examined the biogeography elsewhere (Brun et al.,  
73 *submitted*). We present data coverage as well as trait distributions for the most important  
74 pelagic copepod families and discuss data collection methods as well as limitations. The data  
75 can be found on PANGAEA: doi:10.1594/PANGAEA.862968.

76



## 77 **2 Data**

### 78 **2.1 Origin of data**

79 Our data consists primarily of material from previous data compilations on individual traits,  
80 complemented by information from the primary literature and expert judgements. In total 90  
81 references were consulted, with a few sources contributing the majority of the data (Table 1).  
82 The primary literature was screened mainly for information on the focal traits of body size,  
83 feeding mode, egg size, spawning strategy, and respiration rate. For feeding mode, we also  
84 used expert judgement: feeding modes have been described in the literature only for a minor  
85 fraction of copepod species. Where no information on feeding mode was available, we  
86 studied the morphology of the feeding appendages and, if feasible, grouped the taxa into two  
87 categories of feeding activity (active versus passive feeding, see Sect. 2.2.1).

### 88 **2.2 Trait information**

89 Besides the ecological categorisation shown in Fig. 1, the traits considered may be separated  
90 as categorical/qualitative traits and continuous/quantitative traits, which involve different  
91 ways of data storage.

#### 92 **2.2.1 Qualitative traits**

93 Here, qualitative traits include feeding mode, spawning strategy, myelination, hibernation,  
94 and resting eggs. We treat qualitative traits as unique either on the species level or on higher  
95 order taxonomic levels. For hibernation and resting eggs, we report records on the species  
96 level, including information about the observed life stage in the case of hibernation. Species  
97 for which hibernation and resting egg production has been observed may be considered as  
98 having the potential to express the trait, without necessarily expressing it in every individual.

99 Feeding mode, spawning strategy, and myelination were assumed to be conserved in the  
100 taxonomy, yet we are aware that this is not always the case (Sect. 4.2). Records are therefore  
101 reported also for genera, families and orders, assuming all species from the corresponding  
102 taxonomic branch carry the trait. We distinguish five not-necessarily-exclusive feeding  
103 modes, i.e., ambush feeding, particle feeding, feeding-current feeding, cruise feeding and  
104 parasitic feeding (Kiørboe, 2011). Feeding modes are further clustered into different feeding  
105 activity levels (Table 2). Spawning strategy distinguishes between free-spawner and sac-



106 spawner that may be separated further to ‘single egg-sac’, ‘double egg-sac’ or ‘egg mass’.  
107 Finally, myelination distinguishes between myelinated and amyelinated taxa.

## 108 2.2.2 Quantitative traits

109 Quantitative traits include three size traits, four physiological rate traits, fecundity and number  
110 of generations per year. Where possible, we report mean, minimum, and maximum trait value  
111 as well as standard deviation and sample size for each record. Quantitative traits were  
112 collected mainly for adults, but where available we also include information on juvenile life  
113 stages. Several records may exist for each species and life stage/sex, originating from  
114 different measurements or references. In some cases quantitative traits are reported on  
115 taxonomic levels higher than species. This is usually due to limited taxonomic resolution, and  
116 therefore such records should not be assumed to represent the entire taxonomic branch. For  
117 each quantitative trait, we defined standard units in which the data is reported. Where  
118 conversions were not straight forward, we report different ‘types’ of trait measurements, e.g.,  
119 we distinguish between ‘total length’ and ‘prosome length’ for body size and between ‘outer  
120 diameter’ and ‘ $\mu\text{g}$  carbon’ for egg size. The taxonomic overview of quantitative traits shown  
121 below is based on species-wise averages of the data, restricted to adult individuals where life-  
122 stage matters.

## 123 2.3 Meta information

### 124 2.3.1 Taxonomy

125 Around 10 800 marine copepod species are currently recognised (Walter and Boxshall, 2016).  
126 Taxonomic classification of these small crustaceans is not trivial and has changed  
127 considerably over the past century. In order to ensure consistency, all the taxa reported were  
128 updated based on the latest (June 2 2016) (re)classification by Walter and Boxshall (2016)  
129 with the finest possible resolution on the species level. We also added the full taxonomy of  
130 marine copepods to our data tables in order to allow easy translation of the records to the  
131 desired taxonomic level. However, we encourage readers to use the online version on  
132 [www.marinespecies.org/copepoda](http://www.marinespecies.org/copepoda) instead, to ensure that the information used is up to date.  
133 For simplicity, we restrict the data presentation in this paper to a subset of the taxonomy,  
134 mainly containing families with important pelagic species (Appendix A).



### 135 2.3.2 Life form

136 Copepods undergo a complex life cycle including an egg stage, six naupliar and six  
137 copepodite stages that may show distinct traits. Furthermore, distinct differences between  
138 sexes are possible, for example, through sexual size-dimorphism (Hirst and Kiørboe, 2014). If  
139 necessary, we therefore included information about life stage and sex of an individual in a  
140 ‘life form’ column (Table 3). Some authors distinguish between sexes already in copepodite  
141 stages IV and V (e.g., Conway, 2006). We disregard this separation to optimize consistency  
142 among the different sources.

### 143 2.3.3 Location

144 Traits can vary considerably as a function of the geographical location, in particular if they  
145 are observed on organisms in the field. Information about the geographical location, however,  
146 is not readily available in traditional data compilations. Nevertheless, we reported information  
147 about location where it was available.

### 148 2.3.4 Other

149 Further meta-information includes temperature, body mass and general comments.  
150 Physiological rate traits (growth rate, respiration rate, clearance rate and ingestion rate)  
151 depend on both body mass and temperature (Kiørboe and Hirst, 2014), which we also report  
152 for records of these traits. For body mass, we further distinguish ‘dry mass’ or ‘carbon mass’.  
153 Further relevant meta-information may be provided in the ‘Comment’ field.

## 154 2.4 Data conversions

155 We consider our database to be primarily a source of information, and generally leave it up to  
156 the user to select methods and assumptions for aggregation and conversions, with the notable  
157 exception of physiological rate traits and egg size. Physiological rate traits largely stem from  
158 Kiørboe and Hirst (2014), who converted traits to carbon-specific values and to a standard  
159 temperature of 15 °C. For growth rate, clearance rate, and ingestion rate we included these  
160 converted values, while we recalculated them for respiration rate. We converted weight  
161 information to carbon content based on the empirical relationships provided in Kiørboe  
162 (2013). Temperature corrections were performed based on an empirical estimate of the  $Q_{10}$   
163 value from our data. The  $Q_{10}$  value is the factor by which respiration rates increase when  
164 temperature is increased by 10°C and was estimated to be 2.14 (Appendix B). Egg size was



165 reported in part as carbon content. For comparability, we also report conversions of these

166 values to outer diameters assuming a spherical egg shape and a carbon density of  $0.14 \times 10^{-6}$

167  $\mu\text{g C } \mu\text{m}^{-3}$  (Kiørboe and Sabatini, 1995).

168



## 169 3 Results

### 170 3.1 Data coverage

171 In total, the data tables include 9345 records for the 14 traits investigated. With 7131 records,  
172 by far the most information was available for body size (Fig. 2). However, for taxonomically  
173 clustered traits like myelination, only few records were necessary to cover all marine  
174 copepods. Similarly, relatively few records were available for hibernation and resting eggs,  
175 but they likely cover the existing information in the literature, and therefore the dominant  
176 species expressing these traits. For quantitative traits related to reproduction and physiology,  
177 information was generally more limited. Among taxa, the best data coverage was available for  
178 the order *Calanoida*. But also some non-calanoid families showed a relatively high data  
179 coverage, including *Oithonidae*, and *Oncaeidae*. For non-pelagic copepods, information was  
180 mainly available on myelination, and – for *Siphonostomatioida* – on feeding mode.

### 181 3.2 Body length

182 Total body length varies between 0.095 mm for *Acartia bacorehuiensis* and 17.4 mm for  
183 *Bathycalanus sverdrupi*, and is largest on average for calanoid copepods. Our data indicate  
184 shortest body lengths for the harpacticoid families *Harpacticidae*, *Discoidea*, and  
185 *Euterpinae*, as well as for *Oithonidae* and *Oncaeidae*, with median total lengths of adults  
186 between 0.5 and 0.6 mm (Fig. 3a). Families with largest species are *Megacalanidae* followed  
187 by *Euchaetidae* and *Eucalanidae*, with median adult body lengths of 12.25, 6.51 and 5.54  
188 mm, respectively. The highest interquartile range of body lengths is found for *Lucicutiidae*  
189 with 4.57 mm.

190 Body size does not only vary between species, but also within them. Not surprisingly body  
191 size increases considerably throughout the ontogeny of copepods (Fig. 3b). But significant  
192 variations in body size are also observed as a function of the geographic location. When  
193 compared in space, the prosome lengths of adult females of *C. finmarchicus* vary between  
194 about 2.5 and 3 mm across the North Atlantic, corresponding to a mass difference of a factor  
195 of over 1.7 (Fig. 3c).





### 196 3.3 Egg size

197 Egg diameter varies between 37.3  $\mu\text{m}$  for *Oncaea media* and 870  $\mu\text{m}$  for *Paraeuchaeta*  
198 *hanseni*. The non-calanoid families covered (*Oncaeidae*, *Corycaeidae*, *Oithonidae*, and  
199 *Euterpinidae*) tend to have smaller eggs than the calanoid families (Fig. 6a). With a median  
200 diameter of 51.5  $\mu\text{m}$  *Oncaeidae* is the family with the smallest egg sizes, while *Augaptilidae*  
201 have the largest eggs with a median diameter of 554.3  $\mu\text{m}$ . The highest diversity of egg  
202 diameters is found for *Euchaetidae* with an interquartile range of 365.5  $\mu\text{m}$ .

### 203 3.4 Myelination

204 Myelination only occurs in calanoid copepods and is assumed to be either consistently present  
205 or absent within families. Major families with myelinated axons are *Aetideae*, *Calanidae*,  
206 *Euchaetidae*, *Paracalanidae*, *Phaennidae*, and *Scolecitrichidae* (Fig. 7a).

### 207 3.5 Clearance rate

208 For adult copepods, carbon specific clearance rate corrected to 15 °C varies between 224 ml  
209  $\text{h}^{-1} \text{mg C}^{-1}$  for *Calanus pacificus* and 3067  $\text{ml h}^{-1} \text{mg C}^{-1}$  for *Oithona nana*. On the family  
210 level *Calanidae* show the lowest corrected clearance rates, whereas highest rates are found for  
211 *Acartiidae* (Fig. 4a). The number of data points for adult copepods is only 18 for clearance  
212 rate, as life stage information is missing for most records (Fig. 4b).

### 213 3.6 Ingestion rate

214 Carbon specific ingestion rate at 15 °C ranges between 15  $\mu\text{g C h}^{-1} \text{mg C}^{-1}$  for *Calanus*  
215 *pacificus* and 116  $\mu\text{g C h}^{-1} \text{mg C}^{-1}$  for *Euterpina acutifrons*, when comparing adult  
216 individuals. On the family level, lowest ingestion rates are found *Tortanidae*, and highest  
217 values are found for *Euterpinidae* (Fig. 4c). Again, only 21 data points are available for  
218 ingestion rates of adult copepods, as life stage information was missing for most records (Fig.  
219 4d).

### 220 3.7 Growth rate

221 Specific growth rate at 15°C varies between 5  $\mu\text{g C h}^{-1} \text{mg C}^{-1}$  for *Labidocera euchaeta* and  
222 19  $\mu\text{g C h}^{-1} \text{mg C}^{-1}$  for *Calanus finmarchicus*. In accordance, the families of these taxa,  
223 *Pontellidae* and *Calanidae* have, respectively, the lowest and highest specific growth rates



224 among all families for which we have data (Fig. 4e). The highest diversity of growth rates is  
225 also found for *Calanidae*, with an interquartile range of  $10 \mu\text{g C h}^{-1} \text{mg C}^{-1}$ .

### 226 3.8 Respiration rate

227 Specific respiration rate at reference temperature is lowest for *Hemirhabdus grimaldii* at  $0.2$   
228  $\mu\text{L O}_2 \text{ h}^{-1} \text{mg C}^{-1}$  and highest for *Acartia spinicauda* at  $79.5 \mu\text{L O}_2 \text{ h}^{-1} \text{mg C}^{-1}$ . Among  
229 families, respiration rates are lowest for *Heterorhabdidae* (median =  $0.5 \mu\text{L O}_2 \text{ h}^{-1} \text{mg C}^{-1}$ )  
230 and highest for *Sapphirinidae* (median =  $37.5 \mu\text{L O}_2 \text{ h}^{-1} \text{mg C}^{-1}$ ) (Fig. 4f). The highest  
231 interquartile range of specific respiration rates is found for *Acartiidae*. Most of the records on  
232 respiration rates contain life stage information and are made for adult individuals (Fig. 4g).

### 233 3.9 Feeding mode

234 Feeding modes differ among taxonomic orders (Fig. 5). Calanoid copepods are active feeders,  
235 and in some cases mixed feeders (*Acartiidae* and *Centropagidae*). Active feeding is also seen  
236 in the order *Monstrilloida* and in the family *Oncaeidae* of the order *Poecilostomatoidea*.  
237 Passive feeding prevails in the orders *Cyclopoida* and some families of the order  
238 *Harpacticoida*, as well as in the family *Corycaeidae* of the order *Poecilostomatoidea*. Parasitic  
239 copepods are found in the order *Siphonostomatoidea* and in the family *Sapphirinidae* of the  
240 order *Poecilostomatoidea*.

### 241 3.10 Generations

242 The annual number of generations varies between 0.5 for *Calanus hyperboreus* and 9 for  
243 *Acartia omorii*. On the family level *Eucalanidae* show the slowest life cycle with a median of  
244 0.75 generations per year, while the median for *Centropagidae* is highest with 5.8 generations  
245 per year (Fig. 6b).

### 246 3.11 Clutch size

247 Clutch size is below 35 for all taxa assessed, except for *Heterorhabdus norvegicus* from the  
248 family *Heterorhabdidae*, for which it is 94 (Fig. 6c). Lowest clutch sizes are found for  
249 *Scaphocalanus magnus* (*Scolecitrichidae*) and *Tharybis groenlandica* (*Tharybidae*), with 1.6  
250 and 2, respectively.



251 **3.12 Fecundity**

252 Fecundity ranges from 113 for *Pseudodiaptomus pelagicus* to 2531 for *Sinocalanus tenellus*  
253 (Fig. 6d). The largest interquartile range of fecundity is observed for *Centropagidae*.

254 **3.13 Spawning strategy**

255 Free spawning is only reported for calanoid copepods (Fig. 7b). In most cases spawning  
256 strategy is assumed to be conserved within family with the exception of *Aetideae*,  
257 *Arietellidae*, *Augaptilidae*, and *Clausocalanidae*. Important free spawning families are  
258 *Acartiidae*, *Calanidae*, *Paracalanidae*, *Phaennidae*, *Pontellidae* and *Scolecitrichidae*.

259 **3.14 Hibernation**

260 We found literature reports on hibernation for 28 species, mostly belonging to the family  
261 *Calanidae* (Fig. 7c). Further families with hibernating species are *Acartiidae*,  
262 *Clausocalanidae*, *Eucalanidae*, *Metridinidae*, *Pontellidae*, *Rhincalanidae*, *Stephidae*, and  
263 *Subeucalanidae*.

264 **3.15 Resting eggs**

265 The capacity to produce resting eggs has been observed for 47 species in total. Most of these  
266 species belong to the families *Acartiidae*, and *Pontellidae* (Fig. 7d). Further families with  
267 resting egg producing species are *Centropagidae*, *Sulcanidae*, *Temoridae*, and *Tortanidae*.

268



## 269 4 Discussion

270 We collected information on more than a dozen functional traits of marine copepods, and  
271 combined it into a structured database. Our work complements recent and ongoing efforts to  
272 develop zooplankton trait data collections. As for the collection of Benedetti *et al.* (2015), we  
273 focused on those traits of marine copepods that are the main determinants of fitness, also  
274 referred to as response traits (Violle *et al.*, 2007). However, our collection covered the global  
275 ocean rather than the Mediterranean Sea and a different, though overlapping, set of traits.  
276 Hébert *et al.* (2016) recently published a trait database on marine and freshwater crustacean  
277 zooplankton, which complementarily focuses on effect traits - traits which are expected to  
278 impact aquatic ecosystems. Besides a few overlapping traits, this database mainly contains  
279 information about body composition and excretion rates. Another noteworthy, ongoing effort  
280 is the website maintained by Razouls *et al.* (2005-2016), who provide an impressive  
281 collection of information for around 2600 marine pelagic copepod species. While they focus  
282 on morphological descriptions, they also provide body length information, which in an  
283 aggregated way was also included in this database. In terms of taxonomic breadth and  
284 coverage of key functional traits as defined by the framework of Litchman *et al.* (2013) (Fig.  
285 1), however, the data collection presented here is likely the most extensive. Nevertheless, our  
286 database has several limitations which should be considered.

### 287 4.1 Trait definitions

288 There are uncertainties regarding the definition of some traits and their associated trade-offs,  
289 in particular for hibernation and feeding mode. While we treat hibernation as a discrete  
290 phenomenon, in reality a host of hibernation forms exist, differing considerably in the degree  
291 to which metabolism is reduced (Ohman *et al.*, 1998). Similarly, there are several feeding  
292 mode classifications in the literature. We defined feeding modes after (Kiørboe, 2011), using  
293 trade-offs in feeding efficiency and predation risk as classification criteria. We note that the  
294 separation between cruise and feeding-current feeding is gradual, and that many species are  
295 intermediate between these two categories. This is why we collectively categorize these  
296 feeding modes as active, which is distinctly different from passive ambush feeding.

297 Other classification schemes differ in particular with respect to ambush feeding. We define  
298 ambush feeding as a passive sit-and-wait feeding mode that targets motile prey with raptorial  
299 prey capture, which applies primarily to *Oithona* and related taxa. Alternatively, ambush



300 feeding is sometimes defined solely based on raptorial prey capture (e.g., Benedetti et al.,  
301 2015; Ohtsuka and Onbé, 1991), but raptorial prey capture can also be observed in cruise and  
302 feeding-current feeders. Feeding types are sometimes also classified based on diet, e.g.,  
303 herbivorous, carnivorous, or omnivorous (Wirtz, 2012), however, diet is not a trait in itself  
304 but rather a function of the feeding traits.

#### 305 **4.2 Taxonomic clustering of traits**

306 The assumption that traits are conserved within taxonomic branches may not always hold. A  
307 large part of the diversity of pelagic copepods has only briefly been described in the literature,  
308 and little is known about the biology (Razouls et al., 2005-2016). Deeming a whole family to  
309 carry a certain trait therefore often means extrapolating from a few well known species to  
310 many rare species. While this may be reasonable for strongly conserved traits like myelination  
311 of the nervous system, for feeding mode and spawning strategy the appropriateness is less  
312 clear. Spawning strategy, for example, seems to be homogenous across most orders and  
313 families, yet in some calanoid families, such as *Aetideae*, both free-spawners and sac-  
314 spawners are found. Sometimes heterogeneity is observed even within genera: while the  
315 species *Euaugaptilus magnus* was found to carry its eggs, all other observed species in that  
316 genus are free-spawners (Mauchline, 1998). Our data on spawning strategy largely stems  
317 from Boxshall and Halsey (2004) who defined spawning strategy family-wise but noted in  
318 several cases that the assumption was not certain. We included these remarks in the comments  
319 of the spawning strategy table.

#### 320 **4.3 Variance in quantitative traits**

321 Quantitative traits are subject to measurement errors that may be significant, especially for  
322 traits that are difficult to measure or depend on parameter estimates, such as physiological  
323 rates (Kjørboe and Hirst, 2014). Where possible, we accounted for measurement errors by  
324 reporting standard deviations. However, in many cases this information was either not  
325 available, or it was not retrievable with a feasible effort.

326 Furthermore, most important quantitative traits are strongly modulated by the environment  
327 (Kattge et al., 2011a). For example, we found a substantial intraspecific variation of adult  
328 body size in *Calanus finmarchicus* across the North Atlantic. Such variation is a consequence  
329 of genetic variation and phenotypic plasticity and may optimize fitness in response to biotic



330 and abiotic environmental conditions. It may be interesting to study on its own, however, if  
331 not properly quantified it introduces significant uncertainty to the data: point estimates from  
332 particular individuals and locations that happen to be in the dataset may be an unrealistic  
333 representation of the species (Albert et al., 2010). We tried to account for this problem by  
334 including multiple trait measurements per species or averages over several measurements:  
335 however, for many species no more than one value could be found. The large investment  
336 required to measure copepod traits in the open ocean makes it difficult to overcome this  
337 limitation in the near future.

## 338 **5 Data availability**

339 The data can be downloaded from PANGAEA, doi:10.1594/PANGAEA.862968.

## 340 **6 Conclusions**

341 We produced a database on key functional traits of marine copepods that may currently be  
342 unique in its trait coverage and taxonomic breadth, enriching the field of trait-based  
343 zooplankton ecology. It may be used to obtain an overview over correlations between traits, to  
344 investigate the taxonomic and spatiotemporal patterns of trait distributions in copepods (e.g.,  
345 Brun et al., *submitted*), or to inform and validate trait-based marine ecosystem models.  
346 However, due to environmental modulation of many quantitative traits and the limited data  
347 availability, the database may not always provide robust estimates on the species level,  
348 making more detailed comparisons difficult. A way to overcome this uncertainty may be to  
349 investigate relationships between traits measured for the same individuals or groups of  
350 individuals, where the trade-offs are acting. Flexible structures for trait databases which are  
351 capable to store such information have been developed for plants (Kattge et al., 2011a) and  
352 successfully implemented in comprehensive efforts maintained by the scientific community  
353 (Kattge et al., 2011b). Learning from these experiences may lift the field of trait-based  
354 plankton ecology to the next level.

355



356 **Appendix A: List of important pelagic families considered**  
357 **in figures**

358 *Acartiidae, Aetideidae, Arietellidae, Augaptilidae, Calanidae, Candaciidae, Centropagidae,*  
359 *Clausocalanidae, Diaixidae, Discoidea, Eucalanidae, Euchaetidae, Heterorhabdidae,*  
360 *Lucicutiidae, Megacalanidae, Metridinidae, Nullosetigeridae, Paracalanidae, Phaennidae,*  
361 *Pontellidae, Pseudodiaptomidae, Rhincalanidae, Scolecitrichidae, Spinocalanidae,*  
362 *Stephidae, Subeucalanidae, Sulcanidae, Temoridae, Tharybidae, Tortanidae, Cyclopinidae,*  
363 *Oithonidae, Monstrillidae, Corycaeidae, Lubbockiidae, Oncaeidae, Sapphirinidae,*  
364 *Aegisthidae, Euterpinae, Harpacticidae, Miraciidae, Tisbidae, Misophridae, Monstrillidae,*  
365 *Mormonillidae, Caligidae, Pseudocyclopidae, Peltidiidae, Platycopiidae*  
366



## 367 **Appendix B: Estimation of $Q_{10}$ value**

368 Physiological rates measured at different temperatures were assumed to be related through the  
369 following law:

$$370 \quad R_{T_2} = R_{T_1} * Q_{10}^{\frac{T_2 - T_1}{10}} \quad (A1)$$

371 where R stands for respiration rate at different temperatures T. The  $Q_{10}$  value is the factor by  
372 which respiration rates increase when temperature is increased by 10°C. We estimated  $Q_{10}$   
373 from the data by transforming Eq. (A1) and fitting a linear regression. The regression  
374 equation was

$$375 \quad \ln\left(\frac{R_{T_2}}{R_{T_1}}\right) = \frac{1}{10} \ln Q_{10} * (T_2 - T_1) \quad (A2)$$

376 Reference rates ( $R_{T_1}$ ) and temperatures ( $T_1$ ) were defined species-wise as the record taken at  
377 the minimum temperature and used to calculate differences/ratios for all observations, which  
378 were then used in the regression. Based on this procedure we estimated a  $Q_{10}$  value of 2.14  
379 (adj.  $R^2 = 0.53$ ,  $df = 465$ ).

380





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383 beautiful copepod illustrations. Furthermore, we acknowledge the Villum foundation for  
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385



## 386 References

- 387 Albert, C. H., Thuiller, W., Yoccoz, N. G., Soudant, A., Boucher, F., Saccone, P. and Lavorel,  
388 S.: Intraspecific functional variability: extent, structure and sources of variation, *J. Ecol.*,  
389 98(3), 604–613, doi:10.1111/j.1365-2745.2010.01651.x, 2010.
- 390 Barton, A. D., Pershing, A. J., Litchman, E., Record, N. R., Edwards, K. F., Finkel, Z. V.,  
391 Kiørboe, T. and Ward, B. A.: The biogeography of marine plankton traits., *Ecol. Lett.*, 16(4),  
392 522–534, doi:10.1111/ele.12063, 2013.
- 393 Benedetti, F., Gasparini, S. and Ayata, S.-D.: Identifying copepod functional groups from  
394 species functional traits, *J. Plankton Res.*, 0, fbv096, doi:10.1093/plankt/fbv096, 2015.
- 395 van Bodegom, P. M., Douma, J. C. and Verheijen, L. M.: A fully traits-based approach to  
396 modeling global vegetation distribution, *Proc. Natl. Acad. Sci.*, 111(38), 13733–13738,  
397 doi:10.1073/pnas.1304551110, 2014.
- 398 Boxshall, G. A. and Halsey, S. H.: An introduction to copepod diversity., *Ray Society.*, 2004.
- 399 Brun, P., Payne, M. R. and Kiørboe, T.: Trait biogeography of marine copepods – an analysis  
400 across scales, *Ecol. Lett.*, submitted
- 401 Conway, D. V. P.: Identification of the copepodite developmental stages of twenty-six North  
402 Atlantic copepods, *Occas. Publ. Mar. Biol. Assoc.*, 21, 1–28, 2006.
- 403 Conway, D. V. P.: Marine Zooplankton of Southern Britain - Part 2: Arachnida, Pycnogonida,  
404 Cladocera, Facetotecta, Cirripedia and Copepoda, edited by A. W. G. John, Plymouth., 2012.
- 405 Conway, D. V. P., White, R. G., Hugues-Dit-Ciles, J., Gallienne, C. P. and Robins, D. B.:  
406 Guide to the coastal and surface zooplankton of the south-western Indian Ocean, *Occas. Publ.*  
407 *Mar. Biol. Assoc.*, 15, 354, 2003.
- 408 Hébert, M.-P., Beisner, B. E. and Maranger, R.: A compilation of quantitative functional traits  
409 for marine and freshwater crustacean zooplankton, *Ecology*, (Accepted Author Manuscript),  
410 n/a–n/a, doi:10.1890/15-1275, 2016.
- 411 Hirst, A. G. and Kiørboe, T.: Macroevolutionary patterns of sexual size dimorphism in  
412 copepods, *Proc. R. Soc. B Biol. Sci.*, 281(1791), 20140739–20140739,  
413 doi:10.1098/rspb.2014.0739, 2014.
- 414 Ikeda, T., Sano, F. and Yamaguchi, A.: Respiration in marine pelagic copepods: a global-  
415 bathymetric model, *Mar. Ecol. Prog. Ser.*, 339, 215–219, doi:10.3354/meps339215, 2007.
- 416 Jónasdóttir, S. H., Visser, A. W., Richardson, K. and Heath, M. R.: Seasonal copepod lipid  
417 pump promotes carbon sequestration in the deep North Atlantic., *Proc. Natl. Acad. Sci. U. S.*  
418 *A.*, 112(39), 12122–6, doi:10.1073/pnas.1512110112, 2015.
- 419 Kattge, J., Ogle, K., Bönisch, G., Díaz, S., Lavorel, S., Madin, J., Nadrowski, K., Nöllert, S.,  
420 Sartor, K. and Wirth, C.: A generic structure for plant trait databases, *Methods Ecol. Evol.*,  
421 2(2), 202–213, doi:10.1111/j.2041-210X.2010.00067.x, 2011a.
- 422 Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., Garnier, E.,  
423 Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., van  
424 Bodegom, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D.,  
425 Anand, M., Atkin, O., Bahn, M., Baker, T. R., Baldocchi, D., Bekker, R., Blanco, C. C.,  
426 Blonder, B., Bond, W. J., Bradstock, R., Bunker, D. E., Casanoves, F., Cavender-Bares, J.,  
427 Chambers, J. Q., Chapin III, F. S., Chave, J., Coomes, D., Cornwell, W. K., Craine, J. M.,



- 428 Dobrin, B. H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W. F., Fang, J.,  
429 Fernández-Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.  
430 T., Fyllas, N. M., Gallagher, R. V., Green, W. A., Gutierrez, A. G., Hickler, T., Higgins, S. I.,  
431 Hodgson, J. G., Jalili, A., Jansen, S., Joly, C. A., Kerkhoff, A. J., Kirkup, D., Kitajima, K.,  
432 Kleyer, M., Klotz, S., Knops, J. M. H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D.,  
433 Lee, T. D., Leishman, M., Lens, F., Lenz, T., Lewis, S. L., Lloyd, J., Llusà, J., Louault, F.,  
434 Ma, S., Mahecha, M. D., Manning, P., Massad, T., Medlyn, B. E., Messier, J., Moles, A. T.,  
435 Müller, S. C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R.,  
436 Oleksyn, J., Onipchenko, V. G., Onoda, Y., Ordoñez, J., Overbeck, G., et al.: TRY - a global  
437 database of plant traits, *Glob. Chang. Biol.*, 17(9), 2905–2935, doi:10.1111/j.1365-  
438 2486.2011.02451.x, 2011b.
- 439 Kiørboe, T.: How zooplankton feed: Mechanisms, traits and trade-offs, *Biol. Rev.*, 86, 311–  
440 339, doi:10.1111/j.1469-185X.2010.00148.x, 2011.
- 441 Kiørboe, T.: Zooplankton body composition, *Limnol. Oceanogr.*, 58(5), 1843–1850,  
442 doi:10.4319/lo.2013.58.5.1843, 2013.
- 443 Kiørboe, T. and Hirst, A. G.: Shifts in Mass Scaling of Respiration, Feeding, and Growth  
444 Rates across Life-Form Transitions in Marine Pelagic Organisms, *Am. Nat.*, 183(4), E118–  
445 E130, doi:10.1086/675241, 2014.
- 446 Kiørboe, T. and Sabatini, M.: Scaling of fecundity, growth and development in marine  
447 planktonic copepods, *Mar. Ecol. Prog. Ser.*, 120, 285–298, doi:10.3354/meps120285, 1995.
- 448 Lenz, P. H.: The biogeography and ecology of myelin in marine copepods, *J. Plankton Res.*,  
449 34, 575–589, doi:10.1093/plankt/fbs037, 2012.
- 450 Lenz, P. H., Hartline, D. K. and Davis, A. D.: The need for speed. I. Fast reactions and  
451 myelinated axons in copepods, *J. Comp. Physiol. A Sensory, Neural, Behav. Physiol.*, 186(4),  
452 337–345, doi:10.1007/s003590050434, 2000.
- 453 Litchman, E. and Klausmeier, C. A.: Trait-Based Community Ecology of Phytoplankton,  
454 *Annu. Rev. Ecol. Evol. Syst.*, 39(1), 615–639,  
455 doi:10.1146/annurev.ecolsys.39.110707.173549, 2008.
- 456 Litchman, E., Ohman, M. D. and Kiørboe, T.: Trait-based approaches to zooplankton  
457 communities, *J. Plankton Res.*, 35, 473–484, doi:10.1093/plankt/fbt019, 2013.
- 458 Mauchline, J.: *The Biology of Calanoid Copepods*, Adv. Mar. Biol., 1998.
- 459 Ohman, M. D., Drits, A. V., Elizabeth Clarke, M. and Plourde, S.: Differential dormancy of  
460 co-occurring copepods, *Deep Sea Res. Part II Top. Stud. Oceanogr.*, 45(8-9), 1709–1740,  
461 doi:10.1016/S0967-0645(98)80014-3, 1998.
- 462 Ohtsuka, S. and Onbé, T.: Relationship between mouthpart structures and in situ feeding  
463 habits of species of the family Pontellidae (Copepoda: Calanoida), *Mar. Biol.*, 111(2), 213–  
464 225, doi:10.1007/BF01319703, 1991.
- 465 Razouls, C., de Bovée, F., Kouwenberg, J. and Desreumaux, N.: Diversity and Geographic  
466 Distribution of Marine Planktonic Copepods, [online] Available from: [http://copepodes.obs-  
467 banyuls.fr/en](http://copepodes.obs-banyuls.fr/en) (Accessed 25 June 2016), n.d.
- 468 Verity, P. and Smetacek, V.: Organism life cycles, predation, and the structure of marine  
469 pelagic ecosystems, *Mar. Ecol. Prog. Ser.*, 130(1-3), 277–293, doi:10.3354/meps130277,  
470 1996.
- 471 Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. and Garnier, E.: Let



472 the concept of trait be functional!, *Oikos*, 116(5), 882–892, doi:10.1111/j.2007.0030-  
473 1299.15559.x, 2007.

474 Walter, T. C. and Boxshall, G.: World of Copepods database, [online] Available from:  
475 <http://www.marinespecies.org/copepoda> (Accessed 7 June 2016), 2016.

476 Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A. and Wright, I. J.: Plant Ecological  
477 Strategies: Some Leading Dimensions of Variation Between Species, *Annu. Rev. Ecol. Syst.*,  
478 33(1), 125–159, doi:10.1146/annurev.ecolsys.33.010802.150452, 2002.

479 Williams-Howze, J.: Dormancy in the free-living copepod orders Cyclopoida, Calanoida and  
480 Harpacticoida, *Oceanogr. Mar. Biol.*, 35, 257–322, 1997.

481 Wirtz, K.: Who is eating whom? Morphology and feeding type determine the size relation  
482 between planktonic predators and their ideal prey, *Mar. Ecol. Prog. Ser.*, 445, 1–12,  
483 doi:10.3354/meps09502, 2012.

484



485 **Tables**

486 Table 1: Important references used in the database and their taxonomic and geographical foci;  
 487 a full list of references is given in the data tables

<i>Reference</i>	<i>Trait(s)</i>	<i>Focal taxa</i>	<i>Focal region</i>
Benedetti <i>et al.</i> (2015)	Feeding mode	Abundant copepods	Mediterranean Sea
Boxshall and Halsey (2004)	Spawning strategy	<i>Calanoida</i>	Global
Conway <i>et al.</i> (2003)	Body size	Copepods	Southwestern Indian Ocean
Conway (2006)	Body size	Common planktonic copepods	North Atlantic
Conway (2012)	Body size, spawning strategy	Copepods	Southern Britain
Hirst and Kiørboe (2014)	Body size	Copepods	Global
Ikeda <i>et al.</i> (2007)	Respiration rate	Marine pelagic copepods	Global
Kiørboe and Hirst (2014)	Clearance rate, ingestion rate, growth rate, respiration rate	Marine pelagic copepods	Global
Lenz (2012)	Myelination	<i>Calanoida</i>	Global
Mauchline (1998)	Egg size, clutch size, fecundity, hibernation, resting eggs, generations	<i>Calanoida</i>	Global
Neuheimer <i>et al.</i> (2016)	Egg size	Copepods	Global



Razouls <i>et al.</i> (2005-2016)	Body size	Marine planktonic copepods	Global
Walter and Boxshall (2016)	Taxonomy	Copepods	Global

488



489 Table 2: Feeding modes included in the database and their categorization by feeding activity

<i>Feeding activity</i>	<i>Feeding modes</i>
Passive	Ambush feeding
	Particle feeding
Active	Feeding currents
	Cruise feeding
Mixed	Combination of active and passive modes
Other	Parasitic

490



491 Table 3: Abbreviations used for the classifications of life stage and sex in the database

Abbreviation	Definition
NI, NII, NIII, NIV, NV	Naupliar stages 1-5
N	Nauplius, no information about stage
CI, CII, CIII, CIV, CV	Copepodite stages 1-5
C	Copepodite, no information about stage
A	Adult (copepodite stage 6), no information about sex
F	Adult female
M	Adult male

492





## 493 **Figure captions**

494 Figure 1: Copepod traits included in the database, arranged according to the framework of  
495 Litchman et al. (2013). The vertical axis groups traits by trait type and the horizontal axis by  
496 ecological function. Body size (**bold**) transcends several functions.

497 Figure 2: Trait-wise data coverage for taxonomic families of marine copepods. Top: number  
498 of database records per trait; Left: Taxonomic tree of important families weighted by number  
499 of species, including illustrations of type species for the dominant orders. Illustrated species  
500 are (from top to bottom) *Calanus finmarchicus*, *Metridia longa*, *Oithona nana*, *Microsetella*  
501 *norvegica*, *Monstrilla helgolandica*, *Oncaea borealis*, and *Caligus elongatus*, representing  
502 orders according to their color code; Right: Table indicating the fraction of species for which  
503 data was collected per family and trait. Note that since some traits are taxonomically  
504 clustered, few records for higher order taxa may suffice to describe the entire diversity. \*We  
505 likely covered the vast majority of hibernating species and species with resting eggs that have  
506 been reported in the literature. Yet, future discoveries may expand this list.

507 Figure 3: Variation of body size in marine copepods as a function of taxonomy, life stage and  
508 location. Panel (a) shows boxplots of total body length for the most important families  
509 covered. Thick lines on boxplots illustrate median, boxes represent the interquartile ranges  
510 and whiskers encompass the 95% confidence intervals. Total length of *Calanus finmarchicus*  
511 as a function of copepodite stage in two different areas is shown in panel (b). For males and  
512 females mean values are shown as solid lines and mean  $\pm$  standard deviation are shown as  
513 transparent polygons. Distribution of female prosome length of *C. finmarchicus* in the North  
514 Atlantic is shown in panel (c).

515 Figure 4: Physiological traits of adult copepods grouped by family, and frequency of life stage  
516 information available for the records. Family-wise boxplots for clearance rate (a), ingestion  
517 rate (c), growth rate (e), and respiration rate (f). Illustrated rate values are per mg carbon and  
518 corrected to 15 °C. Thick lines on boxplots illustrate median, boxes represent the interquartile  
519 ranges and whiskers encompass the 95% confidence intervals. Barplots in panels on the right  
520 (b, d, g) indicate frequency distribution of life stage levels for the traits reported.

521 Figure 5: Taxonomic distribution of feeding modes in the most important families of marine  
522 planktonic copepods. Distinguished are active feeders (blue), mixed feeders (orange), passive  
523 feeders (green), and parasites (pink). Taxa for which no information was available are shown



524 in grey. Colors are mixed according to the fractions of trait carrying species in each  
525 taxonomic group.

526 Figure 6: Reproductive traits grouped by family: Family-wise boxplots for egg diameter  
527 including converted values from  $\mu\text{g}$  carbon (a), generations per year (b), clutch size (c), and  
528 fecundity (d). Thick lines on boxplots illustrate median, boxes represent the interquartile  
529 ranges and whiskers encompass the 95% confidence intervals.

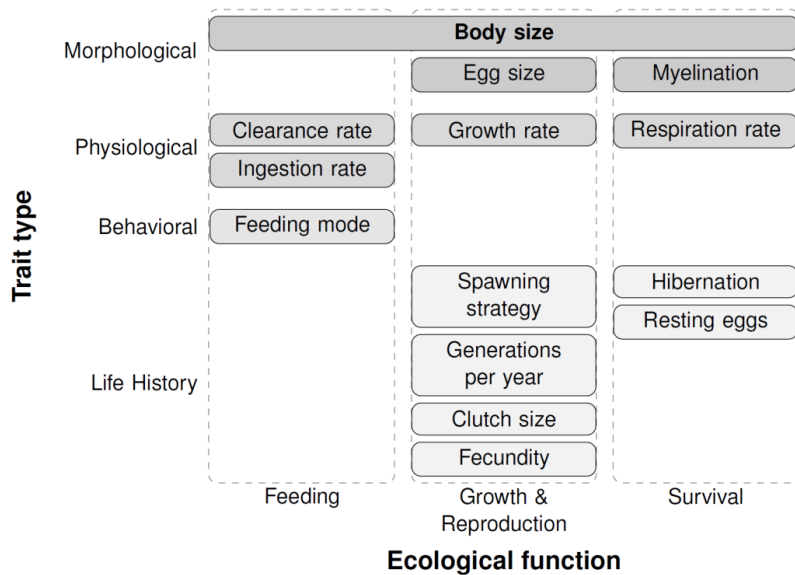
530 Figure 7: Taxonomic distribution of binary traits in the most important families of marine  
531 planktonic copepods. Fraction of trait carrying species is illustrated down to the family level  
532 for myelination (a), spawning strategy (b), hibernation (c), and resting eggs (d). Families in  
533 which the trait is present in at least one species are labelled.

534



535 **Figures**

536 Fig. 1

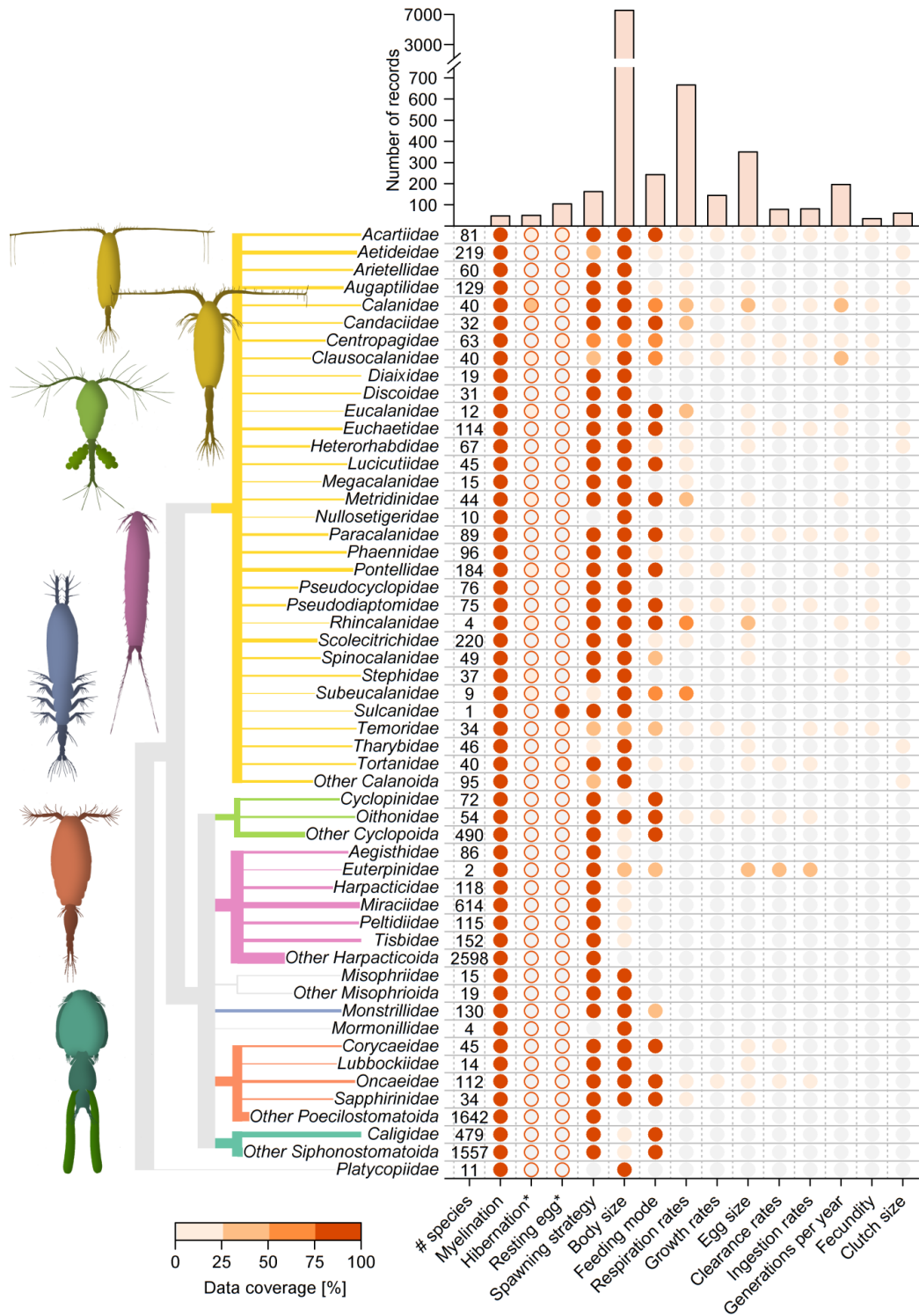


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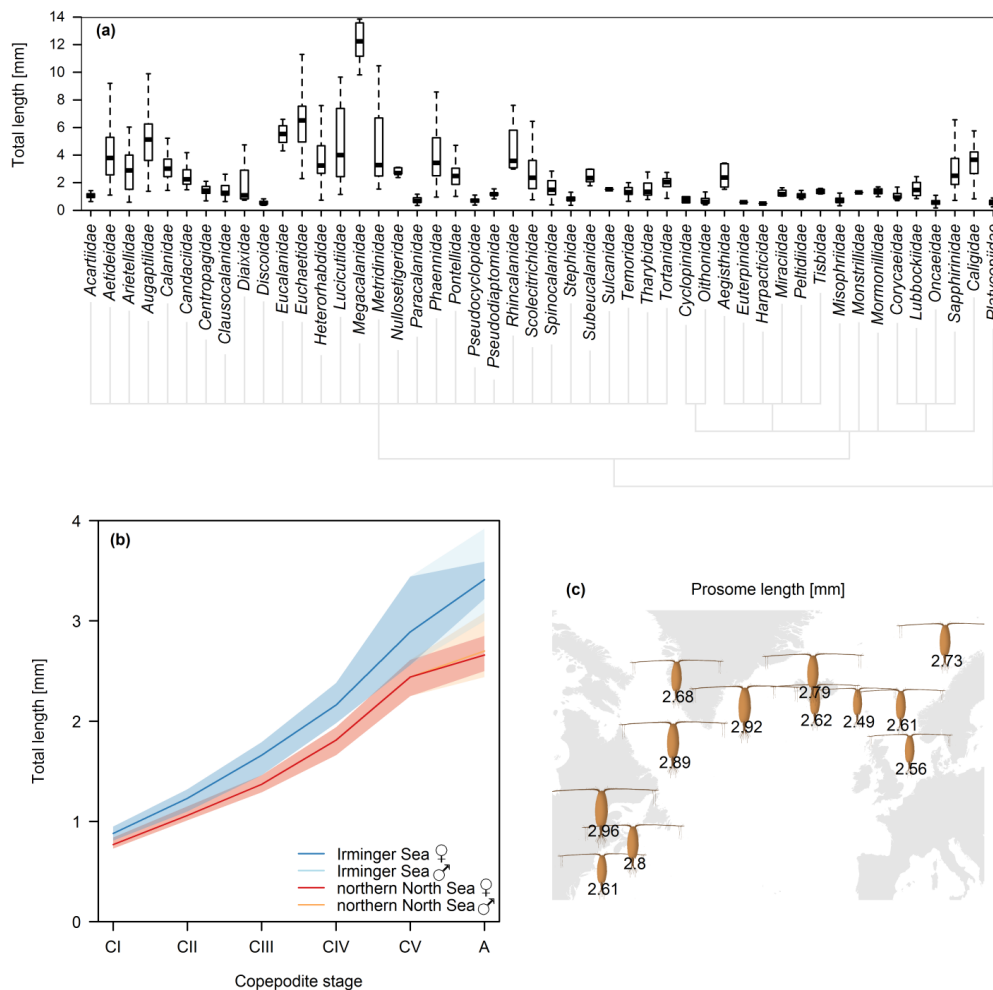
538 Fig. 2

539





540 Fig. 3

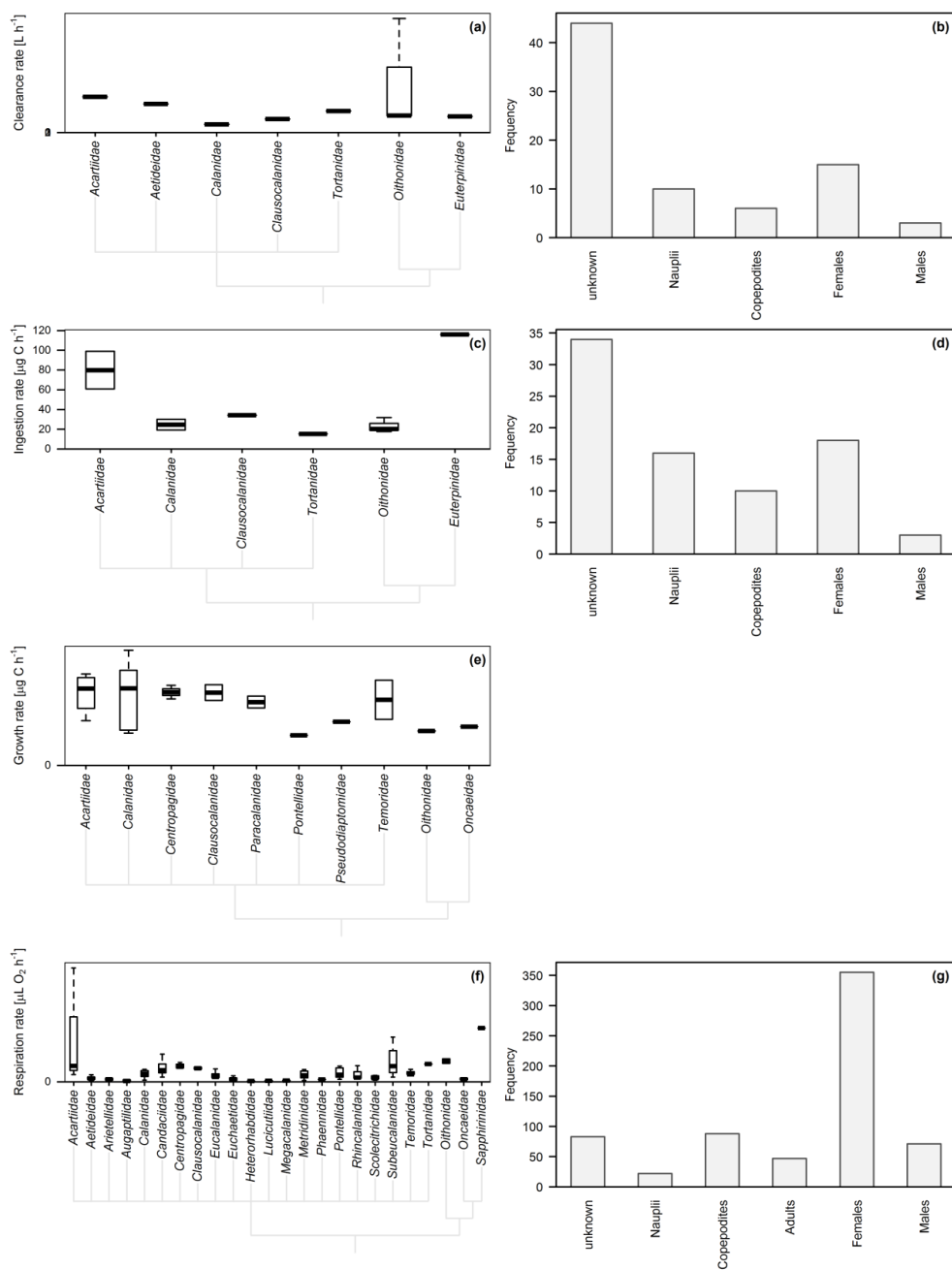


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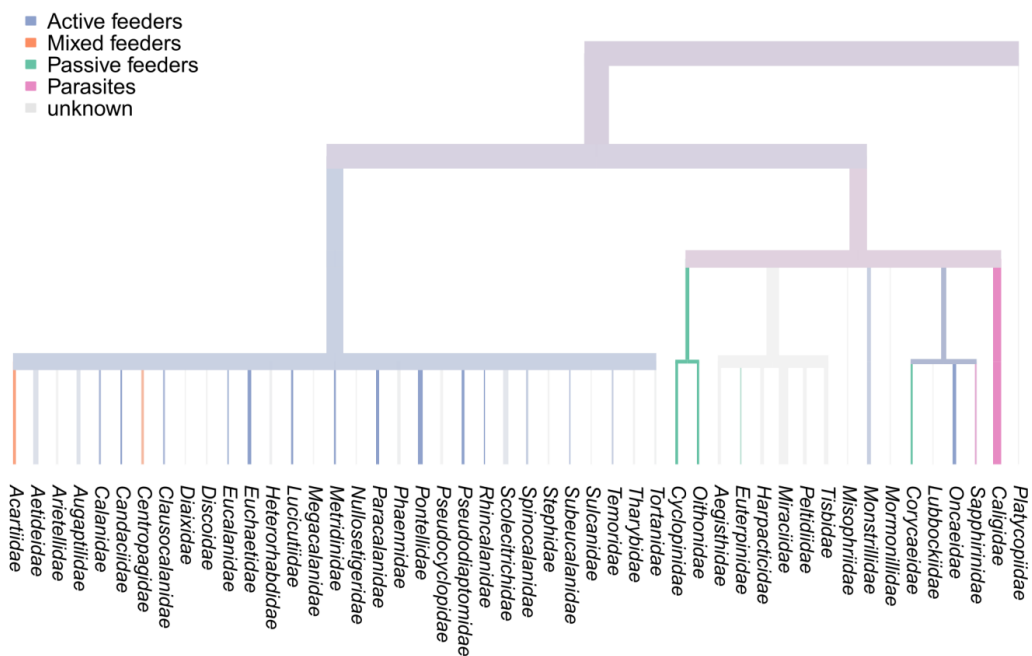
543 Fig. 4



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 545



546 Fig. 5

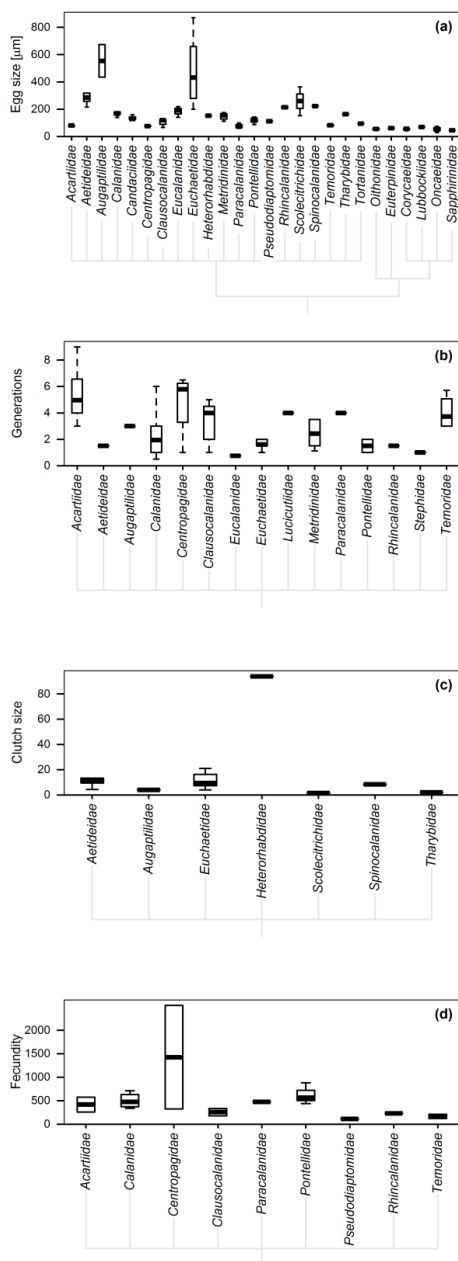


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549 Fig. 6



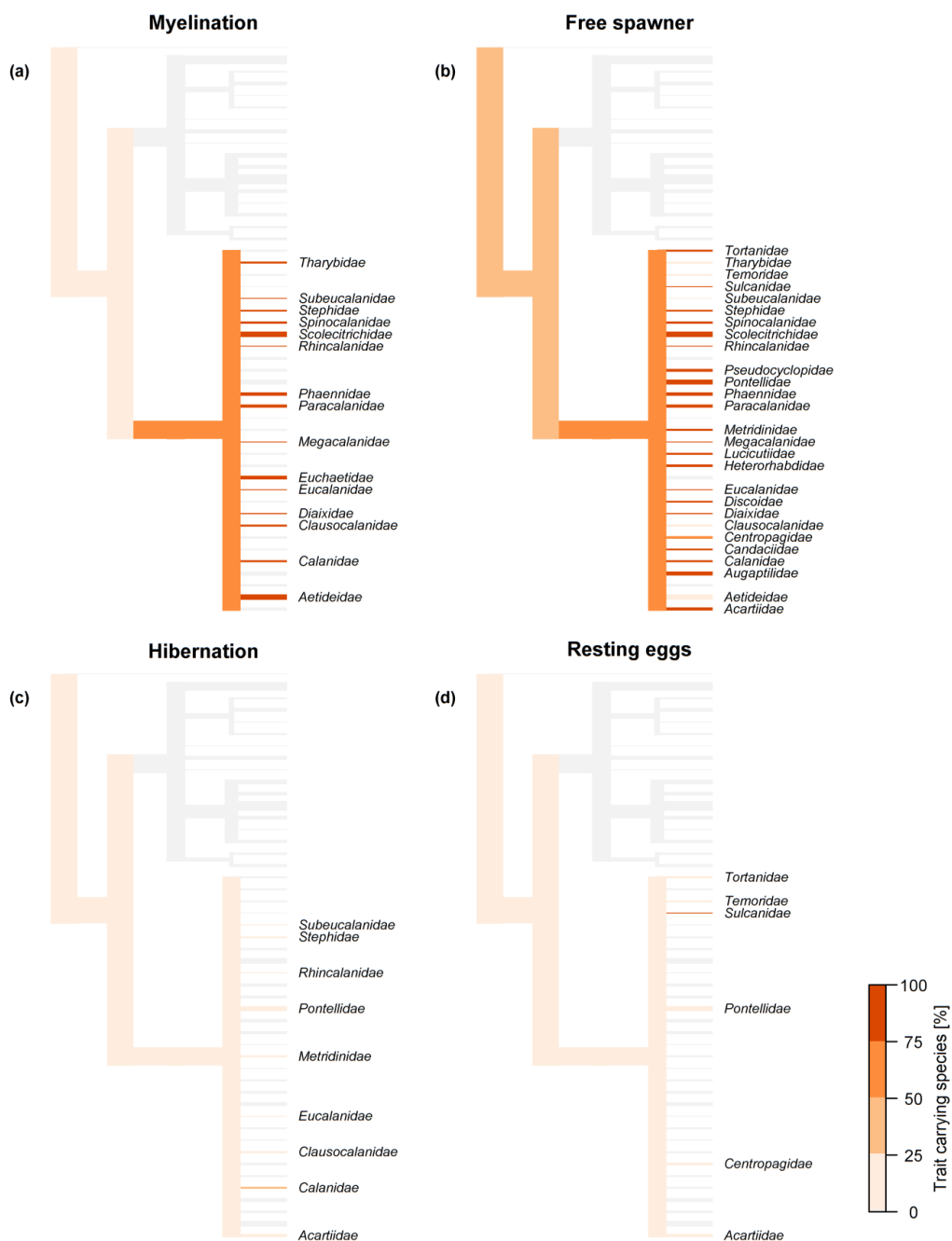
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552 Fig. 7



553