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Disentangling the counteracting effects of water content and carbon mass on zooplankton growth

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26

27 *ABSTRACT*

28 Zooplankton vary widely in carbon percentage (carbon mass as a percentage of wet mass), but are

29 often described as either gelatinous or non-gelatinous. Here we update datasets of carbon

30 percentage and growth rate to investigate whether carbon percentage is a continuous trait, and

31 whether its inclusion improves zooplankton growth models. We found that carbon percentage is

32 continuous, but that species are not distributed homogenously along this axis. To assess variability

33 of this trait in situ, we investigated the distribution of biomass across the range of carbon percentage

34 for a zooplankton time series at station Plymouth L4. This showed separate biomass peaks for

35 gelatinous and crustacean taxa, however carbon percentage varied 8 fold within the gelatinous

36 group. Species with high carbon mass had lower carbon percentage, allowing separation of the

37 counteracting effects of these two variables on growth rate. Specific growth rates, g (d^{-1}) were

38 negatively related to carbon percentage and carbon mass, even in the gelatinous taxa alone,

39 suggesting that the trend is not driven by a categorical difference between these groups. The

40 addition of carbon percentage doubled the explanatory power of growth models based on mass

41 alone, demonstrating the benefits of considering carbon percentage as a continuous trait.

42

43 *INTRODUCTION*

44 Gelatinous zooplankton are a phylogenetically broad and ecologically important group of taxa

45 found throughout the world's oceans. Their prey range from bacteria to fish (Sutherland et al.,

46 2010) and they exhibit an equally diverse range of life history strategies and body compositions.

47 The high water content characteristic of this group can be expressed as carbon percentage (carbon

48 mass as % of wet mass), with some taxa having carbon mass as low as 0.01% of their wet mass

49 (Clarke et al., 1992; Harbison, 1992; Lucas et al., 2011; Kiørboe, 2013).

50

51 Interest in gelatinous zooplankton is linked to a growing appreciation of their impact on pelagic

52 ecosystems and human activities (Richardson et al., 2009; Purcell, 2012, Gibbons and Richardson,

53 2013). For example, the introduction of the ctenophore, *Mnemiopsis leidyi* to the Black Sea has had

54 considerable financial implications for fisheries in the area (Shiganova and Bulgakova, 2000).

55 Research on gelatinous zooplankton has grown apace with basic ecological interest in the

56 physiology, trophic ecology and bloom dynamics of this group (Møller and Riisgård, 2007;

57 Gemmell et al., 2013; Condon et al., 2013).

58

59 Based on a compilation of zooplankton body composition, Kiørboe (Kiørboe, 2013) found that most

60 zooplankton species are either gelatinous (~0.5%) or non-gelatinous (5-10%), with comparatively

61 few intermediates. Indeed, much research has been directed toward comparing and contrasting

62 gelatinous versus non-gelatinous zooplankton. For example, compared to other planktonic animals,

63 gelatinous zooplankton have higher carbon mass-specific feeding rates (Hamner et al., 1975;

64 Acuña, 2001; Acuña et al., 2011), lower locomotion costs and higher specific growth rates (Hirst et

65 al., 2003; Pitt et al., 2013). Indeed, gelatinous taxa such as salps are amongst the fastest growing

66 metazoans (Bone, 1998).

67

68 The use of a categorical approach to zooplankton body composition (i.e. gelatinous versus non-

69 gelatinous) contrasts with the treatment of carbon mass (Peters, 1983), which is used as a

70 continuous variable in many models of growth (Hansen et al., 1997; Gillooly et al., 2002, Hirst et

71 al. 2003). However, the carbon percentage of zooplankton species also varies widely, even among

72 gelatinous taxa (Molina-Ramirez et al. 2015). A recent review suggested that water content was

73 second only to body size in determining key aspects of the biology of zooplankton (Andersen et al.,

74 2015b). So far, empirical models of zooplankton growth use equations that are specific to various

75 taxonomic groups (e.g. Hirst et al. 2003, Kiørboe & Hirst, 2014) and these equations have not yet

76 been unified. As carbon mass and carbon percentage are both variable traits, it is important to

77 consider them together in empirical models of zooplankton growth. Furthermore, quantifying the

78 relationship between growth rate and carbon percentage may help to explain how carbon percentage

79 functions as an evolutionary trait, and, for example, why there are gelatinous representatives from

80 six phyla found in the plankton.

81

82 In this study we have used both a meta-analyses approach and an in-situ time series of zooplankton

83 from weekly sampling at the Plymouth L4 time series (Smyth et al. 2015). We had three objectives.

84 The first was to quantify the degree of variability in carbon percentage both in "trait space" from

85 the meta-analysis dataset and in a natural plankton assemblage, to gauge whether it was appropriate

86 to treat water content as a continuous variable. The second aim was to investigate the degree of

87 collinearity between carbon mass and carbon percentage, again both in a meta-assemblage and in

88 the L4 assemblage. Dependent on the outcome of these two objectives, the third aim was to

89 construct a simple empirical model of zooplankton growth that combines carbon mass and carbon

90 percentage.

91

92 *METHODS*

93 *Carbon percentage data*

94 Ratios of wet mass to carbon mass were combined from a series of recent compilations (Kiørboe,

95 2013;Pitt et al., 2013;Molina-Ramirez et al., 2015). The amalgamated dataset with their sources is

96 presented in Supplementary Information 1. Only concurrent measurements of carbon and wet mass

97 of the same individual were used to calculate carbon percentage.

98 The degree of tissue dilution of zooplankton taxa has been expressed previously as body carbon

99 content (Molina-Ramirez et al., 2015). However to avoid confusion with carbon mass, throughout

100 this paper it is referred to as "carbon percentage" (carbon mass as a percentage of wet mass). For

101 our comparisons the levels of taxonomic organisation were selected based on functional diversity

102 and body form (e.g. phylum for Chaetognatha, but orders Cydippida and Lobata).

103

104 *In situ analysis*

105 To investigate how species biomass was distributed along the spectrum of carbon percentage an in

106 situ community, the L4 zooplankton time series (Western Channel Observatory, Plymouth) was

107 used. The L4 sampling site is approximately 15km south-west of Plymouth and undergoes seasonal

108 stratification (Harris, 2010). Sampling at the L4 site consists of a pair of vertical hauls with a 200

109 µm WP2 zooplankton net from 50 m to the surface (maximum depth 54m). The nets are retrieved at

110 20 cm s^{-1} and are immediately fixed in 4% formaldehyde solution (Maud et al., 2015). The

111 zooplankton are then subsampled, counted and identified (Eloire et al. 2010). This zooplankton

112 abundance times series has high resolution both temporally (weekly sampling) and taxonomically,

113 with many taxa consistently identified to species level since 2009. To determine zooplankton

114 biomass, a total of 3780 individuals from the formalin-preserved catches at L4 taken throughout

115 2014 and 2015 were measured. From standard length measurements (e.g. cnidarian bell height or

116 diameter, copepod prosome length), length-carbon mass relationships from the literature were used

117 to estimate carbon masses per individual. These length measurements were then aggregated into

118 seasons, namely spring (March-May), summer (June-August), autumn (September-November) and

119 winter (December to February) to account for the high intraspecific variability in length observed at

120 L4 (Atkinson et al., 2015). This allowed us to derive season-specific mean carbon masses per

121 individual, which were multiplied by numerical densities to estimate biomass density (mg C m^{-3}).

122 Previously measured, L4-specific seasonal values of individual carbon biomass were used, when

123 available (e.g. *Calanus helgolandicus;* Pond et al. 1996).

124

125 Of the approximately 189 taxa recorded at L4, only 22 contributed more than 0.5% to the total

126 biomass for all species. To examine how biomass was distributed across the spectrum of carbon

127 percentage, these taxa were assigned to log$_2$ classes (0.1 - 0.2%, 0.2 – 0.4%, 0.4 – 0.8%, 0.8 – 1.6%,

128 1.6 – 3.2%, 3.2 – 6.4%, 6.4 – 12.8%, > 12.8%) using the carbon percentage data in Supplementary

129 Information 1. The distribution of carbon biomass in each carbon percentage category across the

130 seasons was then calculated.

131

132 *Growth rate data*

133 Using the references from the appendices of Kiørboe and Hirst (Kiørboe and Hirst, 2014) as a

134 starting point, zooplankton growth rate data were extracted from the original sources and

135 augmented by searching the literature. All growth rate data used here are in Supplementary

136 Information 2.

137

138 To improve comparability of source data we restricted the meta-analysis to data from laboratory

139 incubations with food available in high (assumed non-limiting) concenrations. By using only data

140 collected under these conditions we suggest that the measurements are more directly comparable,

141 with the observed patterns more likely to reflect the intrinsic biology of the species than external

142 factors.

143

144 Published growth rates are normally expressed either as increase in length or body mass over time.

145 When organism size was expressed as length, published length-mass regressions were used to

146 convert to body carbon mass (Hirst, 2012; Kiørboe and Hirst, 2014). To express growth rates in the

147 terms commonly used for zooplankton (as an exponential rate; see Hirst and Forster 2013), the

148 mass-specific growth rate, *g* (d^{-1}) was determined as:

149   $g = (\ln M_t - \ln M_0)/d$

150   where M_t is mass at time t, M_0 is mass at the previous time point, and d is the time period between

151   the two measurements of mass (in days).

152

153   Growth data were temperature-corrected to 15°C using a Q_{10} of 2.8 (following Hansen et al., 1997;

154   Kiørboe and Hirst, 2014). General linear models (GLMs) were constructed in R (R Core Team,

155   2014) to determine the relationships between growth rate, carbon percentage and carbon mass. To

156   determine whether there was collinearity between the predictor variables we examined the condition

157   indices for the variables in the model using the *colldiag* function in the *perturb* package in R

158   (Hendrickx, 2012). A condition index of greater than 30 is considered large (Belsley et al., 1980)

159   and suggests that the variable should be removed from the model.

160

161   When growth data were available for a species but carbon percentage values were not, the latter was

162   estimated using the mean value for the highest level of taxonomic relatedness available. For

163   instance, if composition values for a species were not available, then the composition values for all

164   other species within the genus were averaged and used as an estimate. The estimates were typically

165   at the genus level but no lower relatedness than family (38% estimated at family level, primarily for

166   copepods).

167

168   *Growth rate analysis*

169   Four analyses were performed; the first two were based on mean and maximum growth rates for all

170   zooplankton taxa in the dataset, the second two as above but for the classical gelatinous taxa only

171   (Cnidaria, Ctenophora and Thaliacea). Maximum growth values were defined as the highest

172   temperature-adjusted growth rate value available for each species. Issues of non-independence

173   between data were avoided by using single growth rate values per species per study. For illustrative

174   purposes only (i.e. the plots in Fig. 4), we adjusted all growth rates to a fixed body carbon mass of

175   1mg C after correcting to 15°C. This mass correction was performed assuming $\log_{10}$ mass-specific

176   growth (g) scales against $\log_{10}$ mass with a slope of -0.25 (Brown et al. 2004).

177

178   *RESULTS*

179   *Variability in carbon percentage across the zooplankton*

180   The range in body volume for two animals of equal carbon mass but at either end of the carbon

181   percentage spectrum is demonstrated in Figure 1. For the compiled dataset, the range in carbon

182   percentage extended over four orders of magnitude in zooplankton, from 0.01% in the lobate

183   ctenophore, *Bathycyroe fosteri*, to 19.02% in the copepod, *Calanus hyperboreus* (Fig. 1, 2a,

184   Supplementary Information 1). The intervals between adjacent ranked species were small relative

185   to the range covered (Fig. 2a), suggesting that water content could be considered as a continuous

186   variable. The largest interval between species coincided with the shift from the classic gelatinous

187   taxa to other zooplankton (i.e. from Thaliacea to Chaetognatha). However, this difference between

188   species constituted a relatively small fraction of the total range (6.8%). In addition, there was

189   overlap of classic gelatinous and non-gelatinous groups. For example, some chaetognaths were

190   within the traditional gelatinous range (1.27% and 1.35% for *Pseudosagitta lyra (as P. scrippsae)*

191   and *Pseudosagitta* (as *Sagitta) gazellae* respectively), whereas one tunicate had a carbon percentage

192   which lay within the non-gelatinous range (3.87% for *Doliolum denticulatum*). This overlap of

193   taxonomic groups was extensive across the spectrum of water content, as can be seen by the mixing

194   of colour across Fig. 2. This was particularly the case among the Ctenophora and Thaliacea with the

195   range of both taxa approaching two orders of magnitude in carbon percentage.

196

197   The wide variation in body carbon percentage observed at a species level in Fig. 1a is also

198   summarised at the broader taxon level in Fig. 2b. Median values for groups do loosely cluster into

199   gelatinous and non-gelatinous taxa following the bimodal distribution of species suggested by

200   Kiørboe (Kiørboe, 2013). The ranges of all adjacent taxa (excluding lobate ctenophores)

201   overlapped, with Thaliacea and Chaetognatha bridging the gap between the classical gelatinous and

202   non-gelatinous taxa. The variability within groups was greater for gelatinous taxa, with the greatest

203   range in the scyphomedusae, closely followed by the thaliaceans. The gelatinous taxa sort into their

204   respective phyla when ranked (i.e. Lobata, Nuda, Cydippida for the Ctenophora, then

205   Hydromedusae and Scyphomedusae for Cnidaria) suggesting that taxa within phyla are on average

206   more similar to each other than with other phyla.

207

208   In the natural assemblage sampled at the Plymouth L4 site (Figure 3) we have an alternative picture,

209   namely how biomass is distributed along this spectrum of carbon percentage. At L4, biomass is

210   distributed bimodally. The biomass is primarily concentrated in the categories that are either highly

211 gelatinous (carbon mass $0.1 - 0.8\%$ of wet mass) or non-gelatinous ($6.4 - > 12.8\%$) However, there

212 is considerable variability within the carbon percentage categories, as some gelatinous taxa are as

213 much as 8 times larger in wet mass for the same carbon mass as others. The biomass in the

214 intermediate categories ($0.8 - 1.6\%$ and $1.6 - 3.2\%$) was very low and below our threshold for

215 inclusion. This area of the spectrum is populated by thaliaceans and large rhizostome

216 scyphomedusae, which are either not commonly recorded at L4 (thaliaceans) or are rarely or poorly

217 sampled by the 0.57 cm diameter nets used. Gelatinous taxa comprise a greater proportion of

218 biomass in summer than the other seasons. In winter, chaetognaths (3.56%) have similar total

219 biomass to the dominant copepods. There is also a broad trend of increasing carbon percentage

220 through the year within the gelatinous taxa. In spring, the cydippids (the most gelatinous group

221 frequently encountered at L4) are dominant, followed by Nuda (Beroe) in summer and finally

222 hydromedusae and siphonophores in autumn.

223

224 *Relationship between carbon mass and carbon percentage*

225 There were negative relationships between carbon mass and carbon percentage, both in the meta-

226 dataset (Fig. 4a) and in the in situ dataset (Fig.4b). While the more gelatinous taxa tended to have

227 higher carbon mass there was considerable variability, with some organisms of similar carbon mass

228 differing 100-fold in carbon percentage (Fig. 4). To ensure that collinearity was not influencing the

229 growth model the condition indices for the variables were inspected. The highest condition index

230 observed was 3.05, lower than the threshold of 30 suggested by Belsley (Belsley et al., 1980)

231 confirming that carbon mass and carbon percentage can be used in combination in models of

232 zooplankton growth. As gelatinous and small organisms tend to grow fastest, the tendency for more

233 gelatinous taxa to have higher carbon mass underlines the need to include both as covariates in our

234 growth model.

235

236 *Relationship between carbon percentage and growth rate*

237 We first conducted GLMs on the subset of data comprising the classical gelatinous taxa alone.

238 These showed that mean growth rate declined with increasing mass and increasing body carbon

239 percentage. The GLMs on the whole dataset established that $\log_{10}$ mass-specific mean and

240 maximum growth rate was significantly correlated with both $\log_{10}$ carbon mass and $\log_{10}$ body

241 carbon percentage (Fig. 5, Table I). As expected, there was a negative relationship between $\log_{10}$

242 mass-specific growth rate (g), and $\log_{10}$ carbon mass, in line with the results of Kiørboe and Hirst

243 (Kiørboe and Hirst, 2014). In the analyses of all zooplankton taxa, mean and maximum growth rate

244 decreased with increasing carbon mass and carbon percentage.

245

246 In all analyses, the addition of body carbon percentage to models of growth based on carbon mass

247 alone increased the explanatory power (Table II). The second order Akaike criterion , AICc,

248 (Burnham and Anderson, 2002) was lower in the model including water content in all analyses,

249 supporting the inclusion of this factor in analyses of zooplankton growth. In the maximum analysis

250 including all taxa, Akaike weights (ω_i) were approximately 10 times higher in the models including

251 body carbon percentage (mass $\omega_i = 0.08$, mass + carbon percentage $\omega_i = 0.92$). This suggests that

252 these models were significantly better than models based on mass alone (Royall, 1997). A similar

253 pattern was observed in the analysis of maximum growth rates of the gelatinous taxa however it was

254 not observed for mean growth rates (mass $\omega_i = 0.02$, mass + GI $\omega_i = 0.98$).

255

256 *DISCUSSION*

257 Our study provides strong support for: body carbon percentage being a continuous trait, for a

258 negative relationship between body carbon percentage and growth rate, and for considerable

259 increases in model predictive power as a result of inclusion of this trait for zooplankton. Below we

260 discuss the implications of each of these findings in turn.

261

262 Kiørboe (Kiørboe, 2013) demonstrated that if zooplankton are arranged in a frequency distribution

263 based on body composition, that most taxa are either gelatinous (carbon mass is ~0.5% of wet mass)

264 or non-gelatinous (~5-10%), with little overlap. Our study would appear to contradict this, since we

265 found a fairly continuous distribution of carbon percentage. However, this does not conflict with the

266 findings of Kiørboe (Kiørboe, 2013), since in that study it was emphasised that most taxa are either

267 highly gelatinous or non-gelatinous. Rather, we highlight that, while the most species fall into one

268 of these two groups, there is considerable variability in carbon percentage within each group and

269 there are representatives across much of this spectrum. The distribution of zooplankton biomass at

270 L4 supports both of these views. Biomass is clustered at either end of the spectrum as described

271 previously, and this could suggest that the fitness landscape for this trait favours extremes.

272 However, at either end of the spectrum there is considerable variability. The traditional gelatinous

273 group alone spans an 8-fold range in carbon percentage, with implications for growth rate. For

274   example, there is a trend of increasing carbon percentage among the gelatinous zooplankton through

275   the year, with cydippids being replaced by beroids in summer and finally by hydromedusae and

276   siphonophores in autumn.

277

278   In the meta-analysis compilation, the largest interval occurs between taxa typically considered as

279   gelatinous and intermediate, between the pelagic tunicate, *Thalia* (as *Salpa) democratica* (1.6 %

280   body carbon percentage) and a chaetognath, *Eukrohnia hamata* (2.7 % body carbon percentage.

281   Molina-Ramirez et al. (Molina-Ramirez et al. 2015) stressed that considerable variation in carbon

282   percentage existed even within the classic gelatinous taxa (Cnidaria, Ctenophora and Tunicata). Our

283   results are in agreement, albeit with even higher degree of variability (at 350-fold). Taken together,

284   the relatively small interval between values for gelatinous and non-gelatinous species and the high

285   variability observed within the gelatinous taxa suggest that growth models can indeed incorporate

286   carbon percentage as a continuous trait.

287

288   When $\log_{10}$ mass-specific growth rate was regressed against $\log_{10}$ body carbon percentage as a

289   continuous variable, a negative relationship was observed. Crucially, the pattern persisted when

290   considering the gelatinous taxa alone (Table II). The existence of the relationship among the

291   gelatinous taxa alone, is important as this demonstrates that the relationship is not due to a

292   categorical difference between gelatinous organisms and non-gelatinous organisms.

293

294   One potential mechanism that could explain the relationship between body carbon percentage and

295   growth rate is enhanced feeding rate (Acuña et al., 2011). These authors suggested that the large

296   dilute bodies of gelatinous zooplankton facilitate higher carbon-specific feeding rates than other

297   zooplankton taxa of the same carbon mass. If this increased feeding rate drives faster growth, then

298   this might explain the relationship of increasing growth rate with decreasing carbon percentage (see

299   Fig. 2). As many gelatinous taxa are filter or ambush feeders that rely on capture surfaces to feed,

300   assuming that feeding rate scales with surface area, then we may expect the scaling exponent

301   between surface area and body carbon percentage to match the exponent for growth rate and body

302   carbon percentage. To investigate this we used a simple geometric calculation. Assuming

303   isomorphic growth, surface area (SA) scales with body volume with a power of 0.67. By altering

304   degree of gelatinousness for a fixed amount of body carbon, SA then scales with carbon percentage

305   with a power of -0.67. Hence, with an assumption that growth rate is a fixed proportion of feeding

306 rate, this would give the same slope of -0.67 for $\log_{10}$ mass-specific growth versus $\log_{10}$ carbon

307 percentage (Fig. 2). The exponents that we determined empirically across the various zooplankton

308 taxa are less steeply negative than -0.67 (at -0.18 and -0.16 for mean and maximum respectively),

309 i.e. increasingly gelatinous organisms increase their growth rate less rapidly than these surface

310 considerations would predict. This could indicate a potential feeding inefficiency associated with

311 decreasing carbon percentage or that factors additional to surface area may also be important.

312

313 In common with Ikeda (Ikeda, 2014), we found that species with larger total carbon masses also

314 tended to be more watery. Furthermore, as the larger organisms are typically more watery the

315 effects of carbon mass and carbon percentage tend to counteract, underscoring the need to include

316 these variables together in order to better predict growth. Molina-Ramirez et al. (Molina-Ramirez et

317 al., 2015) found a similar result for tunicates but found that body carbon percentage was invariant

318 with increasing mass for cnidarians and ctenophores. The authors suggested that this might be due

319 to differences between internal filter feeding in tunicates and external ambush or cruise feeding in

320 the other groups. It has been suggested that feeding modes decrease in efficiency with increasing

321 size (Kiørboe et al. 2011), so high water content may help to mitigate this decrease in efficiency and

322 maintain relatively higher carbon specific feeding rate at large carbon masses. This is supported by

323 the findings of Acuña et al. (Acuña et al., 2011), suggesting that gelatinous plankton had higher

324 carbon-specific feeding rates than other zooplankton of a similar carbon mass. Together with higher

325 growth rates, these factors could help to explain how gelatinous zooplankton are capable of forming

326 such high localised increases in species biomass (blooms).

327

328 While the increase in capture surface area and associated feeding and growth rates is one potential

329 advantage of the gelatinous body form, there are other implications. There are potential negative

330 implications also, especially with regard to limited swimming speed and escape responses. While

331 medusae have potential defences in the form of nematocysts, many gelatinous taxa such as

332 ctenophores do not, and may have limited ability to escape from potential predators as a result of

333 their large dilute bodies (Acuña, et al. 2011). Understanding why some taxa are gelatinous is not

334 always straightforward. The most gelatinous mollusc in this analysis is *Clione limacina*, a

335 gymnosome predator that feeds on almost exclusively on *Limacina helicina*. *Clione* does not rely on

336 large capture surfaces or on generating a feeding current as it ambushes individual, relatively large

337 prey items. In this case, water content does not appear to be a derived trait to increase body volume

338 relative to carbon for feeding, suggesting that this may not be the only driver of high water content

339 in zooplankton. It has been suggested that potential other causes include physical or ecological

340 factors such as transparency to impair visual predation (Hamner et al., 1975) or the efficiency of

341 neutral buoyancy (Kiørboe, 2013). Together these factors may help to explain why semi-gelatinous

342 bodies are observed in at least six major planktonic phyla (Cnidaria, Ctenophora, Chordata,

343 Annelida, Chaetognatha, Mollusca, see Supplementary Information 1).

344

345 *CONCLUSIONS*

346 Body size is often described as a master-trait, and is frequently used as the sole intrinsic variable in

347 empirical and simulation models involving zooplankton growth (Kiørboe and Hirst, 2014, Anderson

348 et al., 2015a). But what do we mean by "body size"? Carbon mass is often used as the unit for size,

349 but both our meta-analysis and the real assemblage data show that carbon percentage also varies

350 greatly. It may even vary negatively with carbon mass, levering an opposing effect on growth. We

351 argue that carbon mass and carbon percentage are both key traits, both are intrinsic to the

352 zooplankton and since they are possible to estimate, then we should disentangle their separate

353 effects in a unified growth model. By including carbon percentage to models of growth based on

354 carbon mass alone, we substantially increased their explanatory power, with smaller body masses

355 and lower body carbon percentages leading to higher specific growth rates. Building on the work of

356 previous publications (Kiørboe, 2013, Pitt et al., 2013, Molina-Ramirez et al., 2015) we provide a

357 carbon percentage dataset in Supplementary Table 1. By using these source data alongside carbon

358 masses, the maximum growth rate equation in Table 1 may then be used as a starting point to

359 estimate growth rates attainable by zooplankton.

360

361 Alongside the "size" based simplifications used for modelling, there has also been an increase in

362 "trait-based" modelling in which categorical variables or functional groups are allowed to vary

363 continuously. A purpose of this paper is to allow water content also to be used as a continuous trait;

364 to facilitate its inclusion alongside carbon mass and other traits such as feeding mode (Litchman

365 2013; Andersen et al. 2015a; Hérbert et al., 2016). Since we found that growth rate depended on

366 carbon percentage even among the gelatinous taxa alone, we hope that considering and modelling

367 water content as a continuous trait will reveal the ecological and evolutionary factors that influence

368 the water content of zooplankton.

369

370 *ACKNOWLEDGEMENTS*

379

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490   TABLE AND FIGURE LEGENDS:

491   Figure 1. Comparison of the relative carbon (black) and wet masses (grey) of *Calanus hyperboreus*

492   (left, carbon percentage = 19.02%) and *Bathycyroe fosteri* (right, carbon percentage = 0.01%). The

493   relative area of each shade is scaled as volume so the silhouettes are representative of true size.

494

495   Figure 2. (a) Zooplankton species ranked according to their carbon percentage (CM%WM;$\log_{10}$

496   scale), each horizontal bar represents a single species. Colours indicate taxonomic groups as

497   detailed in the legend. (b) Zooplankton taxonomic groups ranked according to their carbon mass (as

498   % of wet mass; $\log_{10}$scale). Boxes indicate median, lower and upper quartiles with whiskers

499   showing the range. (Vertical lines at 0.5 and 5 CM%WM represent the composition of the

500   gelatinous and non-gelatinous taxa defined by Kiørboe 2013).

501

502   Figure 3. Distribution of carbon biomass (mg C m^{-3}) between $\log_2$ carbon percentage (CM%WM)

503   categories through spring, summer, autumn and winter (2009-2015) at the L4 sampling site,

504   Western Channel Observatory, Plymouth. The same colour coding of taxa is used as in Fig. 1 – see

505   legend. * - Biomass value for the category 0.4 – 0.8 exceeds the scale in summer (34.4 mg C m^{-3}) as

506   a result of 7 high abundance observations of *Beroe spp.* (of total 318 samples). Upper limit of

507   biomass scale in winter is 5 mg C m^3.

508

509   Figure 4. Carbon percentage (CM%WM) as a function of carbon mass (mg) for the meta-analysis

510   dataset (A, log carbon percentage = - 0.26 * log carbon mass –0.18, p = 0.0001, R^2 = 0.21, df = 60)

511   and the L4 assemblage (B, log carbon percentage = - 0.34* log carbon mass – 1.1, p = 0.0026, R^2 =

512   , df = 20). Taxonomic groups coloured as indicated in the legends.

513

514 Figure 5. Specific growth rate, g (d^{-1}) as a function of body carbon percentage (CM%WM). Growth
515 values were temperature-adjusted to 15°C, mass adjusted to 1 mg C and then averaged for each
516 species in each study. (a) mean mass-specific growth rate values for each species in each study and
517 (b) maximum specific growth rate values for each species.

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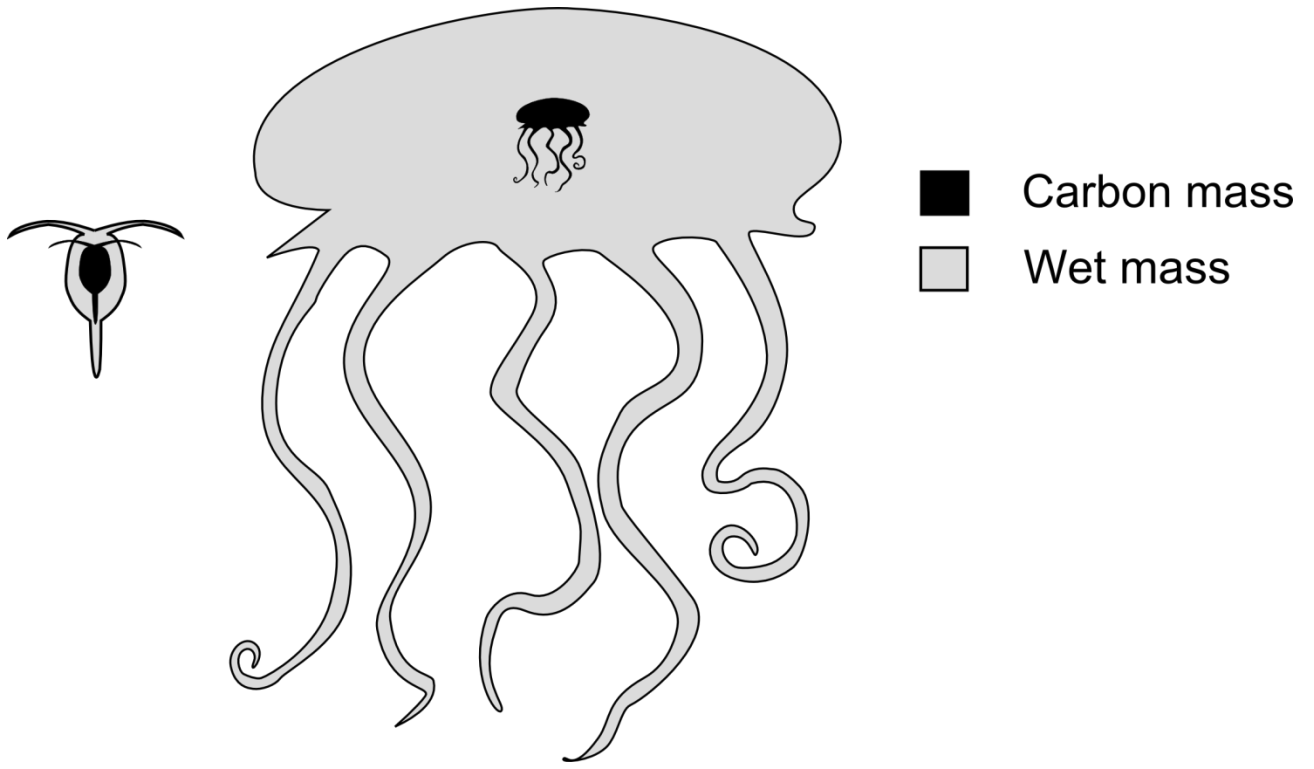
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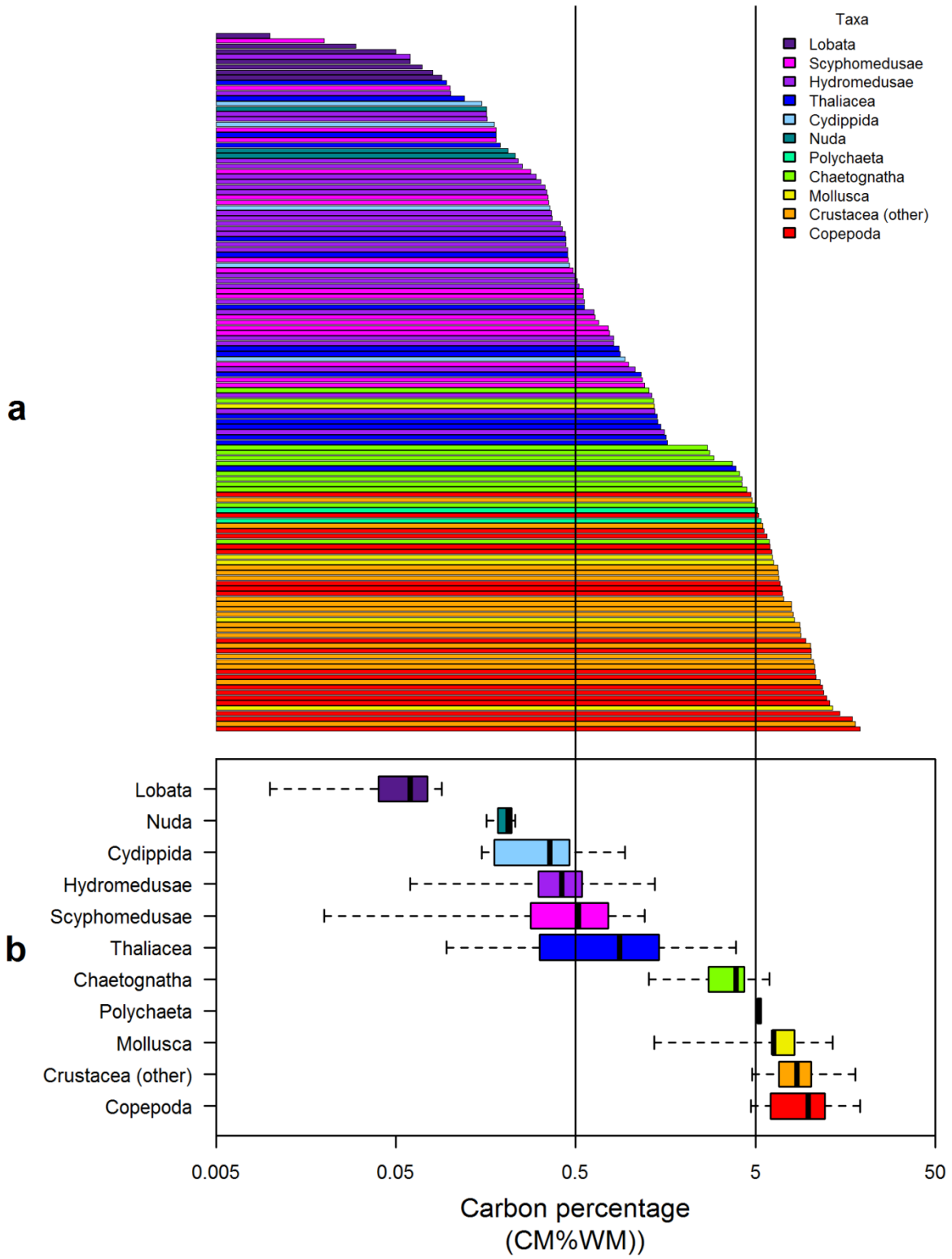525

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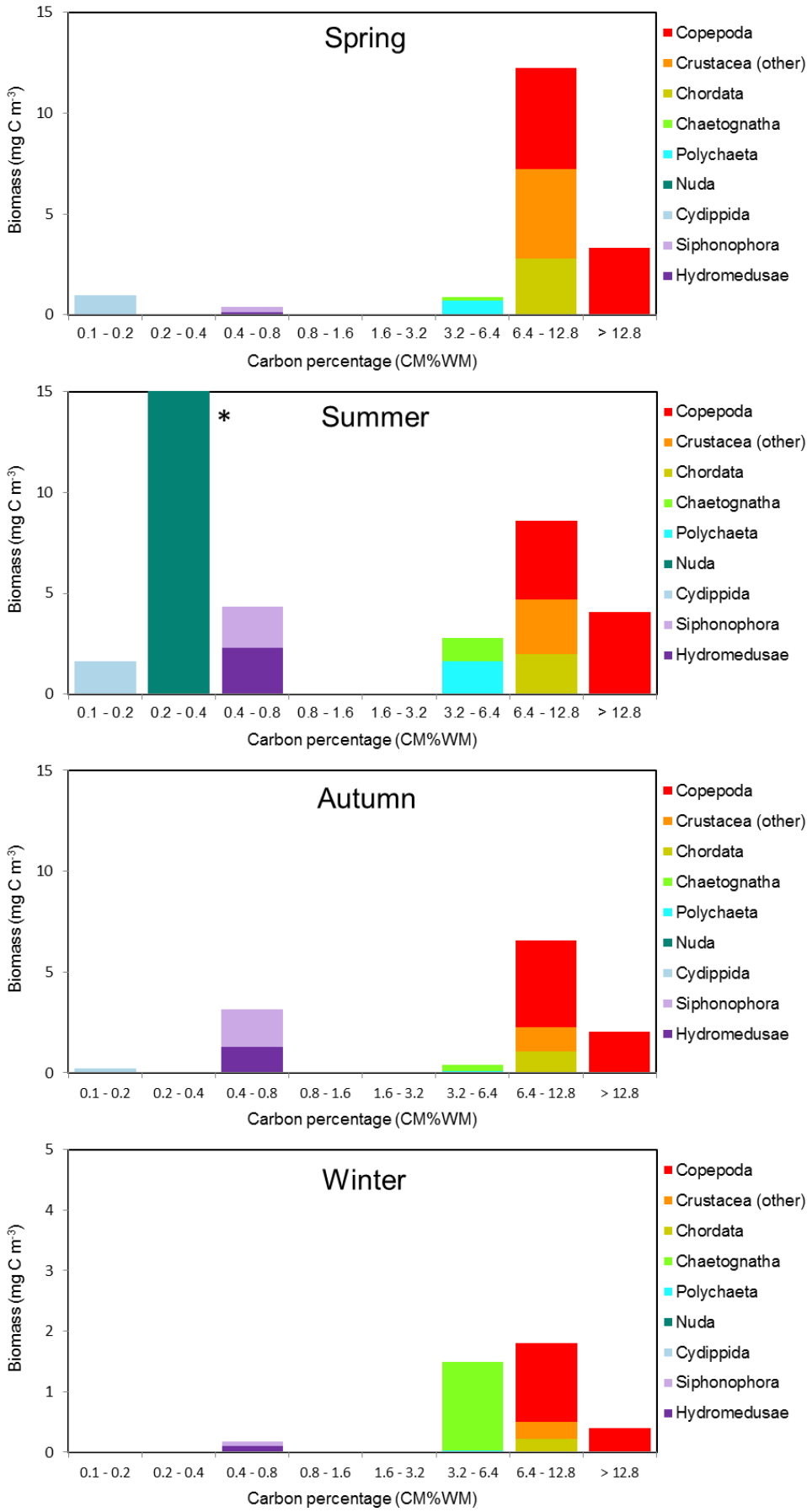531

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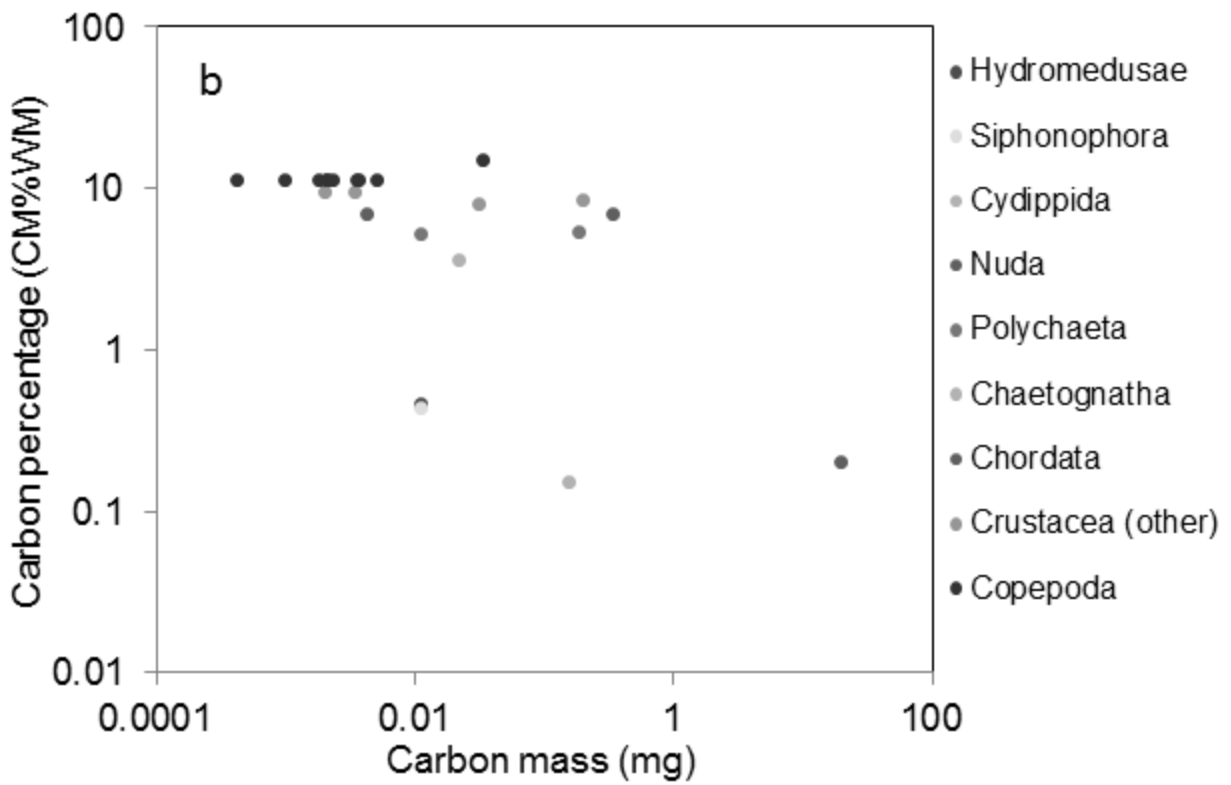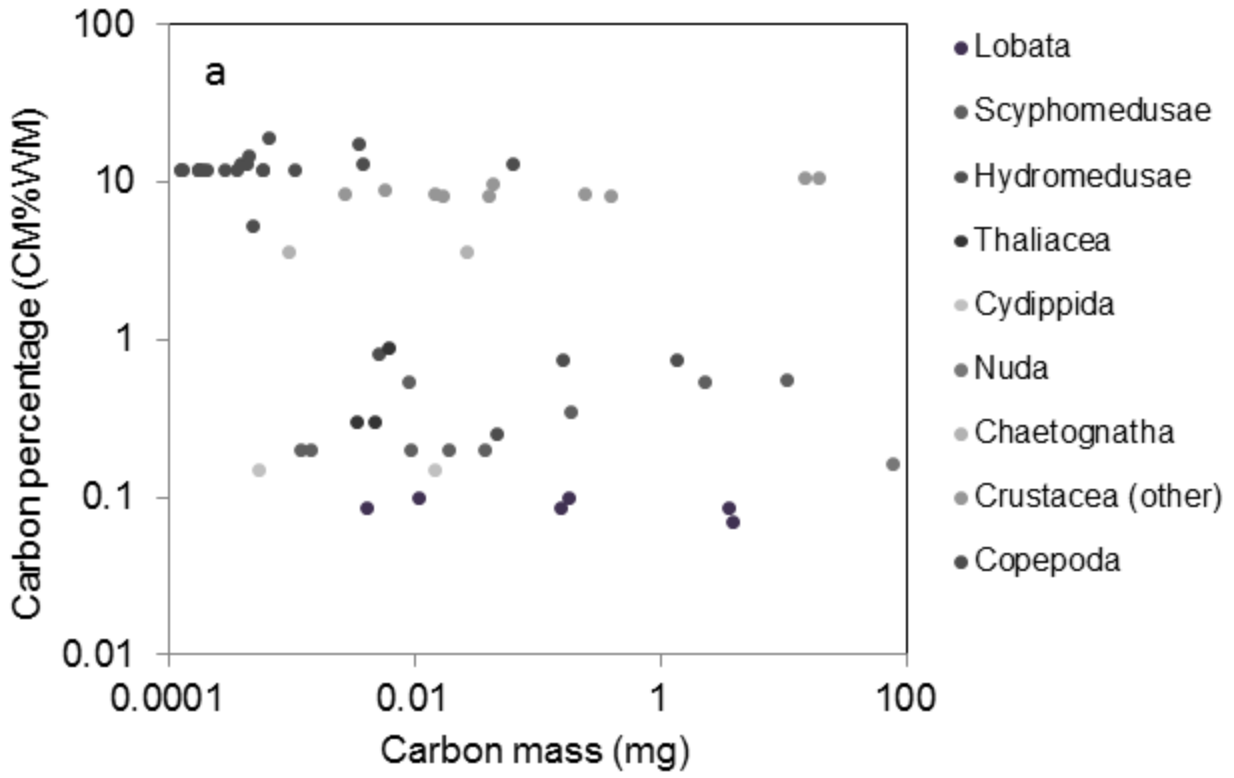
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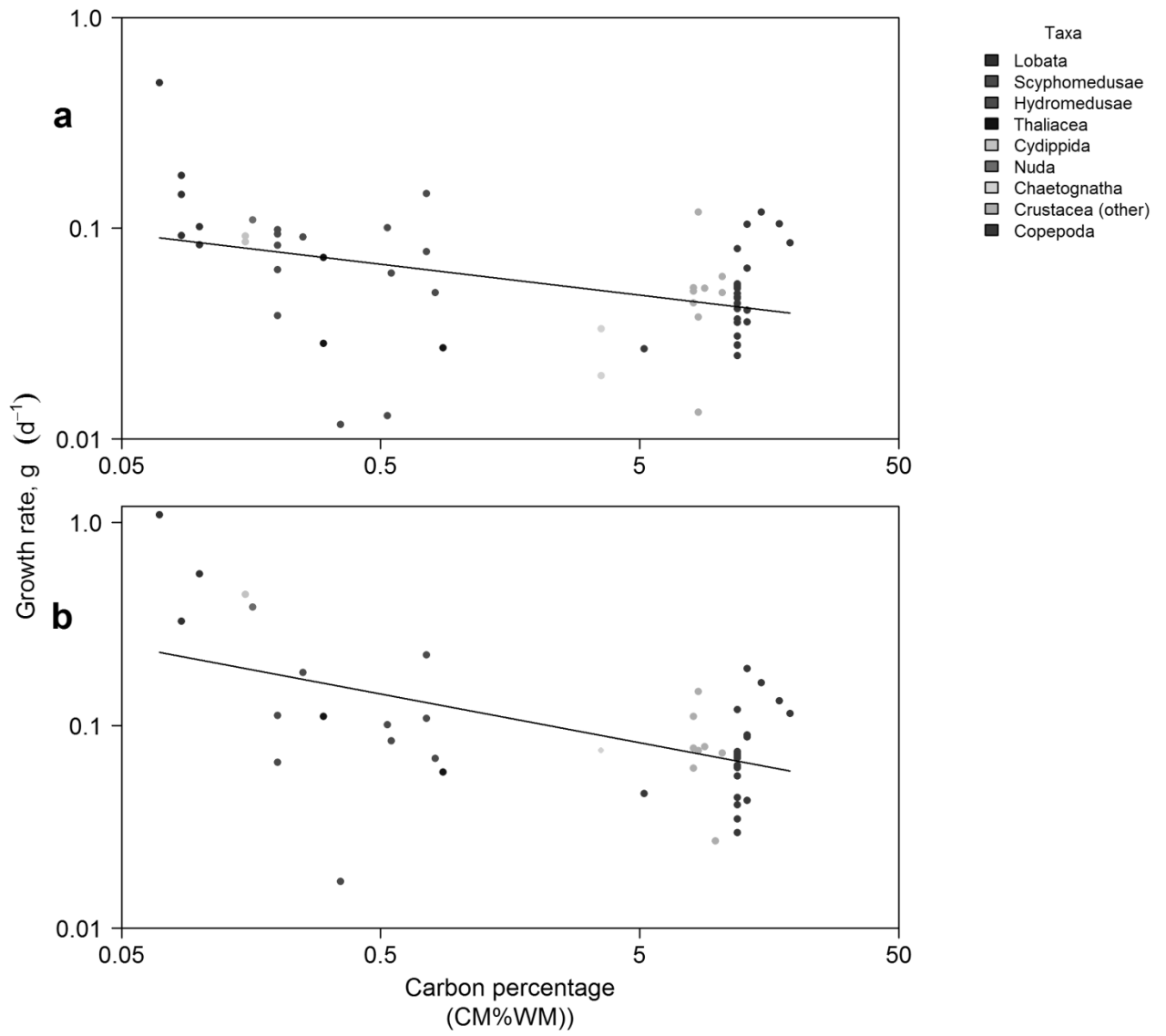
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559 Table I. General linear models predicting $\log_{10}$ mean specific and $\log_{10}$ maximum specific growth

560 rate, g (d^{-1}), as a function of both $\log_{10}$ carbon mass (mg) and $\log_{10}$ body carbon percentage

561 (100*(CM/WM)). All models pertain to growth rate data that were first Q_{10}-adjusted to 15°C.

562

563 Table II. Changes to measures of explanatory power of models of growth based solely on carbon

564 mass when body carbon percentage (CC) was added as a factor. AICc is the corrected Akaike

565 information criterion, Δ_i is the AIC difference, and ω_i is the Akaike weight. Models with Akaike

566 weight values 10 times greater than that of the other models being compared are considered

567 statistically significant as optimal models (mass + GI for mean and max all zooplankton and max

568 gelatinous taxa only). All models pertain to growth data that were first Q_{10}-adjusted to T = 15°C.

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Group		Factor	df	p	Slope	Intercept	Adj R^2
All zooplankton	Mean growth rate,g	$\log_{10}$ carbon mass	58	<0.0001	-0.17	-1.12	0.43
		$\log_{10}$ carbon percentage		0.036	-0.18		
	max growth rate,g	$\log_{10}$ carbon mass	42	<0.0001	-0.16	-0.81	0.31
		$\log_{10}$ carbon percentage		0.013	-0.16		
Gelatinous taxa only	mean growth rate,g	$\log_{10}$ carbon mass	22	0.027	-0.19	-1.18	0.33
		$\log_{10}$ carbon percentage		0.038	-0.17		
	max growth rate,g	$\log_{10}$ carbon mass	13	0.011	-0.16	-1.15	0.42
		$\log_{10}$ carbon percentage		0.018	-0.72		

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Table I

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Group	g	R^2		AICc		Δ_i	ω_i	
		Mass	Mass + CC	Mass	Mass + CC		Mass	Mass + CC
All zooplankton	Mean	0.39	0.43	18.63	16.67	2.47	0.19	0.81
	max	0.22	0.31	21.99	17.57	4.42	0.076	0.92
Gelatinous taxa only	mean	0.33	0.33	18.51	19.96	1.44	0.54	0.46
	max	0.09	0.42	21.55	16.26	5.29	0.019	0.98

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Table II