A global synthesis of seasonal temperature-size responses in copepods

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Key words: body size, temperature, chlorophyll, phenotypic plasticity, temporal, zooplankton

Running title: Seasonal temperature-size responses in copepods

Abstract: 300 | **Main Text:** 5349 | **References:** 65 | **Figures:** 5 | **Tables:** 1

Statement of Authorship

All authors designed the study and wrote the paper. CH collected the data and performed the meta-analysis.

1 **ABSTRACT**

2 **Aim**

3 Body size is a master trait with significant ecological importance. Seasonal changes in body

4 size within diverse ectothermic species can result from different environmental conditions

5 experienced during ontogeny in subsequent generations. Whilst intra-specific changes in

6 adult size have been well studied under controlled experimental conditions and across

7 geographic ranges, comprehensive analyses of temporal changes are lacking, and there

8 remains considerable unexplained variation in body size responses within aquatic taxa.

9 Using planktonic copepods as an exemplar taxon, we quantify variation in adult body mass

10 within seasonally varying marine and freshwater environments. We describe how size

11 variation relates to temperature, food concentration (chlorophyll-*a*) and life history

12 characteristics, including feeding strategy.

13 **Location**

14 Global.

15 **Methods**

16 Using a meta-analytic approach, we extract quantitative data from published literature on

17 seasonal size responses of copepods. We analyse competing models to determine the best

18 predictors of these responses, and compare the relative importance of temperature and

19 chlorophyll-*a* concentration in explaining body size variation.

20 **Results**

21 We quantify 140 seasonal size responses from 33 different global locations, representing 48

22 planktonic copepod species from 4 taxonomic orders. We find that temperature (r^2=0.50),

23 rather than food (r^2=0.22), is the dominant explanatory variable of adult body size variation

24 across seasons. A striking outcome is that current-feeding calanoids exhibit a 4-fold greater

25 reduction in adult body mass per °C (-3.66%) compared to ambush feeding cyclopoids (-

26   0.91%). By contrast, species body size or reproductive strategy did not explain variation in

27   the seasonal temperature-size response.

28   **Main Conclusions**

29   Our findings lead us to suggest that feeding strategies may play a significant role in dictating

30   the magnitude of seasonal temperature-size responses in copepods, with potential

31   implications for other ectotherms with diverse feeding methods. Seasonal temperature-size

32   responses were typically much more variable than responses in laboratory studies providing

33   excess food, suggesting that field conditions modify the temperature-size response.

34

35   **INTRODUCTION**

36   Biologists have long been fascinated by body size variation (Bergmann, 1847; Schmidt-

37   Nielsen, 1984), in part because this 'master trait' affects all vital rates, including feeding

38   (Burns, 1968; Kiørboe, 2011), growth (Poston, 1990; Kiørboe & Hirst, 2014), metabolism

39   (Peters, 1983; Glazier, 2005; Hirst *et al.*, 2014) and reproduction (Honěk, 1993; Arendt,

40   2011), as well as many other aspects of the biology of an organism (Andersen *et al.*, 2016).

41   Consequently, identifying and understanding what drives variation in body size is of

42   fundamental biological importance. Body size is sensitive to environmental conditions, due to

43   the temperature dependence of physiological processes, as well as other effects such as

44   changes in food availability. Ectothermic species that have short life-cycles and inhabit

45   seasonal environments are typically subjected to varying environmental conditions across

46   subsequent generations within a year. This is commonly linked to marked temporal shifts in

47   adult body size over an annual cycle, as sequentially recruited adults are affected by

48   different abiotic and biotic conditions over their ontogeny. Intra-specific variation in size

49   related to seasonal variation in temperature has been found across a wide range of uni- and

50   multicellular organisms, including bacteria (Chrzanowski *et al.*, 1988), rotifers (Diéguez *et al.*,

51   1998), copepods (Liang & Uye, 1997; Hirst *et al.*, 1999; Riccardi & Mariotto, 2000; Dutz *et*

al., 2012), cladocerans (Miyashita *et al.*, 2011) and insects (Kari & Huey, 2000), yet broad-scale analyses of temporal changes in adult body size are lacking.

By contrast, intra-specific variation in size at stage has been well described in the laboratory under different conditions (Atkinson, 1994; Forster *et al.*, 2012), and also spatially over latitude or across regions (Horne *et al.*, 2015). The most frequently observed intra-specific response to warmer temperatures in ectotherms is a reduction in size-at-stage; this has been formalised as the Temperature-size Rule (TSR) (Atkinson, 1994). This phenotypically plastic response can be achieved within a single generation (Forster & Hirst, 2012; Forster *et al.*, 2013), and in many metazoans the proximate cause is attributed to differences in the temperature dependence of growth and development during ontogeny (van der Have & de Jong, 1996; Forster *et al.*, 2011a; Forster *et al.*, 2011b; Zuo *et al.*, 2012). The ultimate cause of this outcome however may be a complex of several factors (e.g. see Forster *et al.* 2012; Horne *et al.* 2015). Uncertainty still remains in the degree to which these responses are found in natural field conditions, where multiple variables can act simultaneously to influence body size. For instance, the relative contribution of food and temperature in determining seasonal shifts in adult size still needs to be resolved. Food availability impacts size at maturity, but while slower growth at lower temperature is frequently coupled with an increase in adult size, slower growth with reduced food availability is typically associated with smaller size at maturity (Berrigan & Charnov, 1994). Further, food quality can dramatically alter the T-S response, even to the extent that the sign of the T-S response can be reversed under poor food quality (Diamond & Kingsolver 2010). Identifying and understanding seasonal variation in body size will not only help to determine the ultimate causes of such variation, but will also aid in predicting future shifts associated with changes in climate (IPCC, 2014) and phenology (Visser & Both, 2005). Our study aims to synthesise and quantify seasonal patterns in adult size of multivoltine species, going beyond previous species- and location-specific studies, so that we might provide a broader understanding of such patterns.

79

80   A recent meta-analysis of terrestrial and aquatic arthropods identified an impressive match

81   between T-S responses measured under controlled laboratory conditions and intra-specific

82   body size clines observed in the field across latitudes (Horne *et al.*, 2015). The magnitude

83   and direction of these responses revealed consistent differences in the strength and sign of

84   the response between aquatic and terrestrial species. These results suggest that laboratory

85   T-S responses and latitudinal body size clines may be driven by similar selective pressures

86   within arthropods, specifically, by voltinism and season length trade-offs in terrestrial species

87   (Kozłowski *et al.*, 2004; Walters & Hassall, 2006), and the need to balance oxygen demand

88   and supply in larger aquatic species (Woods, 1999; Atkinson *et al.*, 2006; Forster *et al.*,

89   2012). However, in many small organisms, in which oxygen diffusion under normoxic

90   conditions is likely to adequately meet metabolic demand, size reductions with warming are

91   still very common; they are for example observed in bacteria, protists and small metazoans,

92   such as copepods (Atkinson *et al.*, 2003; Forster *et al.*, 2012). Copepods are possibly the

93   most numerous metazoan on the planet, are ecologically important, and play a pivotal role in

94   marine and freshwater biogeochemistry and trophodynamics (Banse, 1995). Reduction in

95   size with increasing temperature, consistent with the T-S rule (Atkinson, 1994), has been

96   shown in many copepod species, both in controlled laboratory experiments (Horne *et al.*,

97   2015), and across seasons in the field (Seasonal T-S responses) (Uye *et al.*, 1983; Riccardi

98   & Mariotto, 2000; Hirst *et al.*, 1999; Drif *et al.*, 2010). Furthermore, the strength of the

99   laboratory temperature-size response varies widely between species, to the extent that

100   Horne *et al.* (2015) observed an approximate 30-fold difference between the strongest and

101   weakest copepod T-S responses in their dataset on arthropods. It would appear, therefore,

102   that another factor (or other factors) may be responsible for size reductions with warming

103   observed in these smaller taxa, and identifying the likely causes is an important next step.

104   Planktonic copepods are excellent model organisms in which to investigate seasonal size

105   responses. Temporal changes in adult body size have commonly been examined in this

106   taxon (Figure 1), especially in mid-latitude environments which demonstrate strong shifts in

107   temperature and food, while most species have multiple generations within a year and short

108   generation times of >10 to <100 days (Hirst & Kiørboe, 2002). Thus, here we present and

109   test a number of alternative hypotheses that may help to explain the considerable variation

110   observed in body size sensitivity to warming in planktonic copepods.

111

112   Mature adult size is dependent in part upon obtaining sufficient food to meet maintenance

113   and growth requirements, and size at maturity is controlled by different body size scaling of

114   catabolism and anabolism (von Bertalanffy, 1957; Perrin, 1995):

$$\frac{dM}{dt} = c_s \cdot M^s - c_l \cdot M^l$$

115   where $s > 0$ and $l > 0$ are exponents for energy supply and loss respectively, and $c_s > 0$

116   and $c_l > 0$ represent the temperature dependence of the intercept terms in log-log scale.

117   The point at which metabolic supply and demand intersect defines an organism's asymptotic

118   mass ($\frac{dM}{dt}\big|_{M_A} = 0$). In mathematical terms, the asymptotic mass, M_A, is given by

$$c_s \cdot (M_A)^s = c_l \cdot (M_A)^l \Rightarrow \log(M_A) = \frac{\log(c_s/c_l)}{l - s}$$

119   Temperature changes will affect both energy supply and expenditure, forcing the organism

120   into a new asymptotic mass. Hence, we can predict the induced relative change in

121   asymptotic mass per degree Celsius, noting that f'(x) / f(x) = f'[log(x)]:

$$\frac{1}{M_A}\frac{dM_A}{dT} = \frac{d}{dT}[\log(M_A)] = \frac{1}{l - s} \cdot \frac{d}{dT}\left[\log\left(\frac{c_s}{c_l}\right)\right]$$

122   Thus, the temperature dependence scales inversely with the difference in the mass scaling

123   of supply and demand (*l-s*), and is also influenced by the temperature dependence of the

124   intercepts. Moreover, within this framework, the strength of the T-S cline should be

125   independent of body mass.

126

127   Despite overwhelming evidence in favour of the TSR in a diverse range of ectotherms, there

128   remains considerable unexplained variation in the strength of the response between species

129   and taxonomic groups, which are most likely attributed to key differences in life history traits

130   and their associated metabolic constraints. In copepods and many other small zooplankton,

131   food acquisition is governed by prey availability and uptake. Species within the order

132   Calanoida largely utilise feeding currents to entrain and capture prey (Kiørboe, 2011), with a

133   few exceptions; by contrast, species within the non-Calanoida orders, i.e., the Harpacticoida,

134   Cyclopoida and Poecilostomatoida, lack an ability to produce a feeding current and are

135   either ambush feeders (Cyclopoida; Paffenhöfer 1993), or they feed on surfaces, which in

136   the planktonic environment is provided by marine snow aggregates (Harpacticoida; Koski *et*

137   *al.* 2005), or they are parasitic (e.g. many Poecilostomatoida; Huys & Boxshall 1991). There

138   is evidence that feeding mode is an important correlate of metabolic rates (respiration),

139   clearance, growth and ingestion rates (Kiørboe & Hirst, 2014). Ignoring parasitic copepods,

140   the body mass dependence of clearance rate differs between feeding current feeders and

141   more passive ambush and surface feeders (Kiørboe, 2011), suggesting a possible difference

142   in the temperature-body size sensitivity between different feeding behaviours. We cannot yet

143   predict the magnitude and direction of the T-S response since we do not know how

144   metabolic rates change with mass during ontogeny, and we also do not know how the

145   intercept terms vary with temperature. However, these considerations lead us to suggest

146   that some of the variability in T-S responses may be due to differences in feeding behaviour.

147

148   Another potential influence on the T-S response is reproductive strategy. In copepods,

149   reproductive strategy can be divided into broadcast spawning and sac spawning. Sac

6

150   spawners carry eggs in external sacs, and have much lower fecundity rates than broadcast

151   spawners (Hirst & Kiørboe, 2002). Sac spawners commonly do not lay the next batch of

152   eggs until the previous batch has hatched from the attached sac(s) (Ward & Hirst, 2007),

153   hence egg production is limited by the egg hatch time (Hirst & Bunker, 2003). By contrast,

154   broadcasters have much higher fecundity rates, and are less likely to be limited by clutch

155   size or egg hatch rates in the same way. The potentially different thermal sensitivities of egg

156   development versus egg production rates may produce different solutions for size at maturity

157   (and in turn its temperature dependence) between these two reproductive strategies.

158   However, even in the absence of clear evidence of such a difference in thermal sensitivity of

159   egg production and hatching, optimum size may change to different degrees if the cost of

160   carrying *versus* not carrying egg sacs is temperature dependent. For example, feeding rates

161   of ectotherms, including predators such as fish, typically increase with warming (Barneche *et*

162   *al.*, 2008), and such increased risk of mortality to prey organisms may amplify any small

163   differences in size- and fecundity- related trade-offs observed between broadcast and sac

164   spawners at cooler temperatures. In principle, therefore, differences in the optimum body

165   size response to temperature between the two spawning strategies can be hypothesized.

166

167   Our study therefore aims to: 1. Quantify and synthesise for the first time the seasonal

168   temperature-size responses of a wide range of planktonic copepod species, and to compare

169   these with responses under controlled laboratory conditions. 2. Examine the temperature

170   dependence of size at maturity in copepods, based around major differences between

171   taxonomic orders, species body sizes, modes of feeding (feeding current vs. active ambush

172   feeding), and reproductive strategy. 3. Assess the relative importance of food concentration

173   and temperature in driving seasonal size change.

174

175   **METHODS**

176   We searched the literature for studies in which the adult body size of planktonic copepods

177   was assessed on multiple occasions during an annual cycle. In addition to temperature we

178   also recorded the concentration of phytoplankton pigment chlorophyll-*a* (Chl-*a*) when this

179   was reported. Chl-*a* concentration is commonly used as a proxy for phytoplankton biomass

180   and food availability; indeed, adult fecundity and juvenile growth in many copepods

181   correlates to this term (Hirst & Bunker, 2003; Bunker & Hirst, 2004). To reduce potential

182   sampling bias in the sizes of animals collected, only those studies in which the adults were

183   sampled across the entire depth of the water column, or across most of the depth range of

184   the species, were included. Adult size data were collected as either lengths or dry, wet, or

185   carbon mass. These measurements were subsequently converted to dry mass (mg) using

186   published intra-specific regressions. If these were not available, regressions for closely

187   related species, or more general inter-specific regressions, were used. A list of the data

188   sources is found in Appendix 1. All raw data and conversions are detailed in Data S1 in

189   Supporting Information. Taxonomic order and family were confirmed for each species using

190   the World Registry of Marine Species (WoRMS Editorial Board, 2015).

191

192   In order to test which equation form best describes the relationship between mass and

193   temperature within a species, we used AIC (Akaike Information Criterion) to compare linear,

194   quadratic, exponential and allometric fits to the data. We found that the exponential equation

195   form was overwhelmingly favoured for modelling seasonal T-S responses, as judged by

196   Akaike weights (see Table S1 in Supporting Information for full details). We therefore used

197   an exponential equation form to model the seasonal temperature-size response for each

198   species from each study in our dataset, separating responses by sex. Species-specific

199   slopes of the natural log (ln) of dry mass vs. temperature were determined for all individuals

200   and transformed into percentage change in dry mass per degree Celsius, using the formula

201      $(\exp^{(slope)} -1)*100$ = % change in mass per °C (Forster *et al.*, 2012). This value represents the

202   seasonal temperature-size response, with a negative value showing a reduction in body

203　mass with increasing temperature, and hence following the same trend as the Temperature-

204　Size Rule. Size responses from multiple studies of the same species were then combined

205　into a simple mean to generate a single species-specific seasonal T-S value, separated by

206　sex.

207

208　To quantify relationships between body mass and Chl-*a*, the species-specific slopes of the

209　natural log (ln) of dry mass vs. Chl-*a* concentration (µg per litre) were determined for all

210　individuals and transformed into percentage change in dry mass per $\mu g.L^{-1}$, again using the

211　formula $(exp^{(slope)}-1)*100$ = % change in mass per $\mu g.L^{-1}$, to generate a chlorophyll-size (C-

212　S) response. The mean 95% confidence intervals of T-S and C-S responses, calculated from

213　the 95% confidence intervals of the individual estimated slopes, are presented for each order

214　in Table S2 of our Supporting Information. For all datasets in which we had both a measure

215　of temperature and Chl-*a* concentration (n=80), we compared the coefficient of

216　determination (R^2) of both parameters (i.e. by comparing the R^2 of each seasonal T-S

217　response with its corresponding C-S response), to determine whether one consistently

218　explained significantly more of the variation in seasonal body size clines than the other.

219　Given that temperature is a mechanistic driver of variation in primary productivity, we also

220　utilised an alternate approach to examine these relationships; first we regressed body mass

221　against temperature and then subsequently regressed the residuals from this on Chl-*a*

222　concentration, to determine how much of the seasonal variation in body size could be

223　attributed to Chl-*a* after accounting for temperature.

224

225　All statistical analyses were conducted using the free statistical software package R (R Core

226　Team, 2014). We derived several candidate models to determine the best predictors of

227　seasonal T-S responses based on the Akaike's information criterion (AIC). In order to

228　determine whether species body size impacts the T-S response, we included log_{10} species

229   mass at a reference temperature (15°C) as a predictor, as such an allometric relationship

230   has previously been shown to be significant (Forster *et al.*, 2012; Horne *et al.*, 2015).

231   Taxonomic order, $\log_{10}$ body mass (at 15°C calculated using species and sex-specific

232   slopes) and sex were incorporated as fixed variables in a global linear mixed effects model

233   (using package lme4), with species nested within family, and latitude included as random

234   effects on the intercept. When selecting our random effects, we considered the estimates of

235   variance explained by each of our proposed random variables (environment type (marine vs.

236   freshwater), latitude, and species nested within family) and used stepwise elimination of non-

237   significant terms to determine which parameters to include in the final model. All possible

238   combinations of the global model terms were compared using the dredge function in the

239   MuMIn package in *R*. The best model was identified as that with lowest small-samples

240   corrected AIC (AICc), and Akaike weights (w_i) were used to determine the probability (0-1) of

241   each candidate model being the best fit model (i.e. if w_i=0.9, there is a 90% probability that a

242   given model is the best fit model among those considered and given the data available).

243   Where the difference between a model's AICc and the lowest AICc (i.e. ΔAICc) is <2, a set

244   of best fit models, rather than a single best model, can be assumed, and model averaging

245   may be used to identify the best predictor variables across the top candidate models and

246   determine their relative importance (computed for each variable as the sum of the Akaike

247   weights from all models in which they appear). In addition to AIC, a series of *F* tests (using

248   the 'anova' function in *R*) were used to verify the significance ($p<0.05$) of each parameter's

249   effect on the strength of the seasonal T-S response. *Post hoc* comparisons were made using

250   a Tukey HSD test.

251

252   To compare seasonal T-S responses with laboratory T-S responses, we used the extensive

253   T-S response dataset of Horne *et al.* (2015), supplementing this where possible with newly

254   identified data following identical methods for acquiring data.

255

RESULTS

We derived a total of 140 seasonal T-S responses from 33 different global locations (Fig. 1), within the latitudinal range of 25° to 61°, hence largely falling around mid-latitudes (with a dominance of northern hemisphere locations). This in part reflects well-studied temperate environments with strong seasonality, while also being inhabited by copepod species with multiple generations in a year. The data set included 48 planktonic copepod species from 4 taxonomic orders (Calanoida, Cyclopoida, Harpacticoida, Poecilostomatoida). These species-specific seasonal T-S responses had negative slopes in 87% of cases, with a mean reduction in size of -2.87±0.65% (95%CI) body mass per °C (Fig. 2), reinforcing the generality of the negative T-S response in copepods. The overall strength or direction of the seasonal T-S response did not vary significantly across latitudes ($F_{1,138}$=1.20, p=0.27). Of the 80 seasonal body size clines for which we had a measure of Chl-*a* concentration (corresponding to 33 species), across all orders we observe a mean body mass response of 0.98±2.01% (95%CI) per µg.L^{-1}, which does not differ significantly from zero (t_{79}=0.97, p=0.34) (Fig. 2). On average, across all taxonomic orders temperature explained more of the variation in seasonal body mass than Chl-*a* concentration: this is inferred from the mean R^2 values of each parameter when both were modelled separately (0.44±0.07 vs. 0.22±0.05 respectively (95%CI)), and also when comparing body mass-temperature regressions with regressions of the resulting residuals against Chl-*a* concentration (0.44±0.07 vs. 0.07±0.03 respectively (95%CI)) (see Fig. S1 in Supporting Information). Considering each of the four orders separately, temperature always explained more of the variation in adult body mass than did Chl-a concentration.

In explaining variation in the strength of the seasonal T-S response among planktonic copepods, the model with the lowest AICc includes only taxonomic order as a fixed variable,

281   whilst all other candidate models have a ΔAICc>2 (Table 1). Thus, given the data available,

282   we may reject the other candidate models in favour of a single best fit model in which

283   taxonomic order has a significant independent effect on the strength of the seasonal T-S

284   response ($F_{3,82}$=9.43, p<0.001). *Post hoc* comparisons (Tukey HSD) show that Calanoida

285   (*n*=66, mean=-3.66±0.70% body mass ^{o}C^{-1}; 95%CI) have a significantly stronger negative

286   seasonal T-S response than both Cyclopoida (*n*=12, mean=-0.91±0.59% body mass ^{o}C^{-1};

287   95%CI) and Poecilostomatoida (*n*=6, mean=1.36±3.06% body mass ^{o}C^{-1}; 95%CI), but not

288   Harpacticoida (*n*=2, mean=-1.19±3.60% body mass ^{o}C^{-1}; 95%CI), though our seasonal data

289   for this order are sparse, including only male and female *Euterpina acutifrons*. We note

290   specifically the different temperature response between the calanoids, which use feeding-

291   currents, and ambush feeding cyclopoid copepods, with a 4-fold difference in the strength of

292   the seasonal T-S response observed between these two groups (Fig. 3). We find no

293   significant change in the strength of the response with mean species body mass in either the

294   Calanoida ($F_{1,101}$=0.11, p=0.75) or non-Calanoida orders ($F_{1,35}$=2.75, p=0.11), supporting our

295   prediction that any change in mature body size is independent of mean species body mass

296   in these smaller taxa (Fig. 4).

297

298   Reproductive strategy also varies within and between orders; calanoid species can be either

299   broadcast or sac spawners, but are more commonly the former (n=44 vs. n=22 for broadcast

300   and sac spawners respectively in our dataset), whilst all species in the three remaining

301   orders considered here are sac spawners. Given that taxonomic order and reproductive

302   strategy correlate exactly in 3 of the 4 orders in our dataset, while in calanoids both

303   reproductive strategies occur, we tested for differences in the seasonal T-S response

304   between broadcasters and sac spawners exclusively in calanoids, finding no significant

305   effect ($F_{1,64}$=0.71, p=0.40). Equally, we tested for order-level differences in the seasonal T-S

306   response exclusively in sac spawners (i.e. by excluding any broadcast spawning calanoid

307   species), and find significant differences in the strength of the seasonal T-S response

308   between taxonomic orders, still observing a 4-fold significant difference between calanoids

309   and cyclopoids (t-test; t=-4.51, df=31, p<0.0001). This leads us to suggest that reproductive

310   strategy is not responsible for driving the observed differences in seasonal T-S responses

311   between taxonomic orders and, hence, explains why we chose to exclude the latter from our

312   global linear mixed effects model.

313

314   Despite the numerous other variables that may act to obscure the correlation between body

315   mass and seasonal temperature, we find a strong match between the mean Calanoida

316   seasonal T-S response (-3.66±0.70%) and mean T-S response (-3.20±0.49%) measured in

317   the laboratory under conditions of excess food (t-test; t=-1.09, df=79, p=0.28). However, we

318   note that the two datasets comprise different species. Indeed, when we regress species-

319   specific seasonal T-S responses against laboratory T-S responses for the small number of

320   species for which we have both sets of data (n=12), separating responses by sex, we

321   observe much greater variation in seasonal T-S responses than those measured under

322   controlled laboratory conditions (Fig. 5). This suggests that food quantity/quality, and

323   potentially other environmental variables, are impacting the T-S response in the field. There

324   appears to be no systematic difference in the strength of laboratory and seasonal T-S

325   responses between the sexes, such that sex has no significant effect on the strength of the

326   seasonal T-S response, either across species ($F_{1,84}$=0.03, p=0.86) or intra-specifically

327   (paired t-test; t=1.35, df=37, p=0.19). Unfortunately we are unable to make further

328   meaningful comparisons between field and laboratory responses. For example, we could not

329   compare the broad differences between taxonomic orders we observe in the seasonal T-S

330   data with laboratory data, as very few laboratory studies on species other than calanoids

331   have been conducted; our dataset contains male and female laboratory T-S responses for

332   just 2 planktonic cyclopoid species and a single harpacticoid species.

333

DISCUSSION

Our work combines field data from numerous studies worldwide (Fig. 1), going beyond controlled laboratory-based T-S studies to demonstrate broad patterns in the thermal size responses of marine and freshwater planktonic copepods. Despite numerous other variables that may act to complicate the T-S signal in the field, we show that almost 90% of copepod species in our dataset follow the Temperature-Size Rule (TSR) in seasonal environments, maturing at a smaller adult body mass in warmer conditions. Yet, as we may expect, seasonal T-S responses appear much more variable compared to those measured under controlled conditions in the laboratory (Fig. 5), suggesting that other environmental factors, in addition to temperature, may play a role in driving seasonal body size variation in the field. We should also consider that the temperature at which adults are collected is unlikely to correspond exactly to temperatures experienced during ontogeny, and this may be further complicated by the existence of a winter diapause, during which many copepods will cease recruitment over late winter to early spring. Throughout this period their prosome length will change little, and yet temperatures may vary considerably.

Food availability has also been shown to have a direct influence on body size (Berrigan & Charnov, 1994; Diamond & Kingsolver, 2010), though we find that Chl-*a* concentration explains very little of the seasonal variation in body mass, when both modelled independently and after accounting for the effects of temperature. This suggests that temperature is much more significant in driving body size responses in these natural populations. Higher food quantity typically leads to larger size at maturity in ectotherms, and we observe a positive but non-significant percentage change in adult body mass with increasing Chl-*a* concentration on average (Fig. 2). Chl-*a* concentration commonly correlates significantly with juvenile growth and adult fecundity rates in many natural populations of planktonic copepods (Hirst & Bunker, 2003; Bunker & Hirst, 2004), and hence is generally

360 considered a reasonable proxy of food availability. However, many copepods have an

361 omnivorous diet that does not exclusively include prey containing this pigment (e.g. including

362 heterotrophic ciliates and flagellates (Calbet & Saiz, 2005)), and the proxy also fails to

363 account for variation in prey quality (Pond *et al.*, 1996), which has been shown to alter the

364 temperature-size response, even reversing its sign at times (Diamond & Kingsolver, 2010).

365 Here we find little evidence for sign reversal when comparing laboratory and field animals.

366 Time lags might also obscure the correlation between Chl-*a* concentration and body size. As

367 food availability commonly varies over a much shorter timescale than generation time, whilst

368 temperature varies over a relatively longer timescale, correlations with the latter are likely to

369 be much more reliable. Although greater chlorophyll concentration is often associated with

370 increased growth (Hirst & Bunker, 2003; Bunker & Hirst, 2004), consumer abundance is also

371 predicted to increase with primary productivity (O'Connor *et al.*, 2009). Our analysis does not

372 account for the abundance of the copepods, and hence we are unable to assess the role of

373 food availability on a *per capita* basis. Assuming metabolic rate has a Q_{10} of 2.5 and scales

374 with body mass$^{0.75}$ (Zuo *et al.*, 2012), a simple calculation suggests that an organism would

375 have to decrease its body mass by approximately 11.5% per °C of warming to offset the

376 increase in metabolic rate associated with this temperature increase. Given that calanoid

377 copepods on average reduce their body mass by only 3.66% $°C^{-1}$, this compensates for

378 approximately a third of the increase in metabolic rate per °C of warming. If resources were

379 limiting and kept constant then population abundance would have to fall substantially with

380 warming to accommodate the extra metabolic demand, even with reduced body size of

381 individuals.

382

383 Beyond variation in temperature and food availability, we might expect predation by

384 ectotherms to increase with warming in the field (Kordas *et al.*, 2011). This in turn may lead

385 to increased copepod mortality, selecting for earlier maturation and resulting in a reduced

386 adult body size. Copepods can also detect and perceive chemical signals released by

387 predators, such as fish kairomones, the presence of which has been shown to trigger faster

388 development and earlier maturation at a smaller body size in calanoids (Gutiérrez *et al.*,

389 2010). Thus, increased predation risk in the warm and associated increases in mortality and

390 the presence of chemical cues may amplify the temperature-size response in the field.

391

392 The relative strength of the seasonal T-S response does not vary significantly between the

393 sexes in this study, evidence of which can also be observed in Figure 5. These findings

394 agree with the broader analysis across Arthropoda, for which T-S responses were found to

395 not significantly differ between the sexes (Hirst *et al.*, 2015). Rensch's rule suggests that

396 male body size varies more than female body size, irrespective of which is the larger sex

397 (Rensch, 1960). Applied within species, the rule would predict an increase in sexual size

398 dimorphism (SSD) with increasing body size in species where males are the larger sex, and

399 a decrease in SSD with body size in species where females are larger. Thus males should

400 consistently have the greater size variation, yet we find no evidence to support this pattern at

401 the intra-specific level. Our finding at the intra-specific level here concurs with there being

402 isometry between male and female size seen across copepod species (Hirst & Kiørboe

403 2014), and suggests that the selection pressures on the seasonal T-S response have been

404 equally as strong for both males and females.

405

406 Though recent studies have begun to identify broad trends in both the magnitude and

407 direction of the T-S response, for example between terrestrial and aquatic species (Forster

408 *et al.*, 2012; Horne *et al.*, 2015), there remains a large amount of variation in the strength of

409 the response that is yet to be explained. This is especially true for planktonic species which

410 are only a few millimetres in size or less, where oxygen availability in most conditions

411 appears unlikely to be a driver. Indeed, our most compelling finding is the significant

412 difference in the strength of seasonal T-S responses between species of calanoid and

413　cyclopoid (Fig. 3), both of which typically employ different feeding modes. We find that

414　calanoids exhibit much greater size plasticity upon temperature changes than non-calanoids.

415　This is consistent with the hypothesis that feeding mode may influence the T-S response,

416　since all calanoids can produce a feeding current to harvest prey, while none of the other

417　orders do so. The extent to which the T-S response differs between these two feeding

418　modes depends on the differences in both size-scaling and thermal response of feeding in

419　relation to metabolism. Thus, in order to thoroughly test this hypothesis, one would need

420　estimates of within-species mass scaling and temperature dependence of feeding and

421　metabolism. While some estimates of between-species body mass scaling of respiration and

422　feeding of the two groups exist (e.g., Kiørboe & Hirst 2014), the body mass-dependent

423　changes in vital rates during ontogeny are typically different (Hirst *et al.*, 2014; Glazier *et al.*,

424　2015), and thus needed for these groups. A further complication arises from the fact that

425　feeding mode may change during ontogeny: while all cyclopoids are ambush feeders

426　throughout their development, many calanoids are ambush feeders during the nauplii stage,

427　and feeding current feeders during the copepodite stages; or they may switch between

428　feeding modes in the copepodite stages (Kiørboe, 2011).

429

430　We note the association between taxonomic order and feeding mode in our dataset, and

431　appreciate the potential difficulty in disentangling effects of feeding strategy from other order-

432　specific differences in physiology and behaviour. For example, all cyclopoids in our dataset

433　are sac spawners, whilst calanoid species can be either broadcast or sac spawners, but are

434　more commonly the former. However, we find no substantial effect of reproductive strategy

435　on the sensitivity of mature body mass to temperature. Whilst broadcast and sac spawning

436　planktonic copepods have markedly different rates of adult fecundity (Bunker & Hirst, 2004),

437　egg mass production rates (Hirst & Bunker, 2003) and egg mortality (Hirst & Kiørboe, 2002),

438　they appear to have somewhat similar rates of juvenile growth, development and mortality

439　(Hirst & Kiørboe, 2002; Hirst & Bunker, 2003). The T-S responses of species with

440 determinate growth are largely generated during the juvenile phase of ontogeny (Forster &

441 Hirst, 2012). Similarity of important life history rates during the juvenile phase may therefore

442 explain the lack of difference in the T-S responses within the calanoids based upon

443 reproductive strategy. Expanding our analysis in future to consider ambush feeding calanoid

444 copepods, such as in the genera *Tortanus* and *Pareuchaeta*, will help to more definitively

445 separate effects of feeding strategy from order-level differences. Unfortunately at present,

446 suitable data are not available on these taxa. We recommend that future experimental

447 studies comparing species-specific size variation in response to temperature, both within

448 and between taxonomic orders, should focus on those taxonomic groups that are currently

449 data deficient.

450

451 Given that body size is an important predictor of fitness, and warming is a prominent feature

452 of climate change, there is an urgent need to accurately predict changes in body size with

453 temperature. This is particularly the case in zooplankton which globally represent a primary

454 resource for invertebrates and vertebrates, including fish (Ware & Thomson, 2005). Changes

455 in body size will not only affect individual and population fitness, but may impact feeding

456 rates and alter food web connectivity given the size dependency of trophic processes

457 (Hansen *et al.*, 1994; Rice *et al.*, 2015), as planktonic food webs are especially highly size-

458 structured (Webb, 2012). Measuring and accounting for abundance in the field would also

459 help to define the relationship between food availability *per capita* and adult body size under

460 natural conditions. This may be particularly informative in light of the fact that the

461 temperature-size response in the majority of ectotherms appears to compensate for only a

462 small proportion of the predicted increase in metabolic rate with temperature, whilst

463 metabolic rate in autotrophs (and thus primary productivity) increases substantially less with

464 warming than metabolic rate in heterotrophs (Allen *et al.*, 2005).

465

SUPPORTING INFORMATION

Data S1 Seasonal body size data used in this study

Table S1 AIC output comparing linear, quadratic, exponential and allometric fits for determining seasonal temperature-size responses.

Table S2 Mean 95% confidence intervals of individual T-S and C-S regressions for each taxonomic order.

Figure S1 Comparison of species-specific coefficients of determination for temperature and Chl-*a* concentration in explaining seasonal body mass changes, values averaged by order.

BIOSKETCH

The work presented here results from an ongoing collaboration between researchers from Queen Mary University of London, the University of Liverpool and the Centre for Ocean Life, Technical University of Denmark. We use a range of approaches such as meta-analysis, experimentation, conceptualisation and modelling to establish and test governing rules of ecology and evolution. A major focus is the ecology, physiology and population processes of marine species, especially plankton, including the impact of a changing climate. Further information, including details of our latest research and publications, can be found at our research group website: *www.aquatic-ecology.co.uk*

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656

657 **APPENDIX 1 – Data Sources**

658

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790   Table 1. AIC output comparing the relative strength of candidate models in explaining

791   variation in seasonal T-S responses. The best model, shown in bold, is identified as that with

792   the lowest small-samples corrected AIC (AICc). Given that the difference between the lowest

793   AICc and those of the alternative models (i.e. ΔAICc) is >2, we may favour a single best fit

794   model in which taxonomic order has a significant independent effect on the strength of the

795   seasonal T-S response. An 'intercept only' model, shown in italics, is included for

796   comparison. Akaike weight (w_i) denotes the probability of a given model being the best fit

797   model in the candidate set. The number of parameters (K) in each model is shown. Mass is

798   the species adult body mass at 15°C.

799

Model	K	Log-likelihood	AICc	ΔAICc	w_i
Intercept	*5*	*-328.40*	*667.25*	*5.08*	*0.04*
Order	**8**	**-322.53**	**662.16**	**0.00**	**0.52**
Order+Sex	9	-322.51	664.40	2.24	0.17
Log_{10}Mass+Order	9	-322.53	664.44	2.27	0.17
Log_{10}Mass+Order+Sex	10	-322.51	666.72	4.55	0.05
Log_{10}Mass	6	-327.89	668.41	6.25	0.02
Sex	6	-328.38	669.40	7.24	0.01
Log_{10}Mass+Sex	7	-327.77	670.38	8.22	0.01

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FIGURE LEGENDS

813 Fig.1. World map indicating the location of studies (n=33) from which copepod seasonal size

814 responses were recorded. Studies from freshwater environments are indicated by the light

815 grey circles whilst marine environments are indicated by the dark grey circles.

816

817 Fig. 2. Species-specific % change in body mass (±95% CI) for seasonal T-S (per °C) and C-

818 S (per µg.L^{-1}) responses, averaged by order. Solid grey lines shows the mean seasonal T-S

819 and C-S response across all orders with 95%CI indicated by the shaded area.

820

821 Fig. 3. (A) Seasonal temperature-size responses of adult copepods for individual species,

822 including both males and females, categorized by order (Calanoida, Cyclopoida,

823 Harpacticoida, Poecilostomatoida) and family (Acartidae (Ac), Calaniidae (Ca),

824 Centropagidae (Ce), Clausocalanidae (Cl), Diaptomidae (Di), Paracalanidae (Pa),

825 Pseudodiaptomidae (Ps), Temoridae (Te), Cyclopidae (Cy), Oithonidae (Oi), Euterpinidae

826 (E), Corycaeidae (C), Oncaeidae (On)). Where more than one study has been undertaken

827 on a species, the mean (and ±SE) are plotted. Dashed horizontal lines indicate the mean

828 seasonal T-S response for the Calanoida and Cyclopoida orders. Dashed vertical lines

829 divide taxonomic families. Species names preceded by an asterisk are sac spawners, whilst

830 all other species are broadcast spawners. (B) Species-specific seasonal T-S responses

831 (±95% CI), averaged by order. Different letters above data points indicate significant

832 differences, whilst shared letters indicate no significant difference. Note the significant

833 difference between feeding-current feeding Calanoida and ambush feeding Cyclopoida.

834

835 Fig. 4. Seasonal temperature-size responses (% change in body mass $^{o}C^{-1}$) versus species

836 log$_{10}$ adult dry mass (mg), categorized by taxonomic order. We find no significant

837   relationship between the strength of seasonal T-S responses and species body mass across

838   either Calanoida ($F_{1,101}$=0.11, p=0.75; solid line) or non-Calanoida species ($F_{1,35}$=2.75,

839   p=0.11; dashed line). Data for both females and males are included where possible.

840   "NS"=not significant.

841

842   Fig. 5. Male (M) and female (F) species-specific laboratory temperature-size (T-S)

843   responses versus seasonal T-S responses in planktonic copepods. Seasonal T-S responses

844   are much more variable than laboratory T-S responses and there is a significant positive

845   correlation (RMA regression; R^2=0.25) between the two. Dashed grey line indicates y=x for

846   comparison. There appears to be no significant difference in the strength of seasonal and
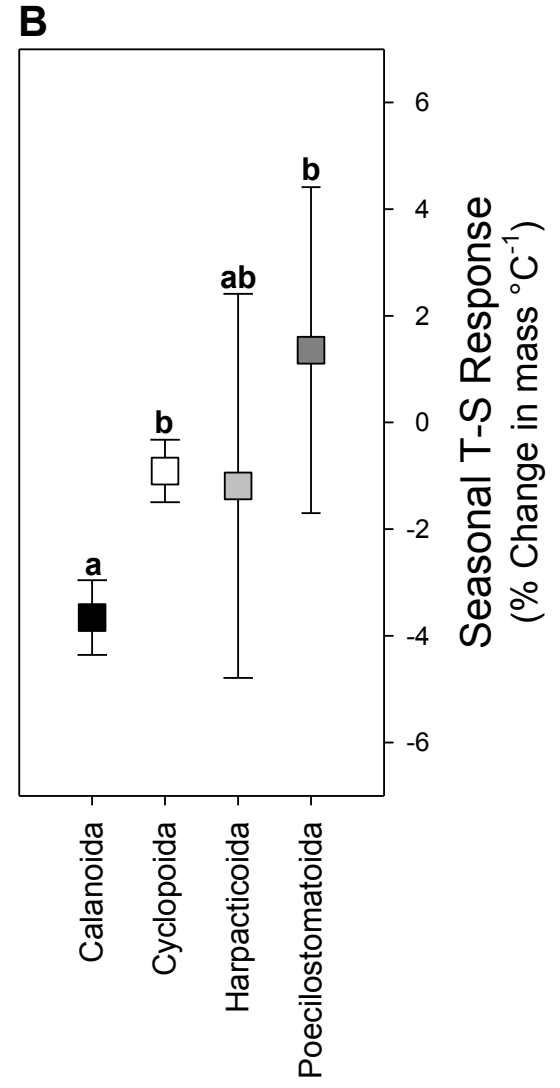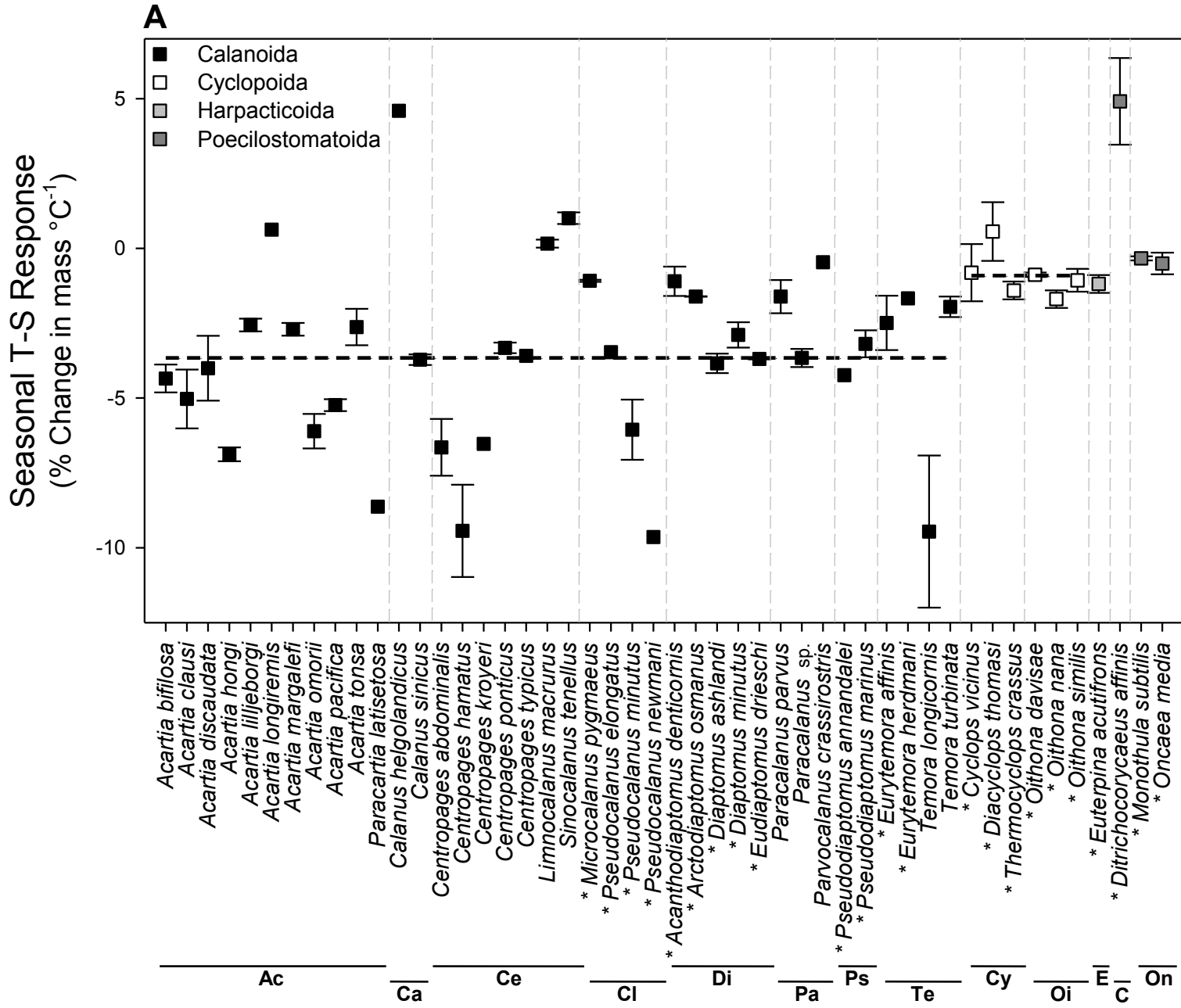
847   laboratory T-S responses between the sexes.
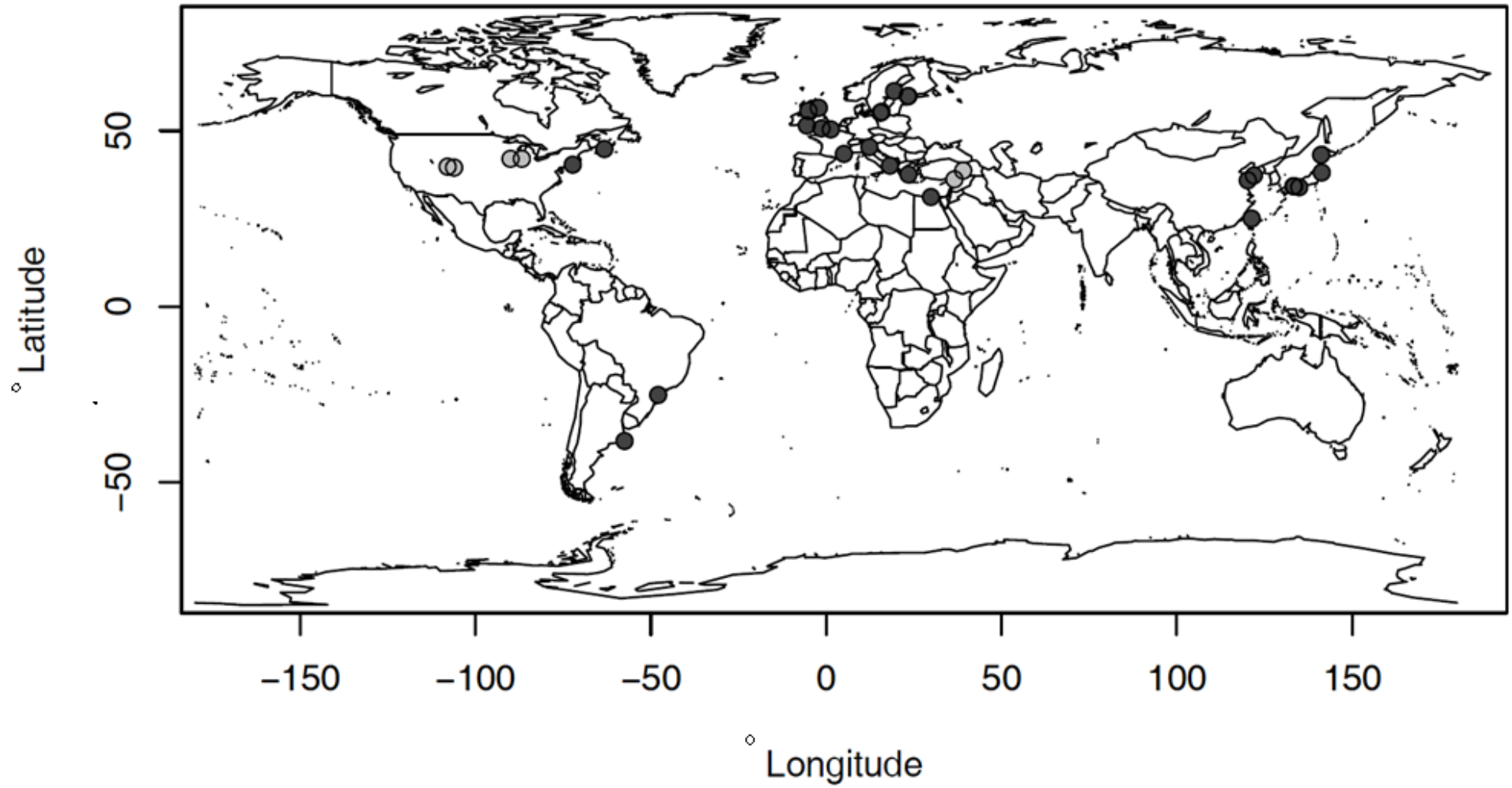
Figure 1
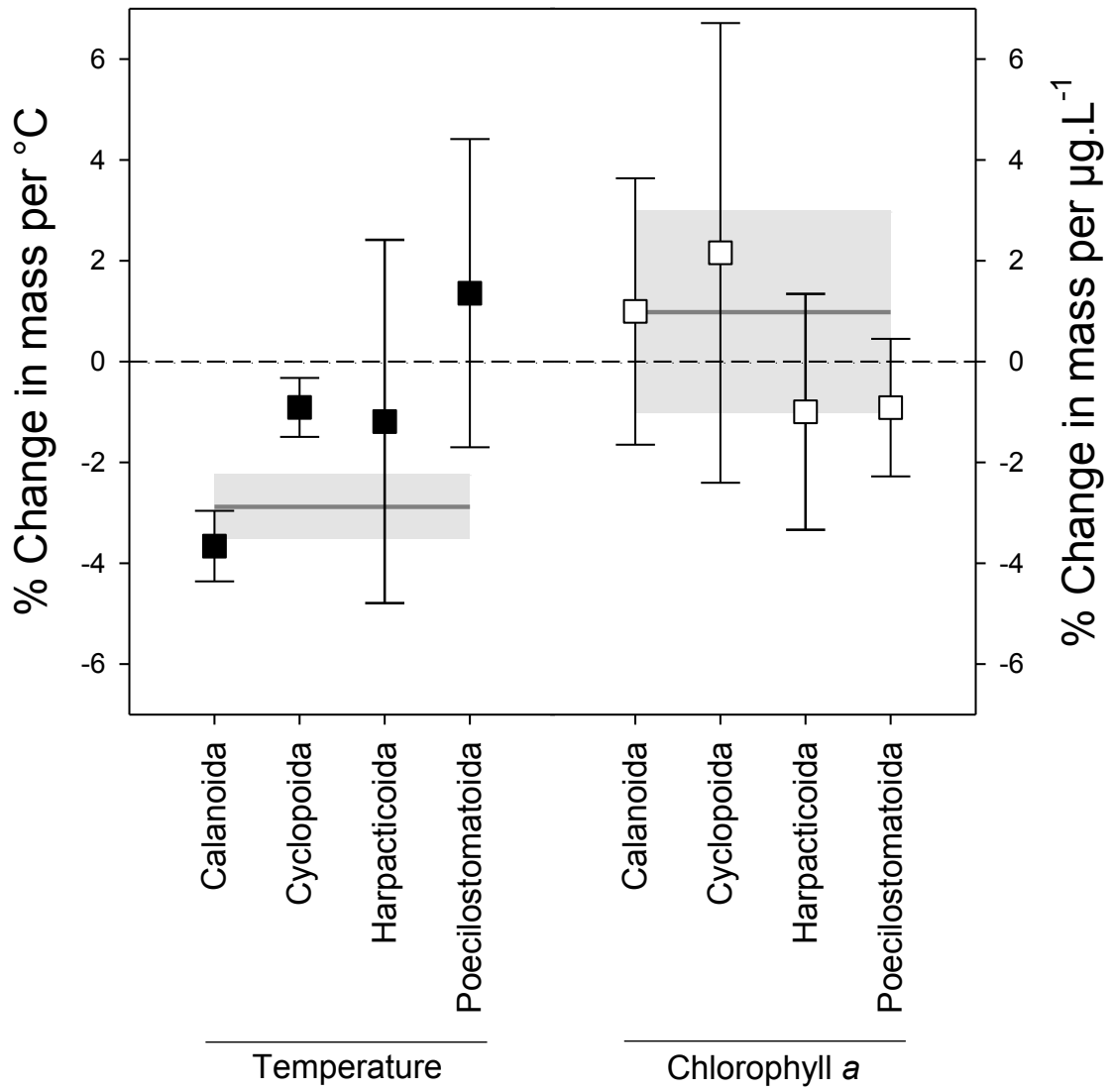
Figure 2

Figure 3

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Figure 5