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Seasonal Body Size Reductions with Warming Co-vary with Major Body Size Gradients in Arthropod Species

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1 **Seasonal Body Size Reductions with Warming Co-vary with Major**
2 **Body Size Gradients in Arthropod Species**

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12 **Keywords:** Body size, plasticity, seasonal, warming, insects, Crustacea

13

14 **Author Contributions**

15 CH, AGH and DA designed the study and wrote the paper. CH collected the data and
16 performed the statistical analyses.

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20

21 ABSTRACT

22 Major biological and biogeographical rules link body size variation with latitude or
23 environmental temperature, and these rules are often studied in isolation. Within multivoltine
24 species, seasonal temperature variation can cause substantial changes in adult body size,
25 as subsequent generations experience different developmental conditions. Yet, unlike other
26 size patterns, these common seasonal temperature-size gradients have never been
27 collectively analysed. We undertake the largest analysis to date of seasonal temperature-
28 size gradients in multivoltine arthropods, including 102 aquatic and terrestrial species from
29 71 global locations. Adult size declines in warmer seasons in 86% of the species examined.
30 Aquatic species show a ~2.5-fold greater reduction in size per °C of warming than terrestrial
31 species, supporting the hypothesis that greater oxygen limitation in water than in air forces
32 aquatic species to exhibit greater plasticity in body size with temperature. Total percentage
33 change in size over the annual cycle appears relatively constant with annual temperature
34 range but varies between environments, such that the overall size reduction in aquatic-
35 developing species (~31%) is almost 3-fold greater than in terrestrial species (~11%). For
36 the first time, we show that strong correlations exist between seasonal temperature-size
37 gradients, laboratory responses, and latitudinal-size clines, suggesting that these patterns
38 share common drivers.

39

40 INTRODUCTION

41 Body size is a 'master trait', affecting vital rates (growth, survival, reproduction) and
42 ecological processes ranging from individual performance (e.g. fitness) to ecosystem
43 function (e.g. food web dynamics, productivity) [1-4]. Biologists have intensively studied body
44 size variation for more than a century [5-8], including describing size clines over latitude and
45 altitude in the field [9, 10]. Populations grown under controlled laboratory conditions show
46 strong associations between mature body size and temperature [11-13], and food [14].

47 These emergent body size patterns have been formalised into prominent biogeographical
48 and biological rules, including Bergmann's rule (inter-specific latitudinal clines: larger bodied
49 species at higher, colder latitudes) [9], James' rule (intra-specific latitudinal clines: larger
50 individuals at higher, colder latitudes) [15], and the temperature-size rule (TSR) (increased
51 size at maturity when grown through ontogeny at decreased temperature) [11]. Furthermore,
52 body size reduction has been described as the third universal response to climate warming
53 [16].

54

55 The drivers of intraspecific body size clines across latitudes can differ from those of size
56 responses to ontogenetic temperature treatments in the laboratory. The former can be
57 influenced not just by phenotypic plasticity, but also by genetic variation among geographic
58 populations [17], as well as many biotic and abiotic factors that could confound the effects of
59 temperature, such as voltinism, season length, food supply, and natural enemies [18-22].
60 Despite these confounding factors, temperature-size (T-S) responses measured under
61 controlled laboratory conditions and latitudinal-size (L-S) clines measured in the field
62 significantly co-vary across taxonomic orders within the Arthropoda. Specifically, taxonomic
63 orders whose species demonstrate particularly strong negative T-S responses (i.e. following
64 the TSR) also show strong intra-specific declines in adult size at lower latitudes (i.e.
65 following James' rule), whereas those with less negative T-S responses tend to show
66 reduced or reversed latitudinal-size clines [13]. This co-variation suggests that similar forces
67 may be driving these important patterns.

68

69 It has been debated whether size responses are adaptive, or a maladaptive outcome of
70 environmental stress or genetic drift [23], or simply a consequence of how constraints
71 imposed by the architecture of the maturation mechanism may affect phenotypic outcomes
72 of selection on body size, growth and development rate [24]. However, given the important

73 influence of body size on vital rates and ecological processes, systematic size responses to
74 temperature are often considered adaptive [25, 26]. For example, variation in the direction of
75 T-S responses and latitudinal-size clines has been attributed to differences in voltinism in
76 terrestrial arthropods, likely an evolutionary adaptation to changing season length [13, 19,
77 27]. Striking differences in the T-S response also occur between environments; aquatic-
78 developing species show greater reductions in adult size per °C of warming, and stronger
79 reductions in size with decreasing latitude towards the equator, than do air-breathing species
80 [12, 13]. Oxygen availability, which includes both its concentration and diffusivity, is
81 approximately 3×10^5 times lower in water than in air [28], and body size reduction with
82 warming is thought to be an important mechanism by which aquatic species maintain
83 aerobic scope when faced with increased metabolic rate at elevated temperatures [12, 13,
84 29]. Indeed, hypoxic conditions also commonly lead to reductions in size within species, both
85 under natural conditions [30] and in laboratory manipulations, especially at warmer
86 temperatures and/or larger body sizes [31].

87

88 Multivoltine ectotherms, which have more than one generation per year, can experience
89 considerable differences in temperature, resources and suitable habitat between seasons,
90 hence between generations. The effects of seasonal changes in temperature on optimum
91 body sizes may therefore be easily confounded by other seasonally varying effects such as
92 food, water, oxygen availability and mortality risks [18]. Nonetheless, seasonal body size
93 variation commonly correlates strongly with changes in environmental temperature in a wide
94 range of uni- and multicellular organisms, including bacteria [e.g. 32], rotifers [e.g. 33],
95 copepods [e.g. 34, 35], cladocerans [e.g. 36] and insects [e.g. 37], examples of which are
96 presented in Figure S1. Yet, despite the huge implications of environmental seasonality for
97 global ecology, no broad exploration of seasonal size gradients has been performed to date.
98 Such intra-annual shifts in size have important physiological, ecological and fitness
99 consequences [18], and the magnitude and variation of such seasonal change across

100 diverse taxa, and between environments, needs to be investigated (cf. with latitudinal and
101 altitudinal descriptions [38, 39]). Moreover, the question of whether the differences in body
102 size gradients observed between environments and taxonomic orders, both in the laboratory
103 and across latitudes, are also observed across seasons still remains unanswered. Improved
104 understanding of size gradients across season will not only help to determine the ultimate
105 causes of body size variation, but will also aid ecologists, including macro-ecologists, in
106 understanding and predicting individual and community level responses to climate change
107 [40]. This is critical given the link between decadal-scale changes in the body sizes of
108 ectotherms and shifts in climate [41-43].

109

110 Our analysis focuses on the Arthropoda, which is the most taxonomically diverse and
111 numerous phylum on earth [44], and which has huge ecological and economic importance
112 [45, 46]. This well-studied group also shares a common ancestry and a related body plan.
113 Here we present, to our knowledge, the largest synthesis of seasonal T-S gradients in
114 multivoltine arthropods to date, including those of marine, freshwater and terrestrial species.
115 Following from the stronger observed laboratory T-S responses and L-S clines in aquatic-
116 developing than terrestrial species [12, 13], we predict that across seasons, species
117 developing in water will also demonstrate a greater reduction in size per °C of warming than
118 will species developing in air. We also assess the extent to which the seasonal T-S gradient
119 depends on mean annual temperature, latitude and species body mass. Finally, we
120 quantitatively compare seasonal T-S gradients with both T-S responses measured under
121 controlled laboratory conditions and with L-S clines, to establish whether differences
122 observed between environments and among taxa are consistent in these three major size
123 gradients.

124

125 **METHODS**

126 We searched the literature extensively using both the Web of Science database
127 (<http://apps.webofknowledge.com/>) and Google Scholar for studies in which the adult body
128 size of multivoltine arthropod species (≥ 2 generations per year) was assessed in nature on
129 multiple occasions during an annual cycle. We used records for which we could model a
130 change in body size that occurred over at least a 3 month period. This criterion for data
131 inclusion increased the likelihood of capturing variation in body size in different cohorts or
132 generations. The primary search term combinations used were: (“seasonal” OR “temporal”)
133 AND “body size” AND (“arthropod” OR “[<insert taxonomic order>]” AND “temperature”. We
134 also identified related studies from reference lists in the papers we found, and sought further
135 direction to key literature from relevant experts. Adult size data were collected as lengths, or
136 dry, wet or carbon masses and subsequently standardised to dry mass (mg) using published
137 intra-specific regressions and conversion factors (see Dataset S1 in Supplementary
138 Information). If regressions for the species were not available, regressions for closely related
139 species, or more general inter-specific regressions were used (in ~26% of cases).
140 Taxonomic order and family were confirmed for each species using the World Registry of
141 Marine Species [47] or the National Center for Biotechnology Information (NCBI) Taxonomy
142 Database for freshwater and terrestrial species. In the case of planktonic species, to reduce
143 potential sampling bias in the sizes of animals collected, only those studies in which the
144 adults were sampled across the entire depth of the water column, or across most of the
145 depth range of the species, were included. Maximum water sampling depth across all
146 aquatic studies in our data set was 125m.

147

148 For each study included in our data set, we derived species-specific slopes of ordinary least-
149 squares (OLS) regressions between ln-transformed dry mass (mg) and environmental
150 temperature at time of collection, using individuals of species as data points. We derived
151 slopes for males and females separately wherever possible. This exponential function is
152 overwhelmingly favoured for modelling seasonal T-S gradients, rather than linear, quadratic

153 and allometric relationships, giving an Akaike weight of 1 (see Table S1 in Supplementary
154 Information). The exponential function is also the best for fitting body size-temperature
155 relationships under controlled laboratory conditions and for latitudinal-size clines, again
156 judged using Akaike weights [13, 48]. This common use of an exponential function allows us
157 to easily compare all three of these size gradients. These 'seasonal T-S slopes' were also
158 transformed into percentage change in dry mass per degree Celsius (hereby referred to as
159 'seasonal T-S gradients'), using the formula $(\exp^{(\text{slope})} - 1) * 100 = \% \text{ change in mass per } ^\circ\text{C}$
160 [12]. A negative gradient shows a reduction in body size with increasing temperature, and
161 hence follows the same trend as the temperature-size rule [11].

162

163 Where temperatures in a study were not reported for the entire year (n=19 of 79), we used
164 high resolution global climate data to estimate mean annual temperature and annual
165 temperature range (ATR) at each sampling location (from NOAA/OAR/ESRL PSD, Boulder,
166 Colorado, USA), available online at <http://www.esrl.noaa.gov/psd/>. Specifically, we used
167 weekly mean sea surface temperatures (SST) from 1989/12/31 to 2015/10/25
168 [year/month/day] (NOAA Optimum Interpolation Sea Surface Temperature dataset; 1.0
169 degree latitude x 1.0 degree longitude global grid) and long term monthly mean air
170 temperature data from 1981 to 2010 (University of Delaware Air Temperature and
171 Precipitation dataset; 0.5 degree latitude x 0.5 degree longitude global grid) to calculate
172 global mean annual ranges in SST for marine environments and surface air temperature
173 ranges for freshwater and terrestrial environments. Surface air temperature has been shown
174 to correlate linearly with water temperature, particularly on a monthly time scale, and thus is
175 a reasonably good indicator of temperature variation in freshwater systems [49]. In cases
176 where the estimated ATR was less than that of the range derived from the original study, we
177 used the latter given that it represents a direct measurement. Sampling locations are
178 presented in Figure 1.

179

180 Statistical analyses were conducted in R [50]. We compared several candidate models to
181 best predict seasonal T-S gradients based on the Akaike's information criterion (AIC). Using
182 seasonal T-S gradient as the dependent variable, developmental environment (aquatic-
183 developing vs. terrestrial-developing), log₁₀-transformed species body mass (at 15°C
184 calculated using species-specific T-S slopes) and mean annual temperature were
185 incorporated as fixed variables in a global linear mixed effects model (using package lme4).
186 Log₁₀-transformed species body mass was included to determine if the seasonal T-S
187 gradient was mass dependent, (i.e. to determine if larger species adjusted their body size
188 more strongly with intra-annual warming), following the results of Forster *et al.*, 2012 [12]
189 and Horne *et al.*, 2015 [13]. Given the strong association between latitude and mean annual
190 temperature, we modelled the effect of latitude on the seasonal T-S gradient separately.
191 Gradients from multiple studies of the same species were included in our analyses. Species
192 have shared evolutionary histories and are not completely statistically independent; we
193 therefore included levels of taxonomic classification (subphylum, class, order, family, and
194 species) as nested (hierarchical) random effects on the intercept in all models to help control
195 for phylogeny [51]. We also included habitat (marine, freshwater, terrestrial) as a random
196 effect on the intercept, to control for the fact that we had aquatic-developing species from
197 both marine and freshwater habitats. Including sex as a random effect did not improve the fit
198 of the model, and so this was excluded. Finally, as the dependent variable in our models (the
199 seasonal T-S gradient) is derived from data that vary between studies and species in their
200 goodness of fit (see Supplementary Information for individual plots of ln-transformed body
201 mass vs. temperature), we accounted for variation in information quality by weighting each
202 seasonal T-S gradient by the inverse of the variance of its T-S slope estimate (using the
203 'weights' function in R) [52]. All possible combinations of the global model terms were
204 compared using the dredge function in the MuMIn package. The best model was identified
205 as that with the lowest small-samples corrected AIC (AICc). Where the difference between a

206 model's AICc and the lowest AICc (i.e. ΔAICc) was <2 , a set of best fit models, rather than a
207 single best model, was assumed. Model averaging was then used to identify the best
208 predictor variables across the top candidate models, and determine their relative importance
209 (computed for each variable as the sum of the Akaike weights from all models in which they
210 appear). In addition to AIC, a series of F tests were used to verify the significance ($p < 0.05$)
211 of each parameter's effect on the strength of the seasonal T-S gradient. *Post hoc*
212 comparisons were made using a Tukey HSD test.

213

214 To estimate the total change in body mass that a species could achieve over a season, we
215 multiplied the seasonal T-S slope by the ATR of the sampling location for each species. This
216 value was transformed into total percentage change in body size using the formula $(\exp^{(\text{slope} \times$
217 $\text{ATR})} - 1) \times 100 = \text{total \% change in mass}$. We compared total percentage change in body size
218 between aquatic-developing and terrestrial species using a two-sample t -test. For both
219 groups, an OLS regression of total % change in mass against ATR was used to determine
220 whether species from more or less thermally variable environments exhibited a greater total
221 percentage change in body size over a season. Given that the slope of this regression did
222 not differ significantly from zero, and thus total percentage change in body size appeared
223 relatively invariant with ATR, we also estimated the maximum total percentage change in
224 body size with warming for aquatic-developing and terrestrial species. To do this, we used
225 package `quantreg` in R to fit the lowest possible quantile regression that complied with the
226 sample size of each data set, following recommendations by Rogers (1992) [53], such that
227 $n > 5/q$ (where n is the sample size and q is the quantile of interest). This gives the most
228 reliable estimate of the edge of the data set appropriate to the sample size. Each quantile
229 regression had a slope that did not differ significantly from zero; thus, we simply used the
230 intercept to estimate the limit to total percentage change in body size over the season.
231 Similarly, we also estimated the minimum total percentage change in body size with warming

232 by fitting the highest possible quantile regression through the data that complied with the
233 sample size of each data set, where $n > 5(1 - q)$ [53].

234

235 To compare seasonal T-S gradients with laboratory controlled T-S responses and L-S clines,
236 we used the data compilations of Horne *et al.* (2015) [13]. Where possible, we added data
237 from our own search to these two body size data sets, using identical methods to screen and
238 quantify size changes. For each of these data sets, we first combined size gradients from
239 multiple studies of the same species into a simple mean to generate single species-specific
240 values. Order-specific gradients were then calculated by averaging species-specific
241 gradients for each taxonomic order, and reduced major axis (RMA) regression analysis was
242 used to compare order-specific seasonal T-S gradients with laboratory T-S responses and L-
243 S clines.

244

245 We note that using interspecific length-mass conversions can increase the likelihood of
246 inaccuracy when determining body size gradients, particularly as any small deviation in the
247 equation's power term can result in substantial over- or under-estimation of the percentage
248 change in body size. Given that we sometimes had to use family- and order-specific
249 conversions, and that authors have employed a variety of equation forms, we repeated our
250 analysis using length in place of dry mass to generate a second set of seasonal
251 temperature-length (T-L) gradients (% change in length °C⁻¹). To do this we used either the
252 original length measurements reported, or calculated the cube-root of mass when this was
253 given. This length-based analysis confirms the difference in responses between environment
254 types (aquatic, terrestrial), and the major findings from this approach are summarised in the
255 Supplementary Information.

256

257 **RESULTS**

258 Our analysis included data from 71 sites in both temperate and tropical habitats between -
259 38.1° and 61.5° latitude, although 52% of all study locations are found either in Europe or
260 North America and hence dominated by northern hemisphere temperate areas (Figure 1).
261 We obtained 3,725 seasonal body mass measurements in nature, representing 30
262 freshwater, 47 marine and 25 terrestrial arthropod species from 9 taxonomic orders,
263 resulting in 225 seasonal T-S slopes (see Supplementary Information for species list and
264 individual plots of ln-transformed body mass vs. temperature). Most species (~86%)
265 conformed to the temperature-size rule; that is 88 of the 102 species exhibited a seasonal
266 decrease in adult body size with increased temperature in the field.

267

268 **Aquatic vs. Terrestrial Species**

269 The best supported model for explaining variation in seasonal T-S gradients contained only
270 developmental environment (aquatic vs. terrestrial) as a fixed variable. Three other models,
271 including an 'intercept only' model, had a $\Delta\text{AICc} < 2$. Therefore, we calculated combined
272 parameter Akaike weights across all four candidate models to determine the relative
273 importance of each variable (Table S2 in Supplementary Information). Developmental
274 environment was the most important variable, accounting for ~30% of the total variance in
275 the seasonal T-S gradient. Aquatic-developing species showed a ~2½-fold stronger
276 reduction in body size with seasonal warming (-3.1% body mass $^{\circ}\text{C}^{-1} \pm 0.8$; 95% CI) than
277 terrestrial species (-1.4% body mass $^{\circ}\text{C}^{-1} \pm 0.9$; 95% CI; $F_{1,211}=16.90$, $p < 0.001$; see Figure 2).
278 Similarly, within the order Diptera, which contains species that develop in water and on land,
279 aquatic-developing species reduced their body size significantly more per $^{\circ}\text{C}$ of seasonal
280 warming than did terrestrial-developing species ($F_{1,34}=10.17$, $p < 0.01$). These differences
281 between aquatic and terrestrial environments were also important in influencing both
282 laboratory T-S responses and L-S clines in the field [13] (Figure 2).

283

284 \bar{T} had no significant effect on the seasonal T-S gradient in either aquatic-developing
285 ($F_{1,172}=0.42$, $p=0.32$) or terrestrial arthropods ($F_{1,35}=2.80$, $p=0.10$). The seasonal T-S gradient
286 across aquatic-developing species became more strongly negative with increasing body
287 mass ($F_{1,172}=6.60$, $p=0.01$), but the goodness of fit was extremely low ($R^2=0.02$). Thus body
288 mass explained relatively little of the variation in aquatic seasonal T-S gradients in our
289 dataset. There was no significant mass-dependence in terrestrial species ($F_{1,35}=0.06$,
290 $p=0.80$). There were significant differences in the strength of the seasonal T-S gradient
291 between taxonomic orders within the sub-class Copepoda; the order Calanoida (-
292 $3.66\pm 0.70\%$ body mass $^{\circ}\text{C}^{-1}$; 95%CI) had a significantly stronger negative seasonal T-S
293 gradient than both Cyclopoida ($-0.91\pm 0.59\%$ body mass $^{\circ}\text{C}^{-1}$; 95%CI) and Poecilostomatoida
294 ($1.36\pm 3.06\%$ body mass $^{\circ}\text{C}^{-1}$; 95%CI). Latitude of the sampling location had no significant
295 effect on the strength of the seasonal T-S gradient ($F_{1,122}=1.13$, $p=0.29$).

296

297 Total percentage change in body size over the annual cycle differed significantly between
298 aquatic-developing and terrestrial species ($t_{223}=-3.52$, $p<0.001$), but did not vary with mean
299 annual temperature range in either group, such that, on average, total size change appeared
300 relatively constant ($t_{180}=0.37$, $p=0.71$ and $t_{41}=0.47$, $p=0.64$ respectively; see Figure 3). Mean
301 overall size reduction in terrestrial species was $-10.7\pm 4.8\%$ (95% CI), whereas overall size
302 reduction in aquatic-developing species was almost 3-fold greater at $-31.3\pm 5.5\%$ (95% CI)
303 (Figure 3c). Additionally, based on the lowest and highest possible quantile regressions
304 through these data (see Methods), we estimated a limit for total percentage change in body
305 mass in aquatic-developing species of $-80.2\pm 22.6\%$ (95% CI), which is more than 2½-fold
306 greater than in terrestrial-developing species at $-29.7\pm 24.9\%$ (95% CI). The lower limit to
307 total percentage change in size with warming did not differ significantly from 0% in either
308 aquatic ($t_{180}=0.17$, $p=0.87$) or terrestrial species ($t_{41}=0.55$, $p=0.58$).

309

310 **Coherence among seasonal, laboratory and latitudinal body size patterns**

311 If temperature is a major driver of seasonal body size variation in the field, seasonal and
312 controlled laboratory T-S responses should be significantly correlated. Indeed, across
313 taxonomic orders these two gradients showed a positive correlation, which did not differ
314 significantly from a 1:1 relationship ($R^2=0.59$; Figure 4a). This 1:1 match was supported by
315 the RMA slope differing significantly from zero but not from 1 (0.73 ± 0.38 ; 95% CI), whilst the
316 intercept did not differ significantly from zero (-0.39 ± 1.16 ; 95%CI) (inferred from 95%
317 confidence intervals; see inset panel in Figure 4a). Given the relatively strong T-S gradients
318 (seasonal and laboratory) of aquatic Isopoda compared with those of the other taxonomic
319 orders, we also tested whether the RMA regression, and hence co-variation between
320 seasonal and laboratory T-S gradients, was dependent on this taxonomic order. The RMA
321 regression did not differ significantly from a 1:1 relationship when the aquatic Isopoda were
322 excluded (slope= 1.31 ± 0.90 ; intercept= 0.56 ± 1.85 ; $R^2=0.41$). The seasonal and laboratory
323 datasets largely contained different species, yet, even for the small number of species for
324 which we had both sets of data ($n=22$), there was positive correlation between the two. Once
325 again the RMA slope differed significantly from zero but not 1 (1.51 ± 0.61 ; 95%CI), whereas
326 the intercept did not differ significantly from zero (1.80 ± 2.28 ; 95%CI).

327

328 Seasonal T-S gradients negatively correlated with L-S clines at the level of taxonomic order
329 ($R^2=0.81$; Figure 4b): those orders (e.g. Isopoda) whose members grew to a smaller adult
330 size in warmer seasons also showed a decrease in size towards lower, warmer latitudes.
331 Although we would not expect a 1:1 relationship between these size gradients (1° increase
332 in latitude does not equal 1°C change in temperature), the gradient of the RMA slope did
333 differ significantly from zero (-0.57 ± 0.28 ; 95% CI), confirming a significant correlation, whilst
334 the intercept did not differ significantly from zero (-0.79 ± 0.93 ; 95% CI; see inset panel in

335 Figure 4b). As before, there remained a significant correlation even when the aquatic
336 Isopoda were excluded (slope= -0.58 ± 0.52 ; intercept= -0.78 ± 1.14 ; $R^2=0.59$).

337

338 **DISCUSSION**

339 Our analysis of seasonal T-S gradients leads us to present four major conclusions: (i)
340 multivoltine arthropod species inhabiting thermally varying seasonal habitats commonly
341 demonstrate a negative seasonal T-S gradient, (ii) aquatic-developing species exhibit a
342 stronger decline in adult body size with seasonal warming than those developing in air, (iii)
343 total size reduction with warming appears relatively invariant despite variation in the annual
344 temperature range experienced, and (iv) seasonal T-S gradients correlate significantly with
345 both laboratory T-S responses and latitudinal-size clines.

346

347 The aquatic-terrestrial differences in seasonal T-S gradients per °C parallel those observed
348 in laboratory T-S responses and latitudinal-size clines [12, 13] (Figure 2). Further, mean
349 overall size reduction through the year is almost 3-fold greater in aquatic (31.3%) than
350 terrestrial (10.7%) arthropods (Figure 3c). The greatest overall reduction in body mass with
351 temperature for an aquatic species in our dataset is 90.4%, estimated for the calanoid
352 copepod *Temora longicornis*, whereas in terrestrial species it is 56.4%, estimated for the
353 isopod *Porcellionides pruinosus*. These consistent differences in seasonal T-S gradients
354 between environments suggest that the drivers of body size reduction with warming are
355 much stronger in aquatic than terrestrial arthropods.

356

357 The difference in seasonal body size change between environments is consistent with the
358 hypothesis that greater constraints on oxygen availability in water than in air have either
359 selected for greater plasticity in adult body size of aquatic species in response to

360 temperature (both per °C and overall), or imposed constraints directly on their growth,
361 compared with terrestrial species [29]. Specifically, metabolic demand increases much faster
362 with increased size and temperature than does oxygen availability in water [12];
363 consequently, aquatic-developing species may have adapted to meet these increased
364 metabolic demands with warming by reducing body size, and/or oxygen limitation may also
365 have limited growth directly. An alternative explanation based on thermoregulatory ability
366 also requires consideration. In the field, behavioural thermoregulation may allow arthropod
367 species to maintain a narrower body temperature range over a season relative to the
368 ambient temperature range, be this through seeking shade or basking in terrestrial species,
369 or vertical / horizontal migration in aquatic species. For this reason, the seasonal T-S
370 gradient in thermoregulating species may seem weaker. Due to the higher heat capacity of
371 water than air, thermoregulation is much more difficult for aquatic than terrestrial species.
372 However, we discount the explanation that thermoregulation may explain the differences
373 seen between environments, because this ability is unlikely to account for a 2½-fold
374 difference in body size reduction with warming between these two groups – such an
375 explanation would imply that, where aquatic species experience an annual temperature
376 range of 30°C, terrestrial species experience a range in body temperature of only 12°C, i.e.
377 are able to reduce their body temperature range by 18°C. At least in some environments,
378 this major reduction in body temperature range is highly improbable [54]. Furthermore, larger
379 aquatic species often exhibit the greatest reduction in body size with warming [12, 13], yet
380 we see no reason why behavioural thermoregulation would be reduced in larger compared
381 to smaller aquatic species. Instead, this pattern supports the prediction that due to their
382 lower surface area to volume ratio, larger species would struggle most to meet their oxygen
383 requirements in the warm, leading to a stronger T-S gradient. Therefore, behavioural
384 buffering does not seem capable of explaining the observed mass-dependence of the T-S
385 gradient in aquatic species, which instead is consistent with the oxygen hypothesis [12].

386

387 Although body size reduction with warming is thought to provide fitness benefits by
388 balancing resource demand and supply at elevated temperatures, this likely comes at a cost,
389 given the link between body size and other vital rates and physiological processes. For
390 example, body size is often strongly positively correlated with fecundity, including in insects
391 [55] and zooplankton [56], whilst smaller body size may also reduce survival during periods
392 of low food availability, or increase vulnerability to predation [18]. Thus, there will eventually
393 come a point at which the fitness benefits of reducing body size no longer outweigh the
394 costs. These widespread fitness trade-offs may dictate overall limits to total proportional size
395 change in arthropods; an optimal point at which the selective pressures in a given
396 environment over the annual cycle no longer favour more extreme size reductions with
397 warming. The relative consistency in total proportional size change in relation to ATR,
398 despite variation in ATR of up to 30°C between sampling locations, may be an indication of
399 such limits (Figure 3). Although these optima vary between species and environments, as is
400 observed in the ~3-fold difference in mean total body size reduction between aquatic and
401 terrestrial species, and in the scatter in total proportional change, the lack of a relationship
402 with ATR suggests that, on average, arthropods from similar environments may share and
403 frequently realize these limits, regardless of the degree of thermal variability across the year.
404 Consequently, species inhabiting environments with a greater thermal range on average
405 reduce their body size less per °C of warming than those from less thermally varying
406 environments.

407

408 Unexplained variation in the magnitude of T-S gradients between species and higher
409 taxonomic groupings is likely to be attributed to differences in life history, physiology and
410 behaviour. Indeed, such effects have been explored in the sub-class Copepoda, in which the
411 ~4-fold difference between the seasonal T-S gradients of calanoid and cyclopoid copepods
412 may relate to differences in the temperature-dependence of energy supply and expenditure
413 in current-feeding calanoids vs. ambush-feeding cyclopoids [35]. Differences in the strength

414 of seasonal variation in resource availability (e.g., food and water in terrestrial species, and
415 food and oxygen in aquatic species) or seasonal mortality risk (e.g. associated with
416 predation, desiccation or both) are also likely to modify the T-S gradient. Although the
417 arthropods in our data set all have more than one generation per year, some groups, such
418 as some of the Lepidoptera species included here, have just two generations in a year,
419 whereas others, including the smaller terrestrial Diptera and aquatic Copepoda, have many
420 overlapping generations. Voltinism is highly temperature-dependent and can constrain body
421 size [19, 27], and differences in perceived seasonality (including temperature and resource
422 availability) between species with these different generation times, might lead to differences
423 in the strength of the seasonal T-S gradient. Specifically, smaller species with short
424 generation times are likely to perceive reduced seasonality within each generation [27].
425 Hence, we might predict that the adaptive advantage of tuning body size to prevailing
426 conditions during development will be strong, leading to a greater reduction in body size and
427 a greater seasonal T-S gradient. Our data largely applies to species with many overlapping
428 generations in a year, making it difficult to assign body size measurements to specific
429 generations or cohorts. A synthesis of changes in mature body size in univoltine terrestrial
430 species, measured over multiple years, would be an informative next step, not least because
431 these species often exhibit a reverse T-S response in the laboratory (i.e. increase in size
432 with warming) and an increase in size towards the equator. In accordance with these
433 patterns, a recent study of a univoltine butterfly species showed that adult male forewing
434 length was positively correlated with temperature during development across multiple years
435 [57]. Whether such an inter-annual size trend extends more generally to other univoltine
436 terrestrial arthropods remains to be tested.

437

438 We note the potential for a mismatch between temperature at the time of collection of adults
439 in the field and the temperature the animals experienced during ontogenetic development.
440 This is particularly true for larger species with longer development times and/or in those

441 species from strongly seasonal environments. However, as discussed above, many of the
442 multivoltine species considered here generally have short generation times, often of just a
443 few weeks; thus, in most cases any temperature fluctuations experienced within a
444 generation should be fairly conserved, and temperature at time of collection of adults should
445 be a reasonable proxy for developmental temperature. Similar issues could arise in species
446 that either undergo extended periods of reproductive diapause, or live a long time as adults,
447 particularly the larger Lepidoptera species in our data set (6 of 10 Lepidopteran species
448 considered), during which time juvenile recruitment to the population is ceased. In this case,
449 adults collected during periods of diapause, or towards the end of long adult lives, may
450 actually develop much earlier in the season, when environmental conditions were very
451 different. This is further complicated because larger individuals generally have a greater
452 chance of surviving periods of dormancy, and this could be an important factor influencing
453 body size variation in diapausing generations, obscuring any effects of temperature and/or
454 resource availability [58]. Yet, when we further explored this issue, by excluding body size
455 measurements recorded during suspected periods of reproductive diapause, we observed
456 no significant shift in the T-S slope in any of the 6 species of Lepidoptera that exhibited this
457 behaviour. These species represent the few extreme cases in our data set where juvenile
458 recruitment is ceased for relatively long periods, giving us confidence in the overall patterns
459 we present.

460

461 Despite the potential pitfalls in our data and the many confounding factors that can influence
462 body size variation in the field, we find a statistically significant match between body size
463 responses measured in the laboratory and in nature, which suggests that they share
464 common drivers. The consistency in both the strength and direction of all three of these body
465 size gradients observed both at the levels of taxonomic order (Figure 4) and of species, as
466 well as between environments, and together with the weighting of data by data quality, gives
467 us confidence that these patterns are unlikely to arise simply from differences in sample size

468 between groups or potential sampling error in the individual T-S slopes. Ultimately, the close
469 match between laboratory and seasonal T-S gradients (see Figures 2 and 4a) suggests that
470 temperature is an important driver of variation in mature body size in arthropods in the
471 diverse seasonal systems we have explored, despite changes in other abiotic and biotic
472 factors that can directly influence body size variation, such as food quantity and quality [59].

473

474 Here we use a simple yet powerful correlative approach to understand major patterns in
475 body size. Although our data set represents only a tiny fraction of all arthropod species
476 globally, we identify important patterns in body size that co-vary with major body size
477 gradients. Evidently, changes in the body sizes of ectotherms associated with climate
478 change can be both substantial [41-43] and widespread [16]. Advancing our understanding
479 of what drives temperature-body size gradients in the field is essential if we are to accurately
480 predict how body size will change with projected increases in temperature and with more
481 extreme seasonality [40].

482

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651 **FIGURE LEGENDS**

652 **Figure 1.** World map (equirectangular projection) indicating the location of studies (n=71)
653 from which seasonal temperature-size gradients were recorded, categorized by environment
654 type. Colour gradient indicates mean annual temperature ranges. Sea surface temperature
655 data was used for marine environments. Air surface temperature data was used for
656 terrestrial and freshwater environments. Data sources are given in the Methods.

657

658 **Figure 2.** Comparison of mean aquatic-developing and terrestrial-developing seasonal
659 temperature-body size gradients (% change in mass per °C \pm 95% CI, left-hand y-axis) in
660 arthropods with laboratory temperature-size responses (% change in mass per °C \pm 95% CI,
661 left-hand y-axis) and latitudinal-size clines (% change in mass per °latitude \pm 95% CI, right-
662 hand y-axis) for multivoltine species, using data from this study and Horne *et al.*, 2015 [13].
663 Different letters above data points indicate significant differences. Dashed grey line indicates
664 no change in body size with warming or increasing latitude. Note the reversal of the right-
665 hand y-axis (for the latitudinal-size cline) for ease of comparison (a reduction in body size
666 with increasing temperature is then comparable with an increase in body size with increasing
667 latitude).

668

669 **Figure 3.** Total change in body mass (%) vs. annual temperature range (°C) for (a) terrestrial
670 and (b) aquatic arthropods. Solid black line represents the OLS regression, the slope of
671 which does not differ significantly from zero in either environment, such that total percentage
672 change in mass appears invariant with annual temperature range. Dashed black lines show
673 the lowest and highest possible quantile regressions through the data and represent the
674 upper and lower limits to total body size reduction with warming respectively (c) Mean total
675 size reduction with warming (expressed as a % change in body mass (\pm 95% CI)) for

676 terrestrial and aquatic-developing species. Different letters above data points indicate
677 significant differences.

678

679 **Figure 4.** Reduced major axis (RMA) regression comparing seasonal temperature-size
680 gradients (% change in body mass per °C ±SE) in arthropods with (a) laboratory
681 temperature-size responses (% change in body mass per °C ±SE), and (b) latitudinal-size
682 clines (% change in body mass per °lat ±SE), categorized by taxonomic order and
683 developmental environment (aquatic=open symbols; terrestrial=filled symbols). Dashed lines
684 indicate a 1:1 relationship. Inset graphs show the intercept and slope values for each
685 regression (±95% CI).

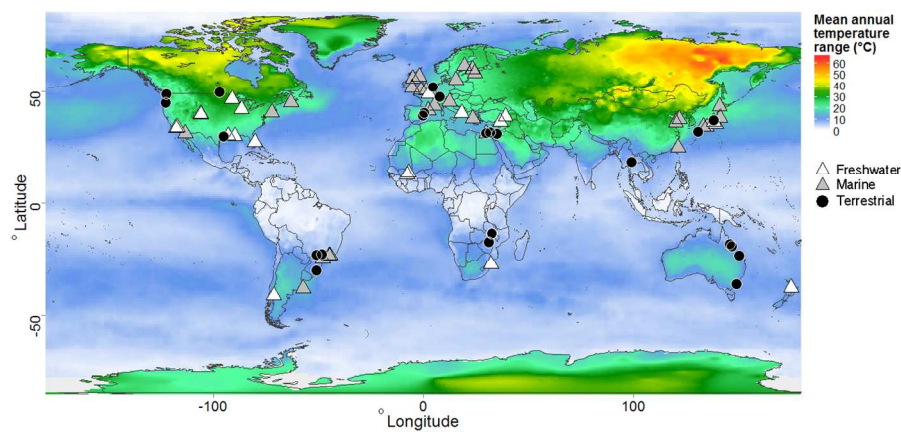


Figure 1. World map (equirectangular projection) indicating the location of studies ($n=71$) from which seasonal temperature-size gradients were recorded, categorized by environment type. Colour gradient indicates mean annual temperature ranges. Sea surface temperature data was used for marine environments. Air surface temperature data was used for terrestrial and freshwater environments. Data sources are given in the Methods.

Figure 1

393x171mm (96 x 96 DPI)

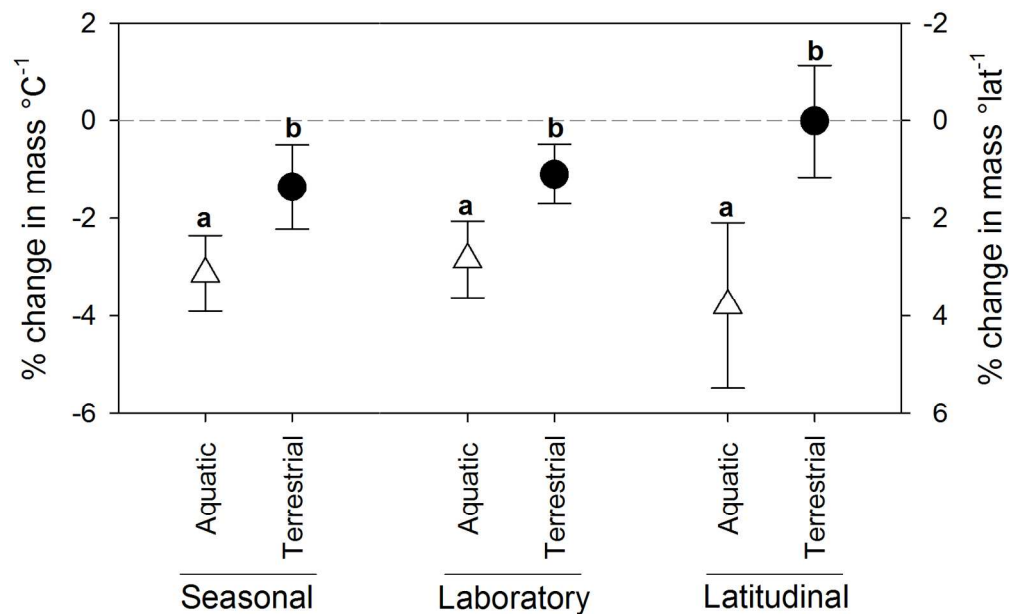


Figure 2. Comparison of mean aquatic-developing and terrestrial-developing seasonal temperature-body size gradients (% change in mass per °C \pm 95% CI, left-hand y-axis) in arthropods with laboratory temperature-size responses (% change in mass per °C \pm 95% CI, left-hand y-axis) and latitudinal-size clines (% change in mass per °latitude \pm 95% CI, right-hand y-axis) for multivoltine species, using data from this study and Horne *et al.* 2015 [13]. Different letters above data points indicate significant differences. Dashed grey line indicates no change in body size with warming or increasing latitude. Note the reversal of the right-hand y-axis (for the latitudinal-size cline) for ease of comparison (a reduction in body size with increasing temperature is then comparable with an increase in body size with increasing latitude).

Figure 2
153x98mm (300 x 300 DPI)

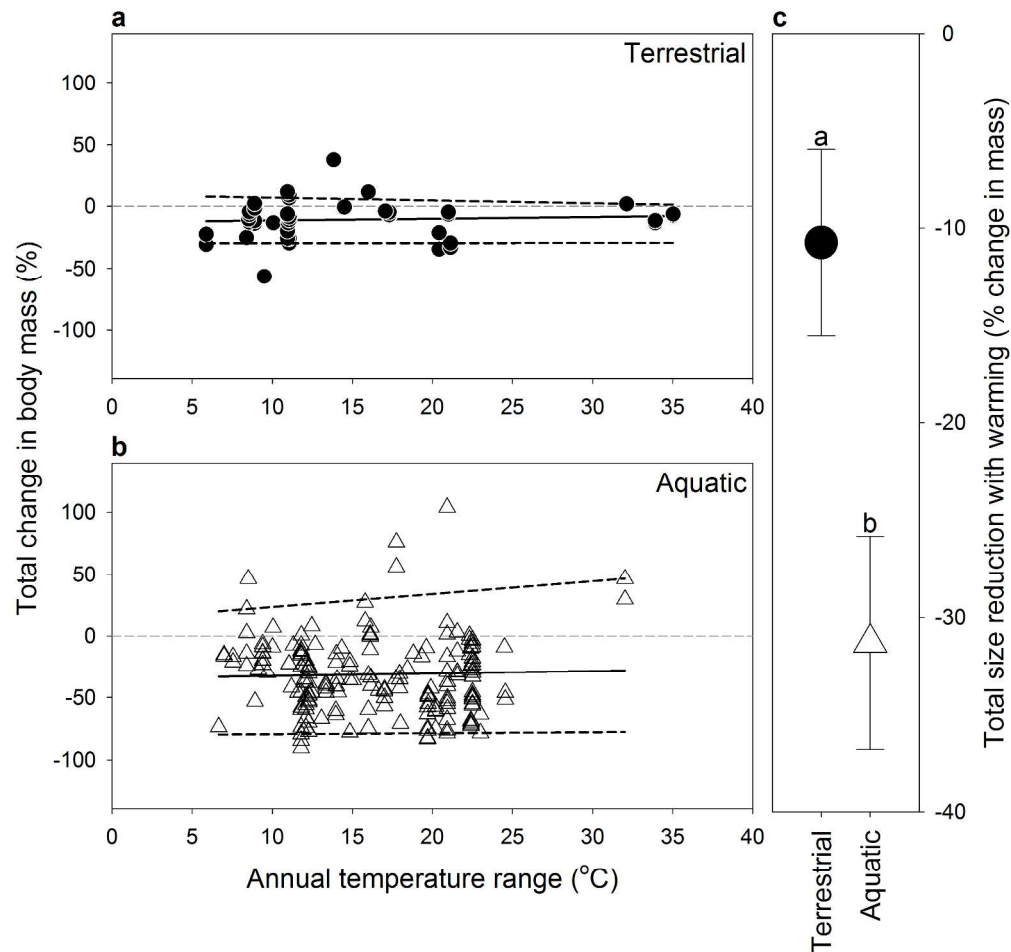


Figure 3. Total change in body mass (%) vs. annual temperature range (°C) for (a) terrestrial and (b) aquatic arthropods. Solid black line represents the OLS regression, the slope of which does not differ significantly from zero in either environment, such that total percentage change in mass appears invariant with annual temperature range. Dashed black lines show the lowest and highest possible quantile regressions through the data and represent the upper and lower limits to total body size reduction with warming respectively (c) Mean total size reduction with warming (expressed as a % change in body mass ($\pm 95\%$ CI)) for terrestrial and aquatic-developing species. Different letters above data points indicate significant differences.

Figure 3
259x255mm (300 x 300 DPI)

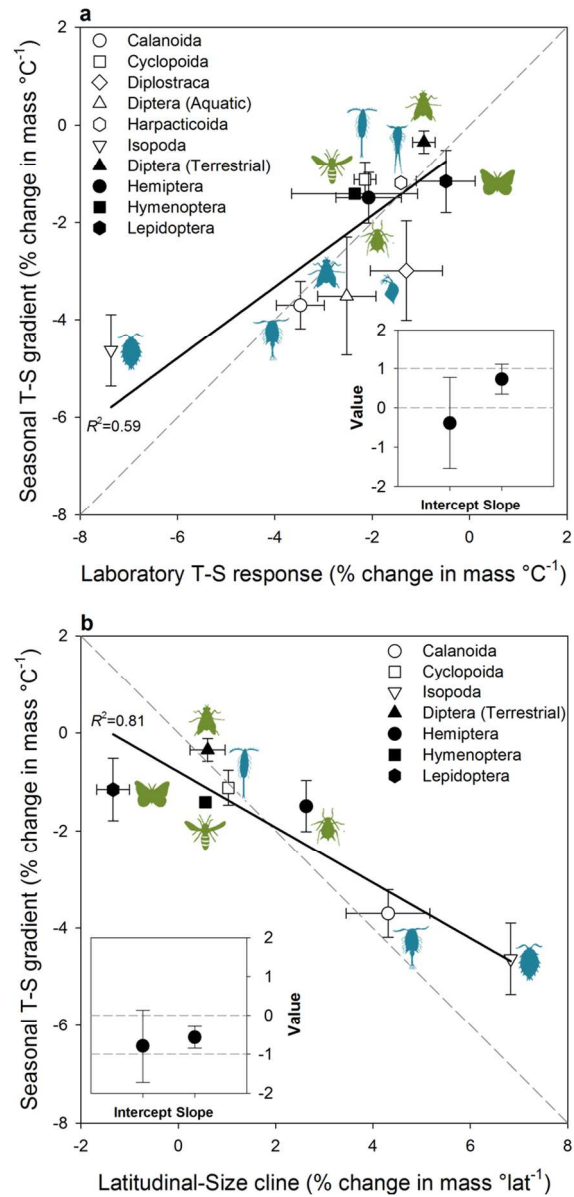


Figure 4. Reduced major axis (RMA) regression comparing seasonal temperature-size gradients (% change in body mass per °C ±SE) in arthropods with (a) laboratory temperature-size responses (% change in body mass per °C ±SE), and (b) latitudinal-size clines (% change in body mass per °lat ±SE), categorized by taxonomic order and developmental environment (aquatic=open symbols; terrestrial=filled symbols).

Dashed lines indicate a 1:1 relationship. Inset graphs show the intercept and slope values for each regression (±95% CI).

Figure 4

218x453mm (96 x 96 DPI)