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16 **Species' distribution and evolutionary history influence the responses of marine**
17 **copepods to climate change: a global meta-analysis**

18

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26 history; phylogenetic signal; ocean warming; ocean acidification

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28

29 **Abstract**

30 Ocean acidification (OA) and warming (OW) are predicted to drive changes to the distribution
31 of species and the structure of biological communities globally. Differences in life history,
32 physical traits, and the phenotypic response of organisms will, however, mean that the effects
33 of OA and OW will differ among species. Geographical differences in environmental
34 characteristics across habitats will also influence the effects of OA and OW, thereby driving
35 inter-population differences in phenotypic response as determined by local adaptations. While
36 is it accepted that the response of species will vary globally, predicting the trends in response
37 of species remains highly uncertain. We undertook a meta-analysis of key biological traits of
38 47 marine copepod species from 88 studies to identify the intrinsic and extrinsic factors
39 influencing the effects of OA and OW on copepod population demographics. Data from OA
40 and OW were analysed independently due to insufficient two-stressor studies. We found that
41 the large disparity in the response of species to OA and OW is largely defined by their
42 environmental history. Additionally, the response of copepod species to OW is related to their
43 evolutionary history which has less influence on their response to OA. Therefore, our study
44 identified that the response of copepods to OA is driven by a combination of biotic and abiotic
45 factors in their habitats. Under OA alone, copepods from less variable environments may be
46 more susceptible but the effects of OA will only be strongly negative at extreme low pH (<7).
47 On the other hand, the response to OW is deeply tied to their phylogeny, whereby closely
48 related species share similar costs and trade-offs. However, the effects of near future OW (+ 2
49 to 4°C) seem mainly positive unless these temperatures exceed a species' thermal limit.
50 Finally, our analysis revealed that OW has a greater influence on key copepod traits than OA.
51 Overall, this study shows that attempting to draw global patterns in the response of species to
52 climate change from a single species or habitat without consideration of environmental and

53 evolutionary history could lead to inaccurate and misleading predictions with respect to the
54 future of biological communities.

55
56

57 **Introduction**

58 Ocean acidification (OA) and ocean warming (OW), two major components of
59 anthropogenic climate change, are predicted to be important drivers of genetic, phenotypic and
60 biodiversity change at a global scale, altering the functioning of marine communities and
61 ecosystems (Parmesan 2006; Hoegh-Guldberg & Bruno 2010; Doney et al. 2012; Nadeau et al.
62 2017; Pecl et al. 2017). The ecological effects of OA and OW are expected to vary among
63 different species depending on intrinsic characteristics of marine organisms such as their
64 physiological tolerance (Pörtner & Knust 2007; Hofmann & Todgham 2010; Sorte et al. 2011),
65 their life stages (Dupont et al., 2010; Byrne & Przeslawski 2013), and their capacity for plastic
66 responses and rapid adaptation (Hofmann & Todgham 2010; Reusch 2014). Moreover, the
67 effects of OA and OW are also expected to vary across temporal and spatial scales due to
68 extrinsic factors such as the rate of environmental change (Hoffmann & Sgrò 2011; Silbiger &
69 Sorte 2018), the degree of environmental variability (Eriander et al. 2015) and the differences
70 in environmental conditions among regions and habitats (Boyd et al. 2015). For instance,
71 populations inhabiting highly variable environments, characterised by high natural
72 environmental variability in sea surface temperature, pH and pCO₂ (e.g., upwelling regions;
73 Sobarzo et al. 2007; Letelier et al. 2009; Kapsenberg & Hofmann, 2016; Chavez et al. 2018),
74 can display greater resilience or plasticity to climate change compared to those inhabiting more
75 stable systems (Berg et al. 2010; Donelson et al. 2018). Nevertheless, these habitat-related
76 responses are not consistent across different regions and taxa (e.g., Cornwall et al. 2020),
77 challenging our capacity to make more accurate predictions of the effects of climate change on
78 populations, communities and ecosystems. In order to address this problem, it is necessary to

79 assess the potential sources and causes that influence the documented heterogeneity in the
80 phenotypic responses of marine organisms to OA and OW.

81 One of the main issues with estimating the effect of climate change on species is that
82 most empirical studies consider species as a single unit where individuals from all populations
83 respond equally to environmental pressures (Valladares et al. 2014). However, populations
84 across the geographical distribution of a species can experience vastly different environmental
85 conditions that influence differences in local adaptation, phenotypic plasticity and the capacity
86 for phenotypic/genetic responses to OA and OW (Boyd et al. 2015; Gaitan-Espitia et al. 2017a,
87 b). In coastal systems, for instance, chemical and physical processes differ across geographical
88 regions but also across ecosystems in close proximity (Gunderson et al. 2016; Fassbender et
89 al. 2018; Silbiger & Sorte 2018). Therefore, coastal zones are influenced by local suites of
90 environmental parameters which can change biological outcomes. For example, in areas where
91 upwelling events are prevalent, ecosystems are naturally exposed to high variation in carbon
92 dioxide concentration, oxygen concentration, pH, and temperature (Sobarzo et al. 2007;
93 Letelier et al. 2009; Kapsenberg & Hofmann, 2016; Reum et al. 2016; Chavez et al. 2018).
94 Conversely, in areas of extensive estuarine discharge, fluctuations in salinity, pH, and turbidity
95 are common (Sarma et al. 2012; Aguilera et al. 2013; Shen et al. 2013; Asp et al. 2018). As a
96 result, species from these different habitats may respond differently to climate change because
97 their tolerances and sensitivities have been differentially shaped by natural selection (Vargas
98 et al. 2017; Gaitan-Espitia et al. 2017a).

99 Heterogeneity in phenotypic responses to OA and OW can also originate from sources
100 of intrinsic biological characteristics such as body size (Daufresne et al. 2009; Garzke et al.
101 2015) and the evolutionary history of the species (Davis et al. 2010; Buckley & Kingsolver
102 2012). Body size is an important determinant of fitness, physiology and performance in many
103 organisms (Roff 2002). It has been documented that intra- and inter-species variation in this

104 important trait can influence the species' and communities' responses to environmental stress
105 and climate change (Daufresne et al. 2009; Garzke et al. 2015; Rice et al. 2015). However, this
106 variation, as well as variation in other phenotypic traits and responses to climate change, are
107 highly dependent on the evolutionary history of species because closely related species share
108 more similar characteristics than distantly related species (i.e., species are not statistically
109 independent) (Felsenstein 1985). Thus, comparative assessments of the phenotypic responses
110 of species to OA and OW in a taxonomically resolved framework is important (Buckley &
111 Kingsolver 2012) whereby exclusion of phylogenetic distribution can potentially hide
112 phylogenetic signals inducing bias in our interpretations of the species' and communities'
113 susceptibility to climate change.

114 Here, we use copepods as model taxon to explore potential intrinsic and extrinsic causes
115 of heterogeneity in biological responses of marine organisms to climate change. Copepods
116 occupy various niches in multiple marine habitats, including coastal, estuarine, oceanic and
117 intertidal habitats (McGinty et al. 2018). As a result, these crustaceans are exposed to a vast
118 array of environments, including fluctuations in salinity, oxygen concentration, temperature
119 and pH level. Some oceanic copepod species, for example, undergo deep diel migrations and
120 are exposed to large variations in temperature and pH on a daily basis (Lewis et al. 2013;
121 Svetlichny et al. 2000). On the other hand, coastal and estuarine species can be exposed to
122 upwelling or high freshwater discharge that drastically change their environmental pH,
123 temperature, oxygen concentrations or salinity (Escribano & Hidalgo 2000; Aguilera et
124 al.2013; Aguilera et al. 2016). Copepod species can also inhabit extreme environments such as
125 intertidal rockpools, characterized by extremely large diel and seasonal changes in pH and
126 temperature linked to variation in sunlight exposure, primary production and respiration
127 (Powlik 1999; McAllen et al. 2009; Willett 2010). The responses of different species of
128 copepods to their abiotic conditions are as varied as the environments themselves (Edmands &

129 Harrison 2003; Brun et al. 2016; Horne et al. 2016; Pereira et al. 2017). While life-history
130 theory predicts that different traits evolve in different environments, concurrently, phylogenetic
131 history may restrict natural selection by dictating the range of phenotypes that selection can act
132 upon (Hairston and Bohonak 1998). Therefore, closely related taxa may share similar traits and
133 trade-offs when exposed to similar variation in their abiotic environment.

134 Since different environments and phylogenetic histories can influence the biological
135 traits of copepods, the effect of climate change on traits can also be expected to vary across
136 habitats and taxa. In fact, short term exposure to OA causes varied effects on the biological
137 traits of different copepod species (Zhang et al. 2011; Lewis et al. 2013; McConville et al.
138 2013; Wang et al. 2018), different populations (Thor et al., 2018) and copepods from different
139 habitats, such as between coastal (Cripps et al. 2014), estuarine (Aguilera et al. 2016; Hemraj
140 et al. 2017) and oceanic habitats (Mayor et al. 2007; Weydmann et al. 2012). Similarly, OW
141 can cause varied effects among species (Chinnery and Williams 2004), populations (Scheffler
142 et al. 2019) and habitats (Han et al. 2018). In addition to short term variation, long-term
143 increases in $p\text{CO}_2$ and temperature are expected to have trans- or multigenerational effects
144 through selection (Thor & Dupont 2015). In contrast to predictions, however, persistent
145 benefits to fitness across generations are not consistently observed (Byrne et al. 2020). Thus,
146 the effects of OA and OW on copepods are not generic and estimating their effects on different
147 species across global oceans is highly ambiguous. Therefore, to understand the potential
148 intrinsic and extrinsic causes of heterogeneity in biological responses of marine organisms to
149 projected climate change, we undertook a global meta-analysis and review of the studies of OA
150 and OW on biological traits of copepods (Figure 1). Data from OA and OW were analysed
151 independently due to insufficient two-stressor studies (Vehmaa et al. 2012; 2013; Hildebrandt
152 et al. 2014; Preziosi et al. 2017; Garzke et al. 2020).

153 First, we investigated the variation in the effects of OA and OW on copepod fecundity
154 (egg production and hatching success) and adult survival across latitudes, marine habitats
155 (estuarine, intertidal, coastal and oceanic), and among taxonomic groups. We used
156 reproduction and adult survival since these are part of the fundamental activities that define
157 fitness in organisms (Litchman et al. 2013). Second, we investigated the influence of the
158 number of eggs produced on the hatching success under OA and OW to identify the extent of
159 investment in reproductive output of different species and how these may drive their fitness
160 under climate change. Finally, we investigated the influence of metabolic scaling across
161 copepod species in defining possible metabolic costs as a trade-off for surviving in acidified or
162 warmer oceans. We, therefore, provide a more comprehensive understanding of the causes of
163 heterogeneity in response to OA and OW observed in copepods.

164

165 **Methods**

166 *Data selection and suitability criteria*

167 Meta-analyses were carried out following the PRISMA (Preferred Reporting Items for
168 Systematic Reviews and Meta-Analyses) and the CEE (Collaboration for Environmental
169 Evidence) guidelines. We undertook a comprehensive search for peer-reviewed papers
170 explicitly investigating the effects of OA and OW on copepods. Searches were carried out on
171 ScienceDirect, PubMed, Microsoft Academic and ISI Web of Science using the following
172 search strings: TS=[("copepod") AND ("climate change" OR "ocean acidification" OR
173 "hypercapnia" OR "pH")], as well as TS= [("copepod") AND ("global warming" OR "ocean
174 warming" OR "temperature")]. Searches included papers published between January 1990 -
175 March 2020, as most climate change studies that manipulated climate change conditions in
176 regard to IPCC AR1 predictions (the first assessment and model of future CO₂ concentrations
177 or temperature increase which are used as baseline conditions to test for organismal response

178 to future climate change) and subsequent updates (IPCC 1990, 2007) were published post 1990.
179 However, we also included experimental studies that investigated the effect of temperature
180 increments on copepod biological response outside of the climate change context, irrelevant of
181 the year, as these experiments were comparable (i.e. account for temperature increments which
182 are within estimates of future ocean warming under climate change) and provided a more
183 comprehensive dataset for investigating the influence of ocean warming on copepods. Our full
184 search yielded 27,273 potential papers. Papers were screened to only include studies that
185 undertook controlled manipulative experiments on trait responses at specific treatment
186 conditions (e.g. response at pH 8.1, 7.7, 7.2 and 6.9; or response at temperature 20°C, 15°C
187 and 10 °C) or undertook measurements of different biological responses directly on organisms
188 across naturally occurring pH or temperature gradients (e.g. comparing traits of a copepod
189 species that naturally has populations occurring in coastal waters and low-pH estuarine waters
190 in close proximity). In addition, we further screened papers to include only those that
191 investigated the influence of OA and OW on fecundity, survival/mortality,
192 respiration/metabolic rates, and feeding rates since these are the only traits analysed in this
193 study. Finally, we only included studies that reported data on adults of a particular species fed
194 *ad libitum* to avoid confounding factors such as life-cycle stage or different food availability.
195 After this manual screening and removal of duplicates, out of 116 papers that investigated the
196 response of copepods to OA or OW, 88 papers remained from which biological response data
197 of interest could be collected (see supplementary materials for the list of papers). In the instance
198 where a study reported multiple independent variables, only data from ‘ambient’ conditions
199 and the variable of interest were used in our analysis. For example, if a study reported biological
200 response data at ‘ambient’ conditions, ‘low-pH’, ‘low-food’, and ‘low-pH × low-food’, only
201 ‘ambient’ and ‘low-pH’ data were used. In the instance where organisms were sampled along
202 environmental gradients, such as a pH gradient, data were collected from each pH value to the

203 closest one decimal point (e.g. 8.1, 8.0, 7.9, 7.8, etc.) or as grouped within the original paper
204 (e.g. in Aguilera et al. 2020 pH > 8 considered as high pH, pH 7.8 – 7.9 considered as low pH
205 group one and pH < 7.8 considered as low pH group two). This was done to account for as
206 much data and variation as possible. Additionally, when repeated measurements were
207 undertaken on the same individuals over time (e.g. egg production rate estimated on day 2, day
208 4 and day 6; at temperature 0°C or 4°C), an average of the measurements was used at each
209 variable level (mean of days 2, 4 and 6 at temperature 0°C and mean of days 2, 4 and 6 at
210 temperature 4°C represented as egg produced per female per day) to ensure we captured the
211 overall response of these individuals rather than individual or diel variations. Alternatively, if
212 cumulative measurements were reported (e.g. percentage eggs hatched from clutch 1 on day 1,
213 3, 5), only the final measurements were used as that denoted the final maximum in that
214 treatment. Several studies included data from multiple species, locations and independent
215 variable levels (e.g. pH 7.8, 7.5, and 7.2). In these cases, all variable levels, species, and
216 locations were included in the analysis as independent measurements if they met the suitability
217 criteria above; each species from each separate population was analysed at each variable level.
218 This approach ensured that we captured the broad range of response in our analysis.

219 Finally, to be included in the analysis, studies that met the suitability criteria had to
220 either provide a full dataset as supplementary or the data had to be reported as mean or median,
221 a measure of variance (standard deviation, standard error, 95 % confidence interval, or range),
222 and sample size (N). Raw data was obtained by searching for supplementary data sets on the
223 journal websites, the Ocean Acidification International Coordination Centre through GOA-ON
224 (<http://portal.goa-on.org/>), or PANGAEA (<https://www.pangaea.de/>). For studies that did not
225 provide datasets, the means, variances and sample sizes were extracted from tables in the paper
226 or from graphical displays using PlotDigitizer™ for windows
227 (<http://plotdigitizer.sourceforge.net/>).

228

229 *Data analysis*

230 The effect size of biological responses between controls and treatments were calculated
231 using the means, standard deviations and sample sizes following Hedges et al. (1999). By using
232 effect sizes in our analyses rather than real measured values, we estimated the change in traits
233 based on different pH or temperature levels directly, therefore, limiting (but not eliminating)
234 the possible effects of confounding factors (e.g. seasons) in our analyses. We selected log
235 response ratio (LnRR) to estimate the effect size because of the capacity to detect true effects
236 and robustness to small sample sizes (Lajeunesse & Forbes 2003). For each biological
237 response, LnRR values were calculated using the following equation:

238
$$\text{LnRR} = \ln (\text{Mean}_T) - (\text{Mean}_C)$$

239 where, Mean_T is the mean of treatment and Mean_C is the mean of control. In some studies,
240 variances were reported as standard error (SE) or as median and ranges. When standard errors
241 were reported, standard deviations (SD) were calculated using the following equation:

242
$$SD = SE \times \sqrt{N}$$

243 where, SE is the standard error and N is the sample size. When median and ranges were
244 reported, means and standard deviation were calculated as per Hozo et al. (2005) with the
245 following equations:

246
$$\text{Mean} = (a + 2m + b)/4$$

247 where, a is the lower range, b is the upper range and m is the median,

248
$$SD = (1/12) \times \{(a - 2m + b)^2/4 + (b - a)^2\}$$

249 for $N < 15$, where, a is the lower range, b is the upper range and m is the median and

250
$$SD = \text{Range}/4$$

251 for $N > 15$. Finally, when 95 % confidence intervals were reported, standard deviation was
252 calculated using the following equation from Higgins et al. (2019):

253
$$SD = \sqrt{N} \times (upper\ limit - lower\ limit)/3.92$$

254

255 Prior to formal meta-analysis, we calculated a Rosenberg Fail-Safe number to test for
256 publication bias. Publication bias may be caused if studies finding non-significant effects are
257 not published (Rosenberg 2005) and are therefore not included in analysis, thus may influence
258 results and interpretation. The Fail-Safe number calculates the number of studies with non-
259 significant effects (effect size of zero) that would be required to change the results of the meta-
260 analysis from significant to non-significant (Rosenberg 2005). The Rosenberg Fail-Safe
261 numbers calculated were larger than $5n+10$, where n is the number of studies included in our
262 analysis (Rosenberg 2005), therefore our analyses are generally robust and publication bias
263 was unlikely to affect our results. Following the publication bias test, we undertook the meta-
264 analyses using weighted random effects models (restricted maximum likelihood) that utilise
265 inverse-variance weighting to account for variation within and between studies (Wallace et al.
266 2017), therefore accounting for random sampling variation within each experiment and
267 variation among studies in estimated effect size (Hancock et al. 2020; Harvey et al. 2013). The
268 weighted random effects model provides wider confidence intervals when there is
269 heterogeneity, thus statistical significance is more conservative. The model calculates the true
270 variation in effect size by the between-study variance (using the ln-transformed response ratios,
271 LnRR), with each study weighted by the inverse sum of the individual study variance (Hancock
272 et al. 2020). This includes a heterogeneity test (Q) that compares the variation in study
273 outcomes between studies and indicates the percentage variation between studies due to
274 heterogeneity (i.e. differences in outcomes between different studies; also denoted as I^2) rather
275 than chance (Wallace et al. 2017). To test for differences between pre-defined groups and
276 perform explanatory analyses for variation in effect sizes, we performed meta-regressions
277 using mixed-effects models (Harvey et al. 2013) using pH, temperature, latitude from where

278 organisms were sampled, habitat from which organisms were sampled, species body size
279 (prosome length), genus and species as explanatory variables. We grouped different species
280 based on their egg production rates (low, medium and high egg production rates (< 10, 10-20,
281 and > 20 eggs per female per day, respectively) and analysed the effects that OA and OW have
282 on their hatching success. We grouped the egg production rates at ambient conditions (control
283 conditions used within studies) for adult females only for each species from different papers
284 and used the mean egg production rate for each species to categorise them within different
285 groups (low, medium, high). All data were converted to the number of eggs female⁻¹day⁻¹ to
286 standardise egg production data for analysis (e.g. if 3 adult females produced 120 eggs at day
287 5 of an experiment, the egg production rate used was calculated as $((120/5)/3) = 8$ eggs female⁻¹
288 day⁻¹). In addition to egg production, we analysed the effects of OA and OW on the hatching
289 success of species based on their spawning mode (broadcast or sac spawners). To test for the
290 influence of metabolic scaling on the metabolic costs of copepods under novel environmental
291 conditions, we analysed the effect size of OA and OW on the metabolism (energy expenditure)
292 and feeding rates (energy intake) of copepods in relation to the species body size (average
293 prosome length). Finally, to test for the effect of evolutionary history on traits, and because
294 we analysed biological responses per species rather than overall response per study, we used
295 phylogenetic analyses throughout the study to reflect evolutionary history whereby closely
296 related species share a common evolutionary history more than distantly related species. We
297 tested for the percentage heterogeneity attributed to phylogeny (phylogenetic heterogeneity) in
298 biological response using both Pagel's lambda (Brownian Motion model) and Martins and
299 Hansen's alpha (Ornstein and Uhlenbeck model) as measure for phylogenetic signal.
300 Phylogenetic signal is a statistical measure of the degree to which evolutionary history has
301 driven trait distribution. Phylogenetic relationships were analysed in MEGA (version 10.1.7),
302 using maximum-likelihood phylogenetic trees, based on best model estimation and accounting

303 for branch lengths and rates of molecular evolution. Molecular data (cytochrome oxidase I)
304 was obtained from NCBI taxonomy database. Calculation of effect sizes, meta-analysis, meta-
305 regressions and analysis of phylogenetic heterogeneity were performed on OpenMEE (Wallace
306 et al. 2017), which is an open-source software specifically designed for meta-analysis in
307 ecology and evolutionary biology, and based on the ‘metafor’ and ‘ape’ packages for R. To
308 ensure the sensitivity of our analyses, we reran analyses by removing the studies showing larger
309 effect sizes (Harvey et al. 2013). In addition, to verify the robustness of the analyses, we used
310 an effect-size correction technique (RR^Δ) as outlined in Lajeunesse (2015) and re-analysed the
311 data. No differences in results were found when RR^Δ was used compared to $\ln RR$, therefore,
312 confirming the robustness of the analyses.

313 314 **Results**

315
316 The 88 papers that passed our suitability criteria assessed the effect of OA and OW on
317 the egg production hatching success, survival, metabolism and feeding rates of 47 species of
318 copepod. Overall, 585 effect sizes were calculated using data from these studies. The majority
319 of the studies were undertaken in the northern hemisphere, investigating the effects of OA and
320 OW primarily on coastal copepod species in temperate regions (Figure 2). Overall, OA and
321 OW had opposing effects on copepod fecundity and survival (Table 1 and 2). When considering
322 all studies, OA decreased both fecundity and survival while OW generally increased these traits
323 (Figure 3). However, there was high heterogeneity in the effects of both OA and OW,
324 confirming variation in the response of different species and studies.

325 Fine-scale analysis revealed that the effect of OA on copepod fecundity (Figure 4) was
326 more marked at lower pH. Nonetheless, this relationship seems to be driven by extreme low
327 pH (pH < 7.0; Table 1), because the relationship was neither significant at pH > 7.7 (estimated
328 end of century OA) or pH > 7.0 (Table 1). Moreover, OA did not have significant overall effect
329 on the fecundity of copepods independent of their different habitats, latitudes or body sizes

330 (Table 1). Although similar findings were documented for survival (Table 1; Figure 5), our
331 results revealed an interesting trend in which copepods living at higher temperatures (lower
332 latitudes) tend to be less affected by OA than copepods from cooler environments at higher
333 latitudes (Mean effect size for latitude > 50 degrees = -0.324, latitude < 50 degrees = -0.107;
334 Table 1). Higher metabolic rates (mean effect size: 0.145) but decreased feeding rates (mean
335 effect size -0.255) in response to OA (Table 3) suggested an energetic mismatch where energy
336 demands increased but energy acquisition was reduced, as seen in Thor et al. (2018). However,
337 these effects were independent of habitat, latitudes and especially body size suggesting a lack
338 of influence of metabolic scaling as observed by the lack of significant relationship between
339 body size and the effect size of OW on metabolism (Table 3). The assessment of other potential
340 sources of heterogeneity in the phenotypic responses of copepods to OA suggests that the
341 species identity and evolutionary history are important factors. For instance, hatching success
342 based on the egg production rate is differentially affected by OA depending on species' specific
343 characteristics. Species with higher egg production rates (> 20 eggs/female/day) endured
344 greater reduction in hatching success (mean effect size: -0.686, -0.142 and -0.11 for high,
345 medium and low egg production, respectively) under OA (Table 4; Figure 6) while no
346 differences were found between broadcast and sac spawners (Table 4). Contrary to fecundity,
347 the effects of OA on survival varied among different genera (Table 1). For this trait, the oceanic
348 genus *Oithona* was more negatively affected by OA than other groups (Figure 5). There was
349 partial phylogenetic influence on the effect of OA on egg production, hatching and survival.
350 Phylogeny explained 18 %, 10 %, and 32 % (average estimated from Pagel's Lambda and
351 Martins and Hansen's alpha) of heterogeneity in the effect of OA on egg production, hatching
352 and survival, respectively (Table 1). When the phylogenetic influence was removed from the
353 models, the overall effect of OA on fecundity and survival remained negative, suggesting that
354 other biotic or abiotic factors are also influencing the phenotypic responses of copepods to OA.

355 OW generally increased fecundity in copepods (Table 2, Figure 7). However, the
356 increase followed a hormesis shape (biphasic, involving an increase followed by a decrease
357 over a temperature gradient; supplementary Figure 3). There were no distinct overall
358 differences in the effect of OW on fecundity among different habitats, but egg production in
359 oceanic species increased significantly more than in estuarine species ($p = 0.034$). In contrast,
360 hatching success of coastal species increased compared to that of oceanic species (+22.7 % and
361 -9.5 % on average, respectively; Table 4). OW increased hatching success in species with
362 higher natural egg production (> 20 eggs/female/day) compared to those with medium and low
363 egg production rates (mean effect size: 0.763, -0.112, 0.154 for high, medium and low egg
364 production, respectively; Table 4) while no differences were found in hatching success between
365 broadcast and sac spawners (Table 4). As for survival (Figure 8), no differences between
366 habitats were observed (Table 2), however, within coastal habitats OW significantly increased
367 the survival of *Acartia* spp. while other coastal copepods had less response ($p < 0.05$).
368 Latitudinal distribution had no influence on the effect of OW on fecundity or survival (Table
369 2). On the other hand, the hatching success of smaller copepods (< 2 mm prosome length)
370 increased compared to that of larger copepods (> 2 mm prosome length) under OW (mean
371 effect size: 0.533 and -0.140, respectively) while metabolic rates of species inhabiting coastal
372 regions increased more than that of oceanic and intertidal species, (mean effect size: 0.855,
373 0.557 and -0.483 respectively; Table 3). There were strong differences among the responses of
374 different genera and species, and strong phylogenetic signals were observed (Table 2).
375 Phylogenetic distribution contributed to 63 %, 14 %, and 86 % (average estimated from Pagel's
376 Lambda and Martins and Hansen's alpha) of variance in the effect of OW on egg production,
377 hatching and survival, respectively. When the phylogenetic influence was removed from the
378 models, the overall effect of OW on fecundity and survival changed from positive to neutral,
379 indicating that closely related species tend to respond similarly to OW.

380

381

382

383 **Discussion**

384 Substantial changes in the pH and temperature of the oceans are among the primary
385 threats predicted to affect marine life at a global scale. Empirical evidence suggests that marine
386 organisms will likely undergo rapid phenotypic changes (e.g., increasing metabolic rates,
387 decreasing body size) in response to OA and OW (Kroeker et al. 2013). Although these changes
388 potentially involve important functional and genetic trade-offs (Gaitan-Espitia et al., 2017a),
389 they provide a mechanism to ameliorate the negative effects of OW and OA on fitness,
390 increasing either their survival or the survival of their progeny. As a consequence, phenotypic
391 changes and the associated trade-offs driven by OA and OW are expected to influence
392 dynamics in natural populations and communities, with profound ecosystem-level effects.
393 Here, we show that OA and OW can drive varied phenotypic responses that are conditioned to
394 some extent by the habitat, life-history traits and the phylogeny of a species. Therefore, we
395 elucidate the importance of incorporating environmental and evolutionary histories into
396 predictions of how species will respond to OA and OW.

397 Our study focusses on traits including reproductive output, survival, and energy intake
398 to identify the effects of OA and OW copepods. While we undertook an in-depth analysis using
399 these traits, our study may be limited by some factors: (1) we did not include all traits under
400 ‘life-history’ and ‘physiology’ therefore our study does not encompass all copepod traits that
401 have been analysed under OA and OW; (2) our study focusses on adult copepods and did not
402 analyse the effects of OA and OW on development and different nauplii and copepodite stages;
403 and (3) we did not include genetic analyses in the meta-analysis. Although our study may lack
404 analysis of some traits, considering meta-analyses may generalise overall effects, we believe

405 we have undertaken thorough analyses to identify the effects of OA and OW as single stressors
406 on the copepod traits included in our study.

407

408 *OA and OW as drivers of phenotypic change in copepods*

409 Heterogeneity in phenotypic responses of marine organisms to OA and OW can be
410 influenced by intrinsic features of the species such as reproductive performance, maternal
411 effects and fecundity (He et al. 2016). While several studies have evaluated the role of maternal
412 effects in the performance of copepods across different environments (Jónasdóttir and Kiorboe
413 1996; Lacoste et al. 2001; Auel 2004; Ianora et al. 2004; Rodríguez-Graña et al. 2010; He et
414 al, 2016; 2020) and experimental conditions (Thor and Dupont 2015; Preziosi et al. 2017), few
415 have directly tested maternal effects in the climate change context (Vehmaa et al, 2012; Cripps
416 et al, 2014; Thor et al 2018). Maternal investment is defined by the balance in energy and
417 resource allocated to either offspring numbers or offspring quality, whereby offspring
418 production by mothers is generally inversely correlated to per offspring investment (Marshall
419 et al. 2006). In invertebrates such as copepods, optimum reproductive investment often
420 involves trade-offs between egg size or quality, and the number of eggs produced which can
421 change depending on factors including food availability, predator avoidance, or environmental
422 conditions (Poulin 1995; Bjærke et al. 2016; He et al. 2016).

423 Here, we evaluated to what extent fecundity, physiology, performance and fitness (e.g.,
424 reproductive effort, survival) are influenced by OA and OW. We found that OA decreases
425 fecundity and survival in the majority of copepod species, a response that is aligned to the
426 negative effects documented for physiological traits. It is well known that OA affects
427 organismal physiology by deviating ion equilibrium, thus influencing changes in intracellular
428 acid-base balance (Pörtner 2008, Melzner et al. 2009) and affecting various cellular processes,
429 including enzyme activity, metabolism and protein synthesis. As a result, functioning of

430 different tissues is altered and energy homeostasis is affected, which can lead to trade-offs
431 between fitness-related traits and maintaining vital functions (Pörtner 2008; Hofmann and
432 Togdham 2010). Thus, the overall phenotypic effects of OA are conditioned by the ability of
433 different organisms to regulate their cellular acid-base equilibrium and manage energy
434 homeostasis. For copepods, the reduction in fecundity and survival caused by OA may be
435 linked to a change in antioxidant enzyme activity and protein synthesis (Lee et al. 2019; Zhang
436 et al. 2016). Despite this mechanistic understanding of the effects of OA on physiology,
437 survival and fecundity, it is important to highlight that the level (e.g. small vs large change in
438 pH) and duration of exposure can contribute to the level of phenotypic responses documented
439 (Pörtner 2008). For instance, we found no significant overall effect of OA on copepods at pH
440 over 7.7 (estimated end of century OA) and even at pH over 7. This confirms the findings of
441 Runge et al. (2016). Thus, acute exposure at more extreme OA levels (lower pH) can
442 substantially affect physiology and survival, whereas minor changes in pH can fall within a
443 species' tolerance windows. However, exposure to minor OA over prolonged periods (weeks
444 or months) may have adverse biological and population-level effects (Pörtner 2008). While it
445 is not known exactly why copepods show such resistance to OA, studies suggest that their
446 ability to regulate their physiology under OA may provide higher adaptability (Engström-Öst
447 et al. 2019; 2020)

448 In contrast to OA, OW causes a significant increase in most physiological processes
449 such as metabolism, protein synthesis, and enzyme activity (Brown et al. 2004). These, in turn,
450 regulate systemic processes and, therefore, influence variations in biological traits (Pörtner and
451 Farrell 2008). For example, temperature induced change in metabolic rates can ultimately
452 control life history traits, behaviour and phenology (Brown et al. 2006; Sponaugle et al. 2006;
453 O'Connor et al. 2007). Our observation of increased egg production and hatching success under
454 warming conditions is aligned with the predicted increase in biological activity due to rising

455 temperature (Brown et al. 2004). In our analysis, positive effect sizes are likely derivative of
456 increased physiological rates which lead to higher fecundity with increased temperature. This
457 increase in copepod fecundity across a large temperature gradient has previously been
458 demonstrated (Bunker and Hirst 2004; Peck et al. 2015). On the other hand, negative effect
459 sizes may denote the response of organisms beyond their thermal tolerance limits, whereby
460 fecundity is severely impacted. This indicates that, under warming conditions alone, copepod
461 fecundity will likely increase until temperatures surpass species- or population-specific
462 tolerance limits. Therefore, like in other ectotherms, raising ocean temperatures that fall within
463 the thermal tolerance window of marine copepods are likely to cause an increase in fecundity
464 under climate change. Simplistic predictions on the effects of OW and OA which take a narrow
465 view of characteristics must, however, be viewed with caution. For example, it is well
466 established that intrinsic characteristics of marine organisms such as body size, life history
467 stage and evolutionary history can differentially influence responses to climate change (Pörtner
468 and Knust 2007; Hofmann and Todgham 2010; Sorte et al. 2011; Dupont et al., 2010; Byrne
469 and Przeslawski 2013; Reusch 2014). Similarly, extrinsic factors such as the level and duration
470 of exposure to environmental stress (Ishimatsu et al., 2008), the rate of environmental change
471 (Hoffmann and Sgrò 2011; Silbiger and Sorte 2018), the degree of environmental variability
472 (Eriander et al. 2015) and the differences in environmental conditions between regions and
473 habitats (Boyd et al. 2015), can play also an important role in determining the phenotypic
474 responses of marine organisms to OA and OW.

475

476 *Do local habitat characteristics influence phenotypic responses to OA and OW?*

477 Coastal and oceanic landscapes are characterized by mosaics of environmental
478 conditions that influence the biology, ecology and evolution of marine organisms (Pittman
479 2017). While there is some evidence of responses of copepods to both OA and OW, our results

480 revealed that this is not a general rule for all species. Significant heterogeneity in phenotypic
481 responses have been documented within the same habitats. This phenotypic variability might
482 be explained by the differences in the level of environmental variation experienced in the same
483 type of habitat in different geographic regions (Vargas et al., 2017). The particular seascape
484 characteristics (e.g., coastal/submarine ridges; river discharges, fjords) of each habitat is
485 therefore an important factor influencing within- and among-habitats differences in phenotypic
486 responses of copepods. For example, the egg production of *Acartia tonsa* is less affected by
487 OA in populations from coastal waters in proximity to an estuarine system with highly variable
488 pH compared to populations residing further from the estuarine system where pH tends to be
489 more stable (Aguilera et al. 2013). Similarly, different populations of *Calanus glacialis* from
490 Kongsfjord, Billefjord and Disko Bay respond differently to pH changes whereby those from
491 Disko Bay may be pre-conditioned to natural pH variation in their environment (Thor et al.
492 2018). Finally, comparison of heat tolerance in populations of intertidal copepods revealed
493 inter-population variation, indicating that the genetic basis for selection were different among
494 populations (Kelly et al. 2012; 2013). Such differences among populations suggest that
495 environmental history plays an important role in influencing local adaptation and the
496 phenotypic responses of copepods to OA and OW (Berg et al. 2010; Donelson et al. 2018;
497 Vargas et al. 2017). For copepods, however, inter-population discrepancies in response to OA
498 and OW based on environmental history remain understudied.

499 Another potential confounding factor in the overall phenotypic responses of marine
500 organisms to climate change is the latitudinal distribution of populations and species (e.g.,
501 Gaitan-Espitia 2017a,b). Latitudinal gradients are characterized by clines in sea surface
502 temperature (SST), aragonite saturation and CO₂ solubility that have important implications in
503 biological characteristics of marine organisms and their susceptibility to climate change (Fabry
504 et al., 2009; Leong et al., 2018). In fact, phenotypic traits of copepods are known to vary across

505 latitudes (Brun et al. 2016). For example, latitudinal variation in diapause egg production
506 (Marcus 1984), growth rates (Lonsdale and Levinton 1985), body size (Brun et al. 2016) and
507 thermal tolerance (Pereira et al. 2017) have been documented for diverse copepod taxa. These
508 are associated to the different thermal regimens experienced by species and populations across
509 latitudes. Despite of this biological trend, here we found that phenotypic effects of increasing
510 SST due to OW are not influenced by latitudinal distribution. This finding could be driven by
511 the limited number of studies exploring the effects of OW on tropical species compared to
512 studies on temperate species. Similarly, to OW, the effects of OA on biological traits, with the
513 exception of survival, were independent of latitude. Higher survival in copepods at lower
514 latitudes under OA conditions may be an indirect result of the influence of higher temperatures
515 on physiological rates, performance and fitness. However, there are some thresholds for these
516 beneficial effects because stressful conditions induced by the interaction of OA and OW have
517 marked negative effects on marine organisms (Harvey et al. 2013; Kroeker et al. 2013).

518

519 *Is body size a good predictor of copepod's susceptibility to OA and OW?*

520 It is well established that body mass is a key determinant of physiological rates
521 (Kolokotronis et al. 2010; Carey and Sigwart 2014), evidenced by a scaling relationship in
522 which these rates change parallel with body mass changes (Gillooly et al. 2001; Kolokotronis
523 et al. 2010). This scaling relationship is temperature dependent (Gillooly et al. 2001), and thus,
524 physiological changes induced by OW and OA are expected to be conditioned by body mass
525 or size. It is often observed that metabolic costs (difference in metabolic rate) is lower in large
526 than small organisms for the same activity or across similar changes in environmental
527 parameters (Carey and Sigwart 2014; Carey et al. 2016). Because of this, body mass is usually
528 incorporated as a predictor of species and community responses to environmental stress and
529 climate change (McCain et al. 2014, Lefort et al. 2015). Copepods generally conform size

530 variation across temperature and latitudinal clines (Evans et al. 2020), as well as to metabolic
531 scaling whereby metabolic rates and energy acquisition increase with body mass (Ikeda et al.
532 2001; Saiz and Calbet 2007). However, in our systematic review, we did not find evidence of
533 the influence of body size on the heterogeneity of phenotypic responses of biological traits to
534 OA and OW in copepods. One potential explanation of this finding is the range of body size
535 that characterize the studied copepods (prosome length ranging 0.31 mm to 4.55 mm) may
536 affect the resolution of the influence of this trait on physiological responses to environmental
537 stress and climate change, therefore rendering precise comparison of physiological costs
538 difficult. Moreover, our study showed that phylogenetic relationships are influential on trait
539 response to OW. Therefore, investigating metabolic scaling within populations of the same
540 species or of closely related species may provide more accurate estimation of the effects of OA
541 and OW on the relationship between body size and metabolic rates. In addition to body size
542 influencing the effects of OA and OW, body size itself can be affected by OA and OW. For
543 example, OW can cause reductions in copepod prosome size in larval and adult stages (Garzke
544 et al. 2015) while a combination of OA and OW can have antagonistic effects on copepod body
545 size (Garzke et al. 2016). Moreover, moulting through nauplii and copepodite stages are
546 positively dependent on temperature, while the intermoult somatic growth is more dependent
547 on other factors such as food concentration (Peterson, 2001). Such variation in size may result
548 from compensation mechanisms to limit other physiological costs from environmental change,
549 thus regulating changes in physiological rates and energy demands.

550

551 *Do phylogenetic relationships matter for the assessment of phenotypic responses to OA and*
552 *OW?*

553 The evolutionary history of organisms define variation in phenotypic traits and
554 responses to climate change because closely related species share similar characteristics

555 compared to distantly related species (Felsenstein 1985). Thus, comparative assessments of the
556 phylogenetic signals in the phenotypic responses of copepods to OA and OW can provide
557 insights and predictive tools to infer how different species will respond to future climate
558 change. One important finding of our study is that phylogenetic relationships partially
559 influenced the response of copepods to OA, but more substantial influences were found for
560 OW. For example, egg production of *Acartia steuri* and *A. tonsa* were significantly affected by
561 OA, followed by *Centropages typicus*. While *Acartia steuri* and *A. tonsa* are very closely
562 related species, *Centropages typicus* is not closely related to the latter two, yet also showed
563 more drastic effects of OA. Therefore, although there is some phylogenetic signal explaining
564 the heterogeneity of responses to OA, it seems that the major physiological costs are broadly
565 shared among species independent, to some extent, of the evolutionary history. As for OW, the
566 genera *Acartia* and *Centropages* demonstrated larger positive response to OW, while the
567 hatching success of the *Pseudocyclops* and *Calanus* changed the least. On the other hand,
568 *Pseudodiaptomus* copepods responded negatively to OW. The differences in response among
569 species and genera are likely due non-independence in the evolution of physiological tolerances
570 and sensitivities to changes in environmental temperature (i.e., closely related species have
571 evolved similar thermal tolerances compared to distantly related species). For example, in the
572 genus *Calanus*, copepods undertake deep diel migrations and therefore are exposed to great
573 variations in temperature and pH (Svetlichny et al. 2000; Maps et al. 2011) while *Acartia*
574 species do not undertake such deep diel migrations (Kouassi et al., 2001; Holliland et al. 2012).
575 Moreover, direct comparison of two species with different modes of life (migrator vs non-
576 migrator; *Calanus* spp. vs *Oithona similis*, respectively) within the same habitat showed that
577 species may have different sensitivities to OA based on their exposure (Lewis et al. 2013).
578 These behavioural traits are the result of the interactions between evolutionary and ecological

579 processes that have shaped the feeding strategies and population dynamics of different species
580 along the water column (Lampert 1989; Ohman 1990; Hays 2003).

581 Overall, here we highlight that the phenotypic cost to OA are partially influenced by
582 the evolutionary history but more importantly by the environmental history. The low
583 phylogenetic signal yet high heterogeneity suggests that the majority of physiological costs are
584 shared among species independent of their phylogenetic relationship and largely explained by
585 other biotic/abiotic factors. On the other hand, the phenotypic response to OW is linked to
586 thermal tolerance which is widely documented to have a deep relationship with the
587 evolutionary history of the species (Kellermann et al. 2012; Grigg & Buckley 2013; Comte &
588 Olden 2017). These findings suggest that more accurate predictions of the response to OA and
589 OW may be obtained by integrating the influence of both the evolutionary and environmental
590 history of the species.

591

592 *Conclusions*

593 Fine-scale analysis of the response of copepods to climate change revealed that the
594 effects of OA and OW differ drastically. While OA has a negative influence on most biological
595 traits, the effects of OW tend to align with the predicted hormesis trend in biological activity with
596 temperature increase. Under future OA levels only, unless copepods develop adaptive
597 responses, they will likely experience decreases in biological traits, thus affecting their
598 population demographics. Such changes in populations will also lead to negative community
599 and ecosystem wide effects. On the other hand, under ocean warming conditions alone, it seems
600 that copepod biological traits will likely increase until temperatures surpass the different
601 tolerance limits of different species. Interestingly, habitat, latitude and body size were only
602 partially influential on the effects of OA and OW on copepods. On the other hand, the
603 phylogenetic relationship partially influenced the response of copepods to OA but more

604 substantially the effects of OW. While OA and OW independently have contrasting effects on
605 copepod biological traits, their future effects will occur concurrently and, therefore, interact.
606 While we analysed the effects of OA and OW independently, other studies suggest that their
607 combined effects on copepod traits can be additive, antagonistic or synergistic, therefore,
608 highly complex with varying interactions between species and the level of change in pH or
609 temperature within the habitats (e.g. Vehmaa et al. 2012; 2013; Hildebrandt et al. 2014;
610 Preziosi et al. 2017; Garzke et al. 2020). Therefore, our findings point to the importance of
611 species- and population-specific environmental history, mode of life and evolutionary history
612 in defining the overall effects of OA and OW on copepod biological traits. More importantly,
613 these findings reveal that assuming general trends in the response of copepods to climate
614 change based on few traits and single habitat or species could be extremely misleading.

615 Finally, while we analysed the effects of OA and OW on phenotypic responses, genetic
616 adaptations will perpetually play a major role in copepod response to these conditions.
617 However, relatively fewer studies have fully examined the changes in genetic pathway leading
618 to adaptations in copepods. Some of the genetic mechanisms that have been found to be
619 involved in the response of copepod to OA include upregulation of genetic pathways to
620 increase ribosomal function, ion transport, oxidative phosphorylation, DNA repair, redox
621 regulation, protein folding, and proteolysis (DeWit et al. 2016; Bailey et al. 2017). As for the
622 response to OW, major pathways that are upregulated include cellular and metabolic processes,
623 catalytic activities, genetic information processing, ubiquitination and proteolysis (Schoville et
624 al. 2012; Ramos et al. 2015; Semmouri et al. 2019). While these studies point out some of the
625 genetic pathways involved in responding to OA and OW, there is still a significant lack of
626 understanding on how these will be involved in defining genetic adaptations in different species
627 and populations of copepods.

628

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634

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636

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1039 Table legends:

1040 Table 1: Weighted random effect models, meta-regressions, and phylogenetic regressions of
1041 copepod egg production, hatching and survival as a function of ocean acidification (δ = overall
1042 effect size, CI= 95% confidence interval, P= p-value, d.f= degrees of freedom, Q= regression
1043 coefficient, σ^2 = variance). Arrows indicate the overall effect of OA (increase or decrease) on
1044 copepod traits. The direction of significant relationships between variables are indicated as
1045 positive or negative signs.

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1047 Table 2: Weighted random effect models, meta-regressions, and phylogenetic regressions of
1048 copepod egg production, hatching and survival as a function of ocean acidification (δ = overall
1049 effect size, CI= 95% confidence interval, P= p-value, d.f= degrees of freedom, Q= regression
1050 coefficient, σ^2 = variance). Arrows indicate the overall effect of OW (increase or decrease) on
1051 copepod traits. The direction of significant relationships between variables are indicated as
1052 positive or negative signs.

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1055 Table 3: Weighted random effect models and meta-regressions of copepod metabolic and
1056 feeding rates as a function of ocean acidification and warming (δ = overall effect size, CI= 95%
1057 confidence interval, P= p-value, d.f= degrees of freedom, Q= regression coefficient). Arrows
1058 indicate the overall effect of OA or OW (increase or decrease) on copepod traits.

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1061 Table 4: Weighted random effect models and meta-regressions comparing the hatching success
1062 as a function of egg production rates (low, medium, high) of copepods exposed to ocean
1063 acidification and warming (δ = overall effect size, CI= 95% confidence interval, P= p-value,
1064 d.f= degrees of freedom, Q= regression coefficient).

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Table 1

Statistical model	Egg Production					Hatching					Survival				
	δ	CI _{low}	CI _{high}	P		δ	CI _{low}	CI _{high}	P		δ	CI _{low}	CI _{high}	P	
Full model (Weighed random effect model)															
Ocean Acidification	-0.408	-0.538	-0.278	< 0.001		-0.298	-0.428	-0.168	< 0.001		-0.241	-0.346	-0.136	< 0.001	
	d.f	Q	P		I ²	d.f	Q	P		I ²	d.f	Q	P	I ²	
	73	812.197	< 0.001	↓	92.96 7	72	6360.785	< 0.001	↓	99.724	18	1705.848	< 0.001	↓	98.628
Meta-regression															
pH	1	6.61	0.01	-		1	8.312	0.004	-		1	1.148	0.284		
pH>7.7	1	0.0154	0.901			1	0.193	0.516			1	0.136	0.712		
pH > 7	1	1.222	0.269			1	3.744	0.053			1	1.704	0.192		
Temperature	1	4.146	0.042	-		1	6.797	0.009	-		1	6.015	0.014	-	
Latitude	1	0.307	0.58			1	0.012	0.914			1	7.075	0.008	+	
Prosome length	1	0.883	0.347			1	1.679	0.195			1	1.336	0.248		
Habitat	2	2.276	0.32			3	3.136	0.371			2	0.802	0.67		
Genus	6	0.009	0.173			5	5.221	0.389			3	12.531	0.006	**	
Species	18	38.78	0.003	**		13	21.188	0.069			7	13.248	0.066		
Phylogenetic regression															
Pagel's $\lambda = 1$		σ^2 between study = 0.2561					σ^2 between study = 0.2988					σ^2 between study = 0.0336			
		σ^2 phylogeny = 0.0497					σ^2 phylogeny = 0.0337					σ^2 phylogeny = 0.0173			
		Percentage variance due to phylogeny = 16.25					Percentage variance due to phylogeny = 10.13					Percentage variance due to phylogeny = 33.99			
		σ^2 between study = 0.2241					σ^2 between study = 0.2886					σ^2 between study = 0.0349			
Martin and Hansen $\alpha = 1$		σ^2 phylogeny = 0.0569					σ^2 phylogeny = 0.033					σ^2 phylogeny = 0.0147			
		Percentage variance due to phylogeny = 20.25					Percentage variance due to phylogeny = 10.26					Percentage variance due to phylogeny = 29.64			

1073 Table 2

Statistical model	Egg Production				Hatching				Survival			
	δ	CI _{low}	CI _{high}	P	δ	CI _{low}	CI _{high}	P	δ	CI _{low}	CI _{high}	P
Full model (Weighed random effect model)												
Ocean Warming	0.58	0.443	0.731	< 0.001	0.309	0.106	0.511	0.003	-0.063	-0.192	0.066	0.338
	d.f	Q	P	I ²	d.f	Q	P	I ²	d.f	Q	P	I ²
	120	25871.94	< 0.001	↑ 99.243	66	330434.6	< 0.001	↑ 99.973	55	1431.391	<0.001	↑ 99.773
Meta-regression												
Temperature	1	0.216	0.642		1	2.011	0.156		1	8.888	0.003	+
Latitude	1	0.726	0.394		1	1.577	0.209		1	0.004	0.948	
Prosome length	1	3.212	0.073		1	4	0.04	-	1	0	0.649	
Habitat	2	4.739	0.094		2	10.29	0.006	**	3	6.593	0.086	
Genus	10	52.457	< 0.001	***	6	20.319	0.002	**	5	71.073	<0.001	***
Species	18	68.887	< 0.001	***	16	35.605	0.003	**	14	113.289	<0.001	***
Phylogenetic regression												
Pagel's $\lambda = 1$	σ^2 between study = 0.4816 σ^2 phylogeny = 1.1834 <i>Percentage variance due to phylogeny = 71.08</i>				σ^2 between study = 0.5865 σ^2 phylogeny = 0.1077 <i>Percentage variance due to phylogeny = 15.51</i>				σ^2 between study = 0.0499 σ^2 phylogeny = 0.418 <i>Percentage variance due to phylogeny = 89.34</i>			
Martin and Hansen $\alpha = 1$	σ^2 between study = 0.4623 σ^2 phylogeny = 0.5645 <i>Percentage variance due to phylogeny = 54.98</i>				σ^2 between study = 0.5847 σ^2 phylogeny = 0.0841 <i>Percentage variance due to phylogeny = 12.57</i>				σ^2 between study = 0.0519 σ^2 phylogeny = 0.2485 <i>Percentage variance due to phylogeny = 82.72</i>			

1074

1075 Table 3
1076

Statistical model	Metabolic rate				Feeding rate			
Full model (Weighed random effect model)	δ	CI _{low}	CI _{high}	P	δ	CI _{low}	CI _{high}	P
Ocean acidification	0.145	0.064	0.227	<0.001 ↑	-0.255	-0.457	-0.054	0.013 ↓
Meta-regressions	d.f	Q	P		d.f	Q	P	
Body Size	1	1.75	0.186		1	2.017	0.156	
Habitat	2	0.356	0.837		3	6.775	0.079	
Latitude	1	0.151	697		1	1.528	0.216	
Genus	5	0.742	0.981		5	2.211	0.819	
Species	7	3.563	0.894		7	2.221	0.947	
Temperature	1	0.326	0.568		1	0.572	0.449	
pH	1	0.645	0.422		1	2.269	0.132	
Full model (Weighed random effect model)	δ	CI _{low}	CI _{high}	P	δ	CI _{low}	CI _{high}	P
Ocean warming	0.666	0.447	0.885	<0.001 ↑	0.155	-0.2	0.51	0.392
Meta-regressions	d.f	Q	P		d.f	Q	P	
Body Size	1	0.344	0.558					
Habitat	2	62.273	<0.001		1	0.43	0.512	
Latitude	1	0.486	0.486		1	1.439	0.23	
Genus	8	59.971	<0.001	***	5	3.076	0.668	
Species	10	70.012	<0.001	***	5	3.076	0.688	
Temperature	1	0.058	0.81		1	0.754	0.385	

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1079 Table 4
 1080

Statistical model	Ocean Acidification				Ocean Warming			
	δ	CI _{low}	CI _{high}	P	δ	CI _{low}	CI _{high}	P
Weighed random effect model per Egg production category								
low	-0.11	-0.207	-0.013	0.027 *	0.154	-0.008	0.315	0.062
medium	-0.142	-0.293	0.009	0.066	-0.112	-0.48	0.257	0.552
high	-0.686	-1.046	-0.326	<0.001 ***	0.763	0.433	1.092	<0.001 ***
Meta-regression	d.f	Q	P		d.f	Q	P	
Egg production category	2	11.615	0.003 **		2	16.836	<0.001 ***	
Spawning mode	1	0.224	0.636		1	1.45	0.229	
pH	1	3.085	0.079					
Temperature					1	3.0842	0.05	

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1085 Figure Legends

1086

1087 Figure 1: (A) Graphical hypothesis displaying the possible factors that influence the response
1088 of copepods and (B) workflow used in the meta-analysis of the effects of Ocean acidification
1089 and Ocean warming on copepod biological traits.

1090

1091 Figure 2: Map of the distribution of copepod populations from studies used for the meta-
1092 analysis. The map was constructed using QGIS and coordinate layers were made from
1093 coordinates extracted from individual papers or estimated using Google Maps based on place
1094 names when no specific coordinates were reported in the paper.

1095

1096 Figure 3: Response of copepod (A) egg production and (B) hatching success to ocean
1097 acidification and warming displayed as mean response ratio with 95 % confidence intervals.
1098 Each blue dot is an effect size calculated for a single study. Red dots represent the overall effect
1099 size of warming or acidification.

1100

1101 Figure 4: The effect of acidification on (A) egg production and (B) hatching success of different
1102 genera of copepods. Mean response ratio with 95 % confidence intervals are grouped by
1103 copepod genus and habitat based on known areas occupied by the species. Arrows indicate the
1104 different effect sizes for each genus. Each blue dot is an effect size calculated for a single study.
1105 Red dots represent the overall effect size for the genus.

1106

1107 Figure 5: Copepod survival as a function of acidification. Mean response ratio and 95 %
1108 confidence intervals are grouped by copepod genus and habitat based on known areas occupied
1109 by the species. Each blue dot is an effect size calculated for a single study and red dots represent
1110 the overall effect size for the genus.

1111

1112 Figure 6: Copepod hatching success as a function of acidification (A) and warming (B). Mean
1113 response ratio and 95 % confidence intervals are grouped by average egg production rates (eggs
1114 female⁻¹ day⁻¹) of the species (< 10, 10-20, and > 20 eggs per female per day, respectively).
1115 Each blue dot is an effect size calculated for a single study and red dots represent the overall
1116 effect size at different egg production rates.

1117

1118 Figure 7: Copepod (A) egg production and (B) hatching as a function of warming. Mean
1119 response ratio and 95 % confidence intervals are grouped by copepod genus and habitat based
1120 on known areas occupied by the species. Arrows indicate the different effect sizes for each
1121 genus. Each blue dot is an effect size calculated for a single study. Red dots represent the
1122 overall effect size for the genus.

1123

1124 Figure 8: Copepod survival as a function of warming. Mean response ratio and 95 % confidence
1125 intervals are grouped by copepod genus and habitat based on known areas occupied by the
1126 species. Each blue dot is an effect size calculated for a single study. Red dots represent the
1127 overall effect size for the genus.

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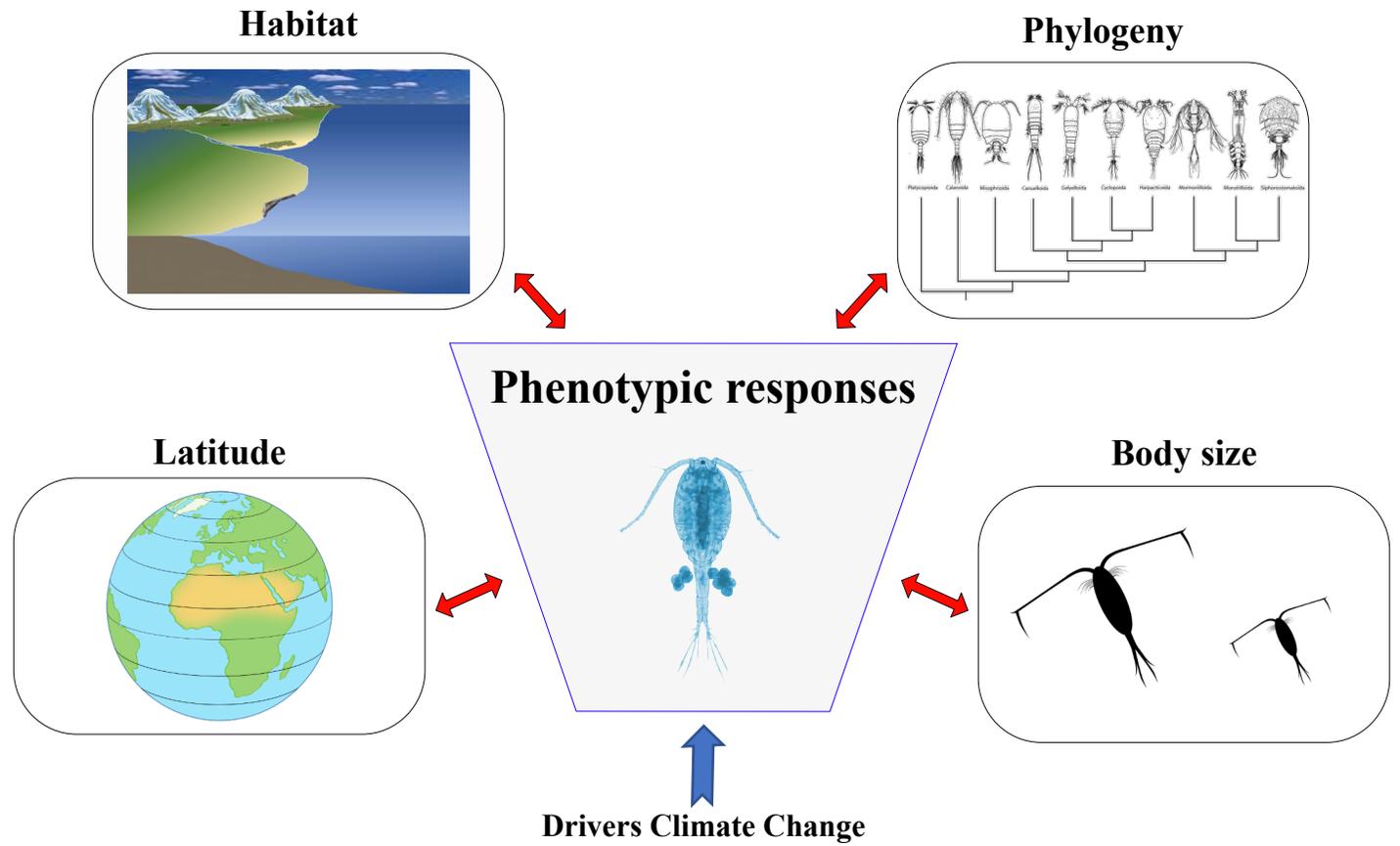
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Fig 1. A)

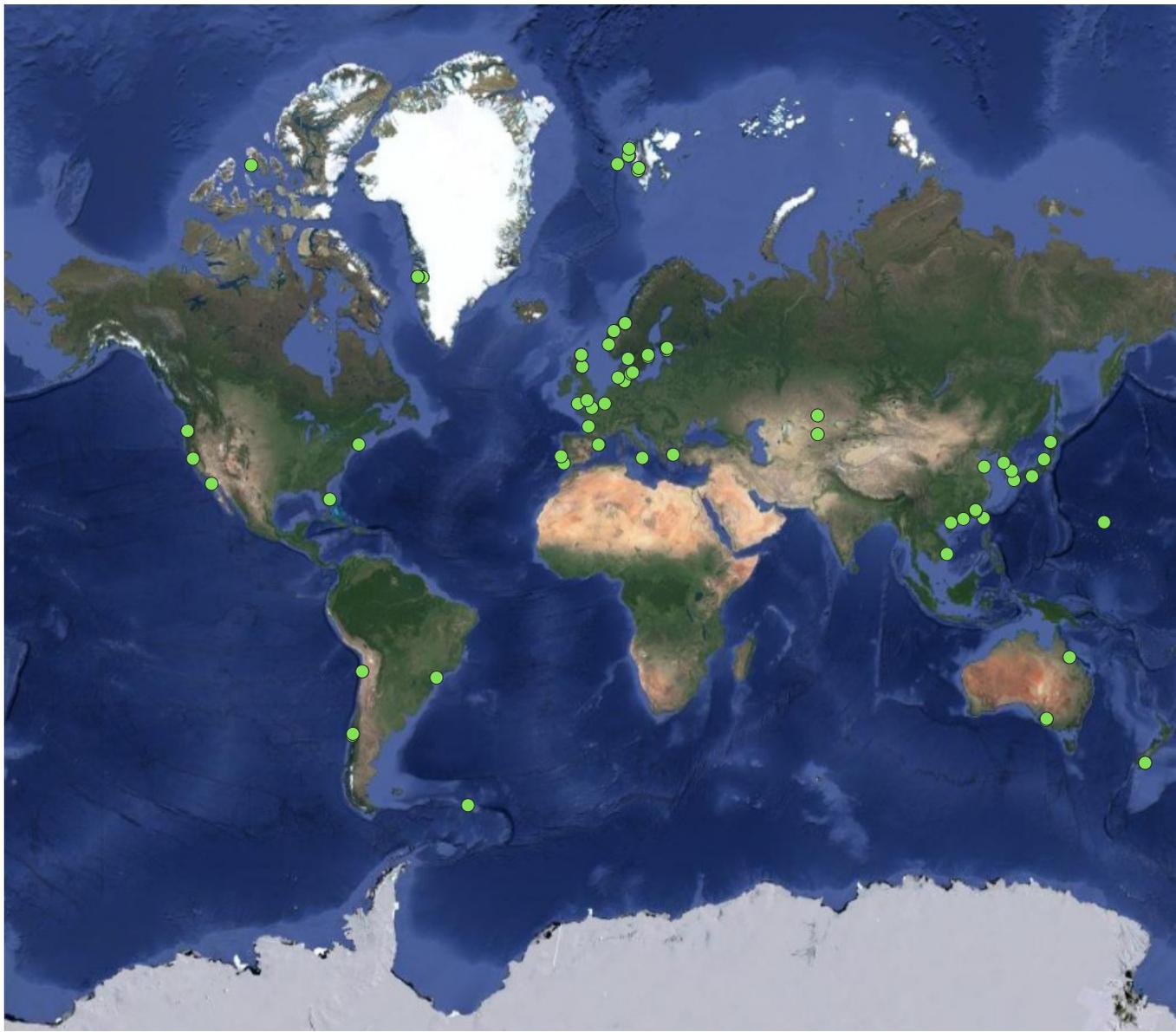


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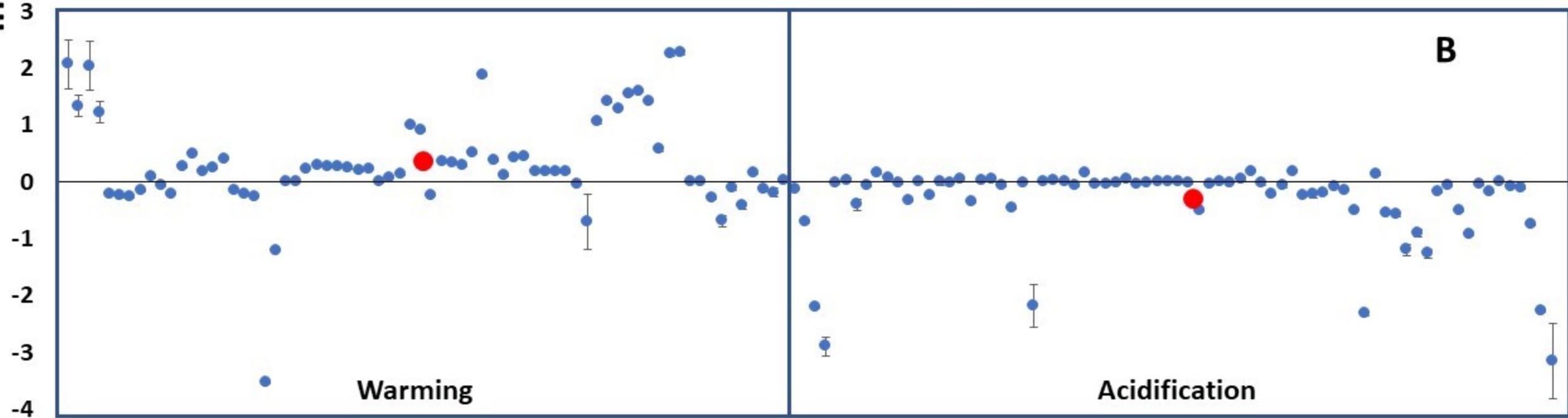
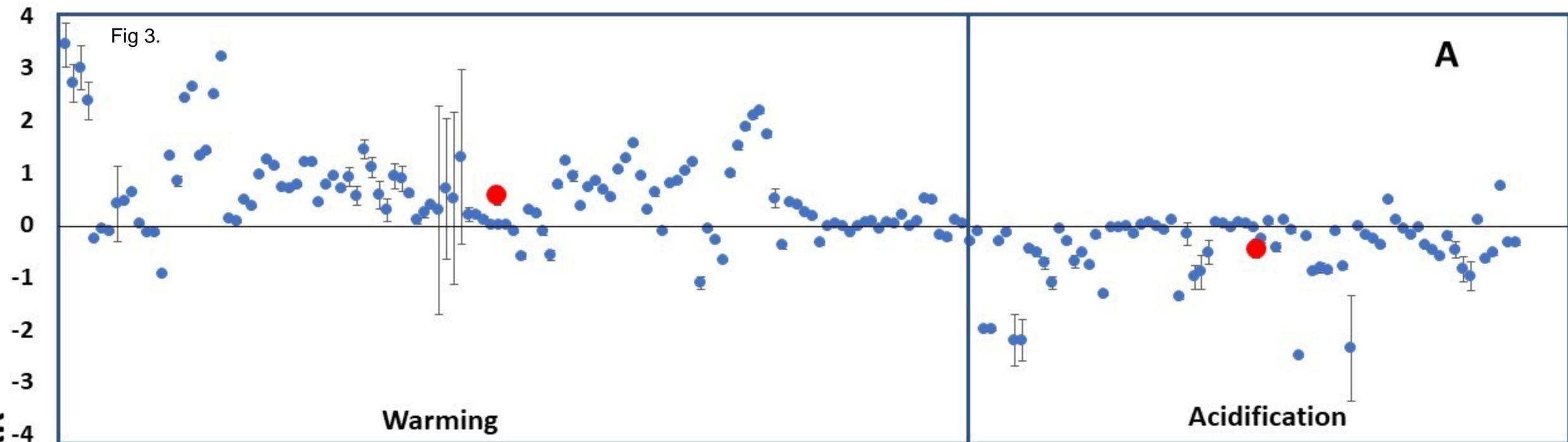
The flowchart details the methodological steps of the study, starting with a literature review and ending with a test for phylogenetic signal. The steps are as follows:

- Literature review
Effects of OA & OW on copepods
- Screening publications
Titles & abstracts for relevant data
- Full text examination & retrieval
of data from tables and figures
- Estimation of effects sizes
of OA & OW
- Check publication bias
- Estimation of overall effects
Random-effects model
- Assessment of heterogeneity
Mixed-effects model
- Test for phylogenetic signal
Brownian Motion
Ornstein & Uhlenbeck models

Fig 2.



InRR



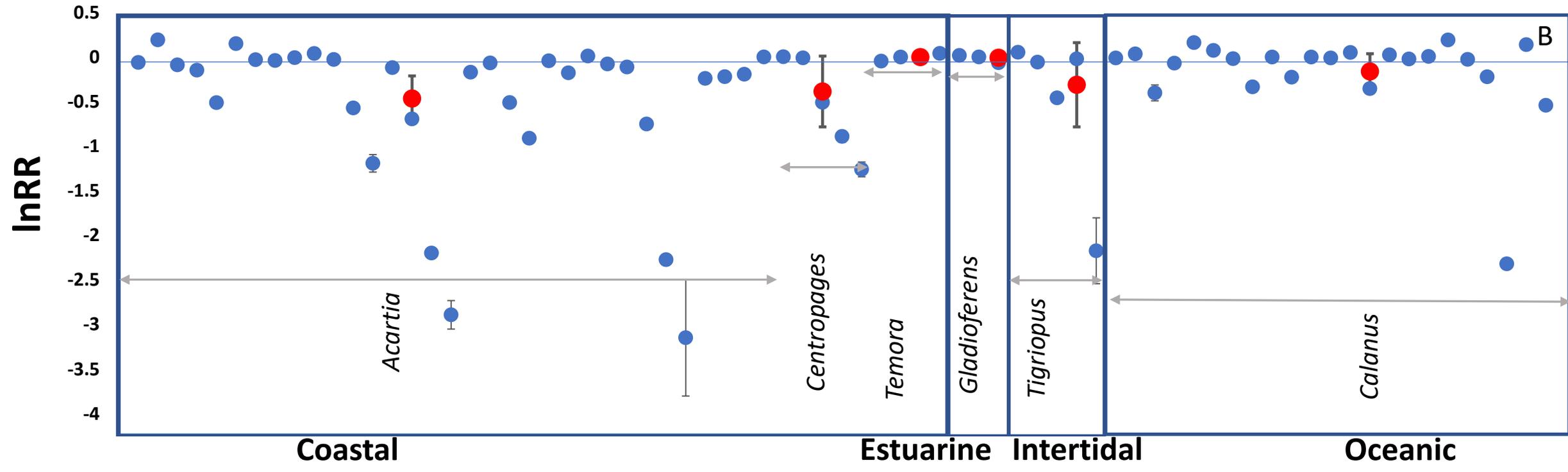
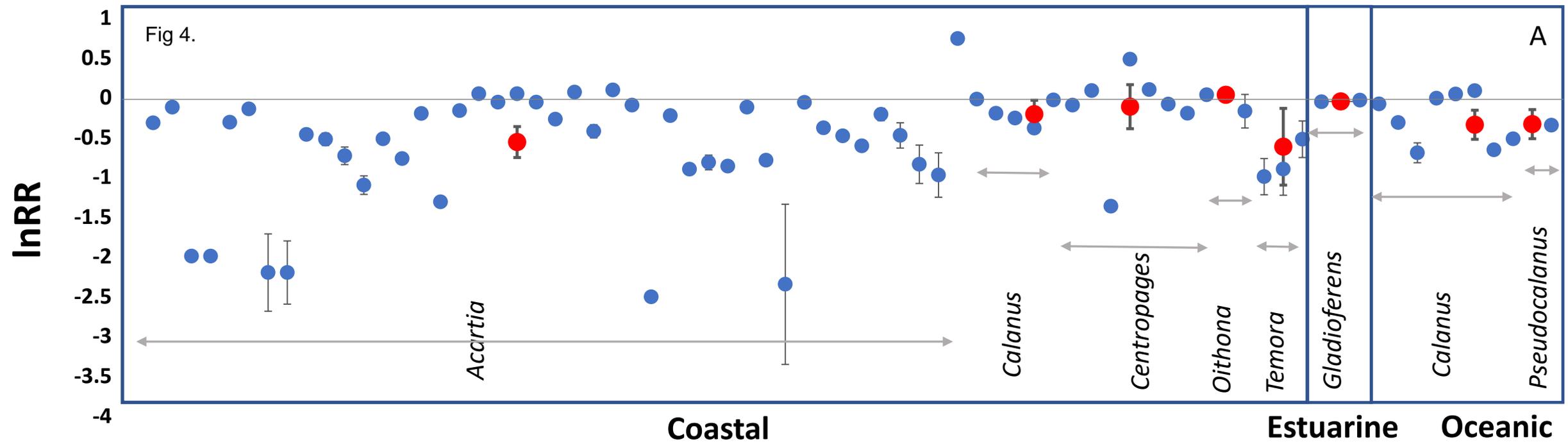
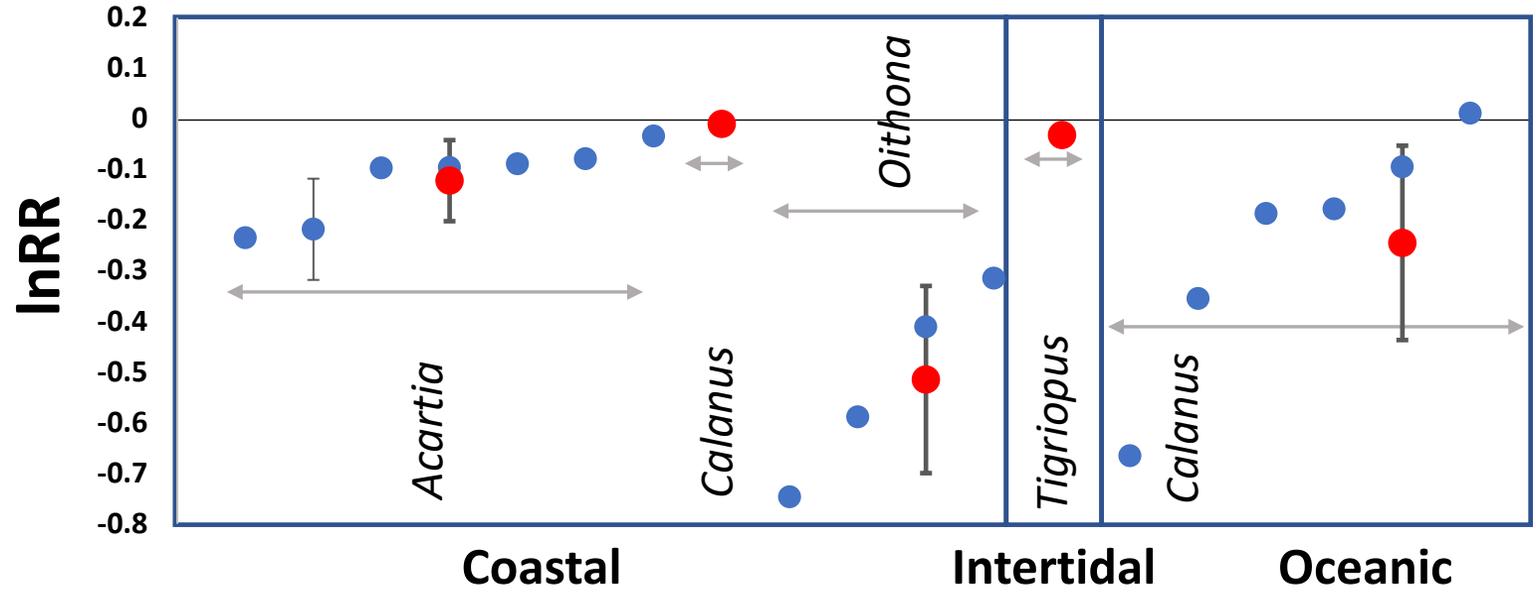
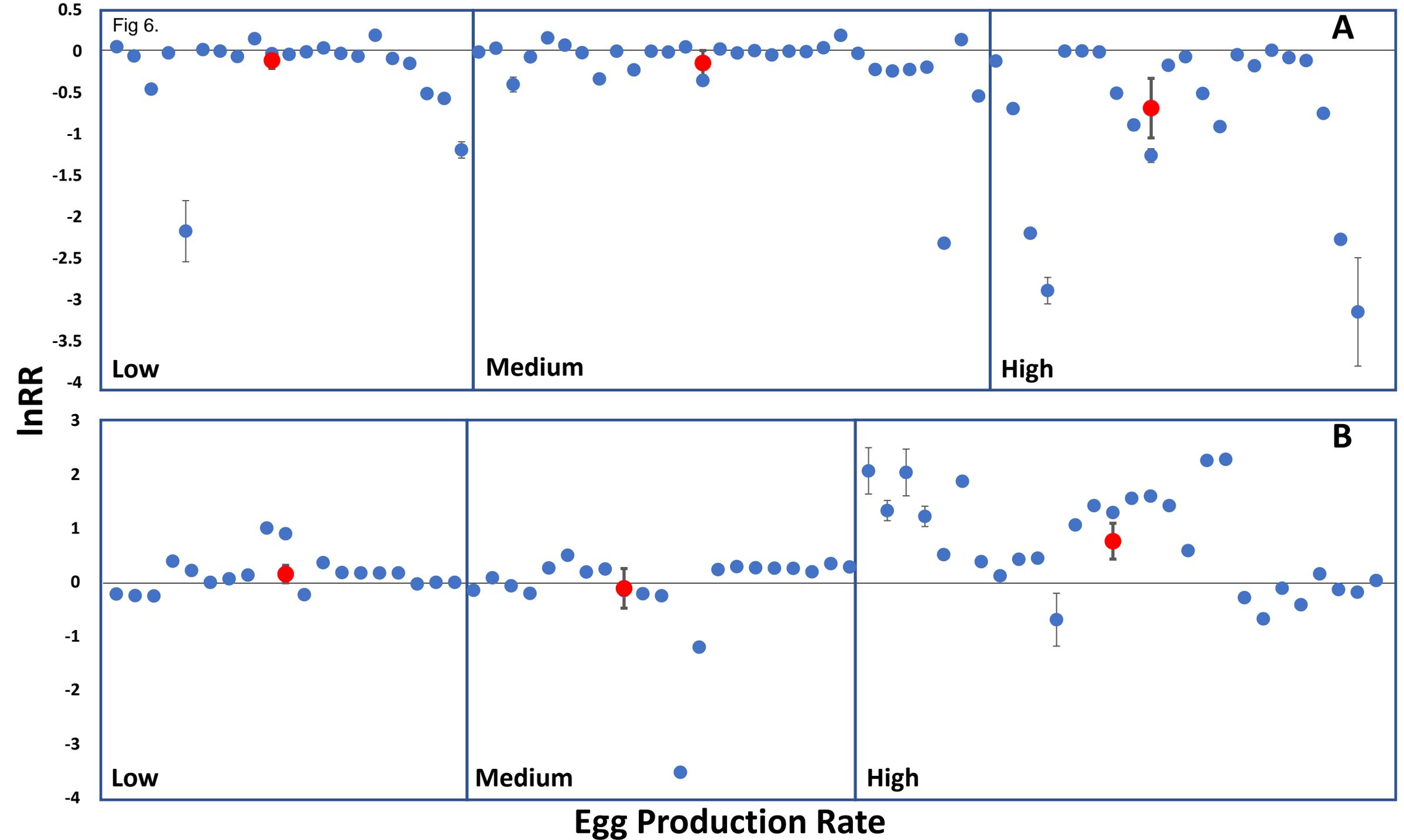


Fig 5.





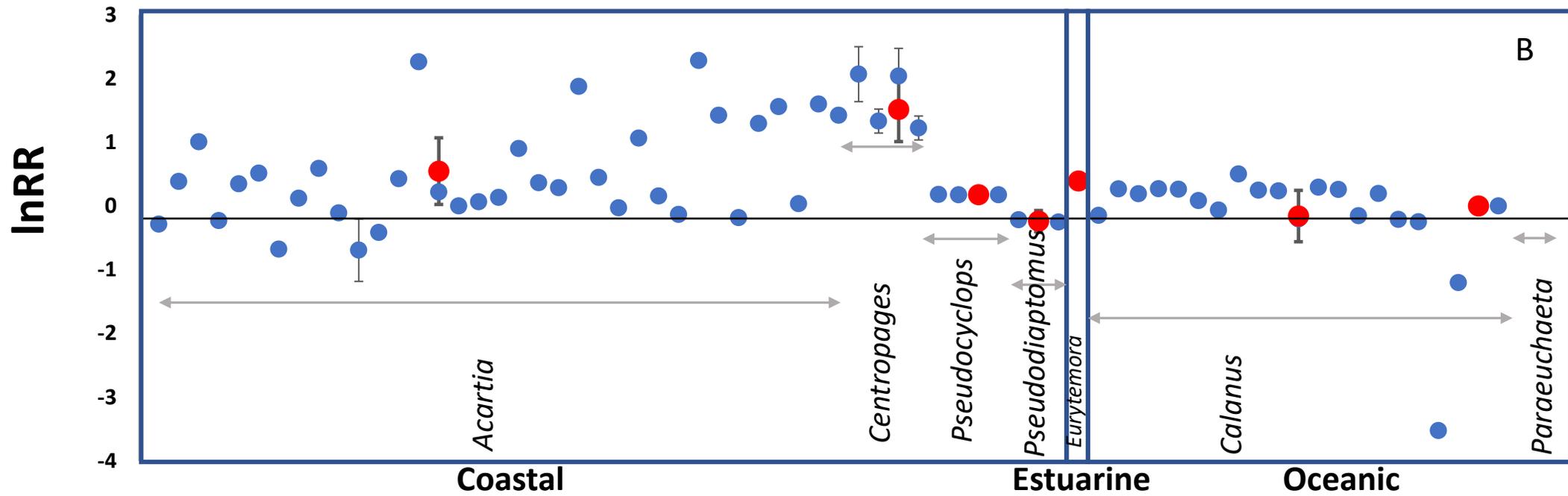
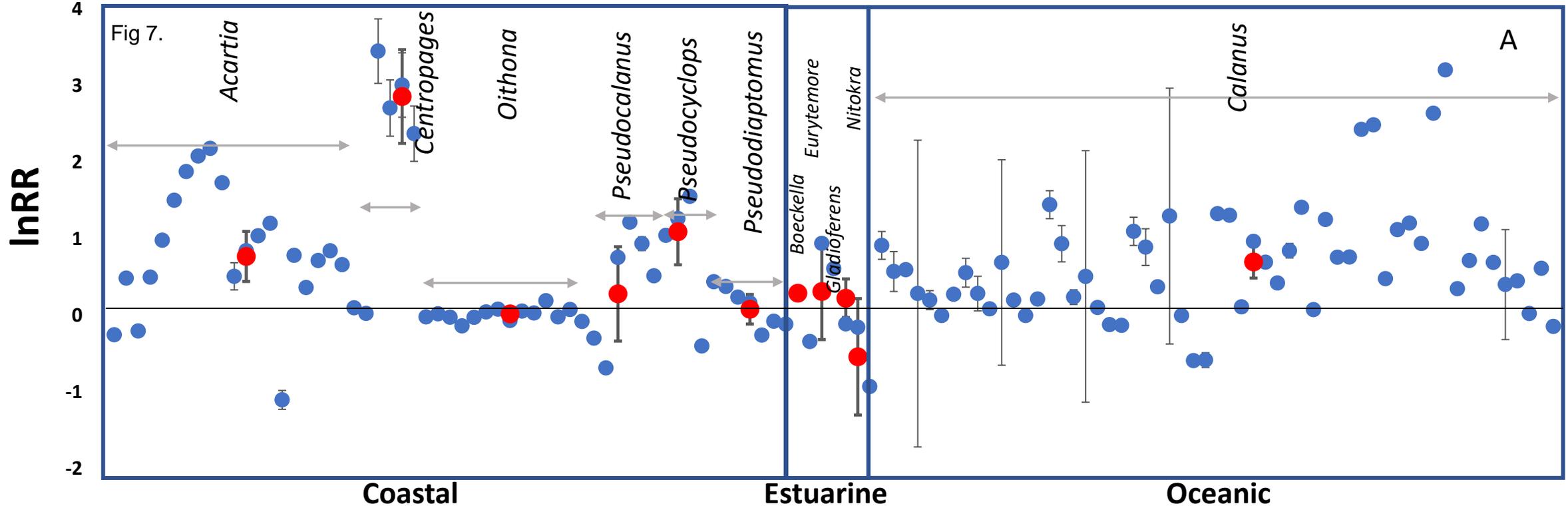


Fig 8.

