The Clam Before the Storm: A Meta-Analysis Showing the Effect of Combined Climate Change Stressors on Bivalves

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Abstract.

Impacts of climate change on marine organisms are increasingly documented in laboratory and experimental studies. The use of different taxonomic groupings and assessment of a range of processes, though, makes identifying overall trends challenging. Meta-analysis has been used to determine general trends but coarse taxonomic granularity may mask phylogenetically specific responses. Bivalve molluscs are a data rich clade of ecologically and economically important calcifying marine taxa, allowing for assessment of species-specific vulnerability across developmental stages. Drawing on the large body of available literature, we conduct a meta-analysis of 203 unique experimental setups, to examine how bivalve growth responds to increased water temperature, acidity, deoxygenation, and changes to salinity in 10 climate change stressor combinations. This is the most complete examination of bivalve responses to date, and shows that anthropogenic climate change will disproportionally affect particular families, suggesting taxonomic differentiation in climate change response. Specifically, Mytilidae, Ostreidae, and Pectinidae (67% of experiments) respond with negative effect sizes for all individual stressors while responses in Pinnidae, Tellinidae and Veneridae are more complex. Our analysis show that earlier studies showing negative impacts on bivalves are driven by only 3-4 well studied commercially important families. Despite the taxonomic differentiation, almost all drivers and their combinations have significant negative effects on growth. The synergistic impacts of deoxygenation, acidification, and temperature results in the largest negative effect size. Infaunal taxa, including Tellinidae and Veneridae, appear more resistant to warming and oxygen reduction than epifaunal or free-swimming taxa but this assessment is also based on a small number of datapoints. The current focus of experimental set-ups on commercially important taxa and families within a small geographic range creates gaps in understanding of global impacts on these economically important foundation organisms.

1 Introduction

Rising levels of atmospheric carbon dioxide will alter the marine environment over the coming decades. Sea surface temperatures are projected to rise 2–4°C globally by the end of the century depending on region and emission scenario (IPCC, 2021) with some areas, such as the Gulf of Mexico, already suffering frequent, severe deoxygenation events (Breitburg, et al., 2018). Higher latitudes will be exposed to more severe warming than the tropics (Meredith et al., 2019), resulting in sea ice and glacial melting, raising global sea levels, and increasing runoff and freshwater influx into marine settings (Lu et al., 2022). Ocean pH will decline by between 0.3–1 units by the end of the 21st century, with coastal regions expected to experience greater pH decreases than the open ocean (IPCC, 2021). Oxygen levels in the ocean are projected to decrease by up to 7% leading to an expansion of 'dead zones' (Breitburg, et al., 2018; Messié and Chavez, 2017; Schmidtko et al., 2017). The heterogeneous nature of change in each environmental driver will result in location-specific combinations and extent of stressors. This complexity presents a significant challenge for decision-makers in fisheries and marine conservation. Therefore, it is increasingly important to identify how stressors arising from climate change work both individually and in different combinations on communities and organisms in different settings.

At the intersection of the marine and terrestrial realms, shallow marine and coastal settings typically exhibit large spatiotemporal variations in physicochemical conditions such as pH, oxygen, and temperature (e.g., Hoffmann et al., 2011). This variability is exacerbated by anthropogenic climate change leading to more frequent extreme climate events, as well as redistribution of upwelling zones, circulation and currents, and alterations to both the quantity and quality of terrestrial runoff (Sydeman et al., 2014). Therefore, environmental changes are projected to especially impact shallow marine and coastal habitats, which harbour socially and economically important ecosystems. Up to 40% of the world's population lives within 200 km of the coastline (Neumann et al., 2015), and an estimated 775 million people globally have high dependence on these systems and their services (Selig et al., 2019). Costal ecosystems are estimated to contribute more than 60% of the total economic value of the biosphere (Martínez et al., 2007) but organisms adapted to live in these systems are predicted to suffer large alterations in their population fitness in response to future climate change (Kroeker et al., 2013; Sampaio et al., 2021; Hoppit and Schmidt, 2022).

Bivalve molluscs (Class Bivalvia) are cornerstones of coastal and shallow marine ecosystems, with representatives in all marine biomes where they provide provisioning and regulatory services (Olivier et al., 2020; Carss et al., 2020; Vaughn and Hoellein, 2018). Bivalves are a key global food source, with production for human consumption growing from 51 thousand tonnes in 1950 to more than 12.4 million tonnes today (Smaal et al., 2019). As a result, bivalve aquaculture has an estimated global market value of $17.1 billion (van der Schatte Olivier et al., 2018).

Additionally, there is a growing awareness of the wider ecosystem benefits of bivalves as habitat formers. Their biogenic three-dimensional reefs formed by sessile epifaunal taxa such as oysters increase surrounding biodiversity (Fariñas-Franco and Roberts, 2014). Complex reef frameworks and individual bivalve shells in soft-substrate environments can act as microhabitats to other invertebrates through creation of new hard substrates and by altering local flow regimes or even temperature (McAfee et al., 2017). Filter-feeding bivalves can reduce pollution and clear large particulates out of the water column (Smyth et al., 2018). They enhance or change local marine productivity (Donnarumma et al., 2018; Strain et al., 2021) via selective removal of specific species of

68   phytoplankton (Ward and Shumway, 2004). Deposition of bivalve faeces and pseudofaeces, along with

69   burrowing activity of motile infaunal deposit or suspension feeders, can lead to changes in the local flux or

70   enrichment of organic matter into the sediment and biogeochemical cycling (Smyth et al., 2013), and ultimately

71   habitat suitability for other benthos.

72   Anthropogenic pressures including coastal development, overfishing, and pollution have resulted in

73   demonstrable decreases in global bivalve populations (e.g., De Groot, 1984; Baeta et al., 2014). Akin to other

74   calcifying invertebrate organisms, it has been hypothesised that the physiochemical changes resulting from

75   climate change will reduce bivalve growth, impair maintenance of shells (Maynou et al., 2020; Knights et al.,

76   2020), and disrupt larval settlement patterns and spawning (Bascur et al., 2020; Figueirodo et al., 2022). In

77   recognition of the environmental, social, and economic benefits bivalves produce, and the current and future

78   pressures they face, the group is a focus for conservation efforts (zu Ermgassen et al., 2020; Buelow and

79   Waltham, 2020, Gagnon et al., 2020). However, despite extensive study there remain important gaps in our

80   understanding of their response to climate change across different bivalve families.

81   Current understanding of how bivalves will respond to various climate change stressors is based on field studies

82   and lab-derived experimental data focused largely on ocean acidification and response to warming, generally

83   observing negative responses (e.g., Beukema et al., 2009; van Colen et al., 2012; Addino et al., 2019; Eymann et

84   al., 2020). Synthesis work through meta-analysis supports the notion that bivalves overall will respond

85   negatively to climate change (Kroeker et al., 2013; Harvey et al., 2013; Sampaio et al., 2021; Hoppit and

86   Schmidt, 2022; Leung et al., 2022). These studies have shown that the synergistic effects of ocean acidification,

87   ocean warming, and an increase in hypoxic events decrease the growth rates of calcifying marine organisms

88   (Kroeker et al., 2010; Maynou et al., 2020; Knights et al., 2020; Sampaio et al., 2021). However, these analyses

89   have been conducted at high taxonomic rankings, e.g., examining changes at phylum level, thereby risking

90   averaging differential outcomes at finer taxonomic resolution. Organisms experience disparate responses to

91   environmental drivers based on local phenotypic expression (Dong et al., 2017) and environmental influences

92   (Genner et al., 2010) resulting, for example, in species-specific mortality risk to extreme heat based on local

93   microclimates and adaptation (Montalto et al., 2016). 'Clumping' these diverse responses make high level

94   analyses and their generalized trends difficult to interpret (Helmuth et al., 2005). Therefore, our current

95   understanding of how bivalves respond to climate change based on broad scale synthesis work might not capture

96   the granularity and diversity of responses this group exhibits.

97   We aimed to fill this gap by employing a meta-analysis methodology to explore the effects of marine climate

98   stressors, and combinations thereof, on bivalve growth at both the whole-group and family levels. Our analysis

99   explores 10 stressor combinations, greatly expanding earlier work examining only four stressors (Sampaio et al.

100   2021). For the first time in a meta-analysis of impacts of marine climate change, we explore taxonomic

101   sensitivities within a family and identify large gaps in taxonomic understandings of how response to climate

102   change in this very well-studied group. Our aim is to determine whether a negative response to climate change is

103   intrinsic to the group or driven by specific taxa. We focused on studies that emphasize bivalve growth rates; a

104   commonly studied trait that offers insight into organism vulnerability to answer how these growth rates are

105   impacted by climate stressors, and whether different families or developmental stages are more sensitive to

106   climate stressors than others. Additionally, we examine taxonomic diversity of the experiments available in the

published literature for meta-analysis. We hypothesise that a focus on commercially important bivalve taxa may be creating a bias in current observations. Our findings encourage a new approach to meta-analysis by moving towards more differentiated taxonomic understandings of a group's responses to future conditions, while still providing a summative response above the individual species level needed for conservation decision making.

2 Methods

The data and code is accessible in the Github folder https://github.com/georgehoppit/Bivalve-meta-analysis.

2.1 Study selection criteria

Primary literature focusing on bivalve growth was identified using Web of Science Core collection. The keywords used were "bivalve", "Bivalvia", "meta-analysis", "acidification", "pH", "hypercapnia", "ocean change" "temperature", "salinity", "oxygen", "deoxygenation", "hypoxia", "anoxia", and combinations thereof. Articles collected ranged from 1997–2020. Articles were screened initially through title relevance, then abstract content, and finally full-text content (Fig. 1), from which individual experimental set-ups were extracted. Article lists from previous meta-analyses with similar scope (Kroeker et al., 2013; Harvey et al., 2013; Sampaio et al., 2021) were additionally consulted to identify material missed from initial search strings. For a list of included articles used for analysis please consult 'Data availability' section.

[Figure 1] PRISMA flow diagram of screening process for the present study following recommended guidelines (Page et al., 2021). Relevant articles on Bivalvia growth experiments were identified from the Web of Science Core Collection using a series of keywords (see main text). Screening resulted in the identification of 79 relevant articles with 203 experimental set-ups that were included in our meta-analysis.

When extracting data from papers, we selected experiments that represented plausible end-of-century climate conditions or their location specific expression, and excluded physiological stress experiments which often subject animals to artificially unnatural conditions. Data were extracted from studies which maintained constant experimental conditions, thereby also not exploring the natural diurnal variability which is large in coastal settings (Dong et al., 2017; Hofmann et al., 2011) especially for species which are exposed to air at low tide. The data overview for individual species is available in our accompanying data.

We used growth as a broad measure of organism physiological response to climate stressors (and not more specific measures like shell thickness or soft tissue mass) for two main reasons. Disentangling specific growth measurements would weaken our analysis due to the wide disparity in approaches measuring growth responses to climate stressors. Additionally, using growth in this manner keeps our study in line with previous meta-analyses (Krocker et al., 2013; Harvey et al., 2013; Sampaio et al., 2021), allowing direct comparisons with past work with different foci. We opted against using survivorship as death often recorded just as a percentage which is not sufficient for this type of analysis, as meta-analysis requires means, standard deviation, and sample size being reported to calculate effect size.

141 We included articles with lab-based studies that focused on direct measurements of Bivalvia growth including

142 length, mass, condition index, or shell thickness. Proxies for growth were excluded, such as scope for growth or

143 RNA production, as these introduce additional uncertainties and variability to the growth signal and were not

144 directly comparable to absolute measures of growth. Only studies where the bivalves were fed and studies on

145 larvae that develop without feeding were included, as nutrient intake has a strong impact on growth (Norkko et

146 al., 2005; Thomsen et al., 2013; Ballesta-Artero et al., 2018). Study sample size, mean growth value of both

147 control and treatment groups, and indication of the variation of growth values (confidence intervals, standard

148 error, and standard deviation) were extracted from articles. Absolute values were used, as percentage data could

149 not be combined with absolute measurements within the Metafor package. Data were extracted directly from

150 result text, tables, or supplementary data when possible. Data from figures was collected using WebPlotDigitizer

151 v. 4.4 (Rohatgi, 2022). Control values for climate stressors for each article were based on authors' determination

152 of control conditions. Climate stressor values were based on realistic end of century projections based on

153 author's determination for that experimental setup or study location. The phylogeny and column chart (Fig. 2)

154 were plotted using R v. 4.1.0 (R Core Team, 2021) and the packages ggplot2 v. 3.3.5 (Wickham, 2016), ggtree

155 v. 3.2.1 (Yu et al., 2017), ape v. 5.6.1 (Paradis and Schliep, 2019), and patchwork v. 1.1.1 (Pederson, 2020). The

156 topology is taken from the time-scaled 'budding II' family-level phylogeny of Crouch et al. (2021).

157 [Figure 2] Experimental representation of 18 Bivalvia families in 203 unique experimental setups from 79

158 relevant articles found in Web of Science Core Collection. **A**, time-scaled 'budding II' phylogeny of extant

159 Bivalvia from Crouch et al. (2021). The root age is 485.4 Ma. **B**, number of experiments representing each

160 extant family.

161 **2.2 Statistical analysis**

162 We preformed meta-analysis on the impacts of climate stressors on the growth of Bivalvia at whole-class and

163 family levels following methods described in Hoppit and Schmidt (2022). Stressors identified from the included

164 experiments are water oxygen depletion (O_2), increased acidity (decreased pH), salinity change (S), and

165 temperature increase (T), and combinations of these stressors (indicated as, e.g., O_2 + pH) (Figs 3–5; Table 2).

166 Stressor effects could be synergistic (additive) or antagonistic (reductive) (*sensu* Harvey et al., 2013), or

167 dominated by one stressor (unaffected by changes in another stressor). Additionally, we separated out the effect

168 sizes of these stressors on different growth stages (egg/larva, juvenile, adult) for the entire class Bivalvia.

169 Analyses used R v. 4.0.3 (R Core Team, 2020) and the package Metafor version 3.0-2 (Viechtbauer, 2010).

170 Metafor function escalc was used to calculate effect size and sampling variance. We chose Log Response Ratio

171 (LnRR; the natural log of the response ratio) as the measure of effect size to measure the proportion of change

172 between the mean of the treatment and control responses to experimental intervention. An effect size of zero

173 corresponds to a statistically insignificant effect. Multivariate meta-analytical models (function rma.mv) were

174 used to calculate mean effect sizes of climate stressor impacts on bivalve growth rates for three subsets of data:

175 all bivalves pooled, different developmental stages, and families with sufficient sample sizes ($n \geq 7$). Significant

176 results were identified when model 95% confidence intervals did not overlap zero effect size. Models used

177 random intercepts for articles and species intercepts for each treatment to compensate for similarities introduced

178 by studies, as data originating from the same experimental setup or from the same species are assumed to be

179   more likely similar than data from different articles or species. Residual heterogeneity (QE), calculated as part
180   of the meta-analytical models, was used to determine whether additional study moderators not considered might
181   be influencing study results (Hedges and Olkin, 1985).

182   Publication bias was tested using Egger's regression test. Following Habeck and Schultz (2015), function
183   rma.mv was extended using the square root of effect size variance in the model moderator variables to conduct a
184   regression test. Egger's regression test looks at the symmetry of the data published and determines whether there
185   are statistically 'missing' studies within the spread of the papers published (Egger et al., 1997). We used meta-
186   regression to determine whether published results had changed over the 25 years from which studies had been
187   collated, using study year as a moderator variable. This would indicate whether increasingly detailed knowledge
188   has altered the overall picture with regards to the effect of each climate change stressor.

189   **3 Results**

190   Our literature search produced the most detailed examination of bivalve growth rates under multiple climate
191   stressors to date. We identified 79 studies with 203 unique experiments meeting the criteria, comprising 18
192   families and 37 species (Figs 1, 2; Table 1). Sampling of families was highly uneven: Mytilidae make up 36% of
193   the experiments and 81% of the experiments include just four families: Mytilidae, Ostreidae, Pectinidae, and
194   Veneridae; including Pinnidae and Tellinidae increases the total to 88% (Table 1).

195   We find consistent and significant negative effects of all single stressors and most combinations acting on the
196   entire class Bivalvia, in agreement with previous meta-analyses (Fig. 3; Table 2). At the class level, many
197   combinations of stressors increase the negative effect on growth in a synergistic way (Fig. 3; Table 2). For
198   example, pH and O_2 treatments are greater in combination than either alone, as were salinity + temperature and
199   pH + temperature. The effect of pH + salinity is intermediate between that of the two single stressors, , while
200   O_2 + temperature causes a smaller effect than either single stressor. The combination of three stressors, O_2 +
201   pH + temperature, causes the strongest negative effect size to both individual stressors and any combinations.
202   While low heterogeneity is preferable in terms of data validity it is rarely achievable in environmental meta-
203   analyses. Therefore, the significant heterogeneity in the data is expected given it is drawn from so many
204   disparate studies: QE = 300509.7155, df = 148, $P < 0.0001$.

205   [Figure 3] Effect size (log-response ratio, LnRR) for individual and combined effects of temperature (T), acidity
206   (pH), oxygenation (O_2), and salinity (S) as stressors on bivalve growth rates for all Bivalvia. Points represent
207   mean effect size with error bars indicating 95% confidence intervals. Numbers indicate number of included
208   experiments. Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

209   [Table 1] Representation of bivalve families across 203 experimental studies included in this meta-analysis.

210   [Table 2] Single and combined stressor effect sizes from a meta-analysis of 203 experimental set-ups (log-
211   response ratio, LnRR). Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

212   Thirty-one of the 203 experimental set-ups involve adult Bivalvia, 14 on unspecified ages/stages, 45 on eggs/
213   larvae, and the remaining 113 focused on juvenile stages. Separating by growth stage shows that the

214 combination of pH and O_2 stressors causes significantly negative effect size at all points in the life cycle (Fig.
215 4). Salinity is not an important stressor for larval or juvenile bivalves but causes a reduction in growth in adults.
216 Juveniles show responses to most stressors, whereas egg/larvae and adult bivalves have much smaller sample
217 sizes, and do not show significant effect size responses across the stressors.

218 Families do not all respond in the same way as the whole class Bivalvia, and stressors affect different families in
219 unexpected ways (Fig. 5). Mytilidae, Ostreidae, and Pectinidae (67% of experiments) respond with negative
220 effect sizes for all individual stressors (Fig. 5A–C). Pinnidae show positive responses for single stressors
221 temperature and pH, but negative when combined (Fig. 5D). Tellinidae show positive responses for oxygen and
222 O_2 + pH (Fig. 5E). Veneridae (14% of experiments) show mixed results with significant negative effect sizes of
223 salinity, pH + S, O_2 + pH, and O_2 + pH + T, but strong positive responses to temperature and O_2 + T (Fig. 5F).

224 [Figure 4] Effect size (log-response ratio, LnRR) for individual and combined effects of oxygenation (O_2),
225 acidity (pH), salinity (S), and temperature (T) as stressors on Bivalvia growth rates at different life stages
226 (egg/larval, juvenile, adult). Points represent mean effect size with error bars indicating 95% confidence
227 intervals. Numbers indicate number of included experiments. Significance is indicated with asterisks: * $P <$
228 0.05, ** $P < 0.01$, *** $P < 0.001$.

229 [Figure 5] Effect size (log-response ratio, LnRR) for individual and combined effects of oxygenation (O_2),
230 acidity (pH), salinity (S), and temperature (T) as stressors on Bivalvia growth rates separated by family. **A**,
231 Mytilidae. **B**, Ostreidae. **C**, Pectinidae. **D**, Pinnidae. **E**, Tellinidae. **F**, Veneridae. Points represent mean effect
232 size with error bars indicating 95% confidence intervals. Numbers indicate number of included experiments.
233 Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

234 Publications with significant results are published more often than would be expected by chance, suggesting
235 negative observations are less frequently reported (see Appendix A; Table A1), as shown by highly significant
236 Egger's regression test ($P < 0.001$) results for every stressor. Meta-regression analysis of publication by year and
237 stressor showed that no individual stressor is changing in effect size signal through time, supporting consistency
238 in findings over the years (see Appendix B; Fig. B1 and Table B1).

239 **4 Discussion**

240 The impact of individual and combined climate stressors on growth rates of all bivalve molluscs in our study
241 concurs with previous meta-analyses on marine calcifying invertebrates. Our analysis demonstrates that
242 increased incidences of deoxygenation, pH decrease, as well as changes to temperature and salinity in nearshore
243 marine environments in the future will inhibit the growth of bivalves. However, by separating out both bivalve
244 family-level response and different life stages, we build upon previous synthesis work by revealing previously
245 unappreciated complexity in responses. Effects of climate change for bivalves will in addition to the physico-
246 chemical environment, depend on the varied ecological and taxonomic makeup of specific habitats and will also
247 vary across growth stages which exploit the marine habitat differently. We also highlight numerous biases that
248 exist in currently available studies (taxonomic, ecological, geographic) which hinder upscaling of individual
249 bivalve responses to a true global picture. Furthermore, our analysis hopes to move synthesis literature studies

250 towards higher taxonomic understanding of an individual group's responses to future ocean conditions, by
251 showing the level of variability that can be present once taxonomic distinctions within a group are teased out.

4.1 Climate change stressors will negatively impact bivalve growth

253 Our findings clearly show that growth rates in Bivalvia are negatively affected by climate stressors (Fig. 3). By
254 exploring responses at family level, we confirm our hypothesis that negative growth responses to climate change
255 are likely inherent to this taxonomic group as a whole, despite the experimental bias in the published literature
256 towards key families. Previous meta-analyses that incorporated bivalves did not focus on the group specifically
257 but include them alongside numerous other taxa (i.e., within phylum Mollusca) (Harvey et al., 2013; Kroeker et
258 al., 2013; Sampaio et al., 2021). These analyses found little evidence for significant effect sizes except in a few
259 single stressors (pH and temperature: Harvey et al., 2013; hypoxia: Sampaio et al., 2021).

260 Unsurprisingly, the effect of temperature on bivalve growth is the most studied stressor in the experiments
261 included in our meta-analysis (35 experiments: Fig. 3) – a feature seen in other studies of the effects of marine
262 climate change (Borges et al., 2022). This bias is likely because temperature-altering experiments require less
263 complex equipment and sensors than pH or oxygen manipulation, have been performed over decades, and target
264 the most obvious effect of climatic change i.e., global warming. Inclusion of a substantially greater number of
265 previous experiments within our meta-analysis (over 200 specific bivalve growth observations versus 45, 46,
266 and 34 Mollusca for Kroker et al. (2013), Harvey et al. (2013), and Sampaio et al. (2021) respectively) confirms
267 that all single climate stressors show significant negative effect sizes in bivalves (Fig. 3). Our analysis also
268 shows that in many cases this effect prevails when individual growth stages (Fig. 4) and the families containing
269 the largest number of experiments or observational data (Table 1; Fig. 5) are examined separately.

270 An important result is the identification of synergistic, additive, and antagonistic effects between different
271 stressors which in all cases in our analysis increase the negative response (Gobler et al., 2014; Stevens and
272 Gobler, 2018) (Table 2). For example, we identify significant negative effect sizes for O_2 + pH, and temperature
273 + salinity when analysing overall bivalve responses (Fig. 3). The combination O_2 + pH has a stronger negative
274 synergistic effect size compared to either oxygen or pH individually in all analyses (Figs. 3-5). Decreases in pH
275 restrict growth via restricting availability of CO_3^{2-} and increasing HCO_3^{-} ions making shell building more
276 metabolically expensive and increasing shell dissolution (Ivanina et al., 2013; Byrne and Fitzer, 2019). Internal
277 tissues also require buffering against pH changes, incurring a further metabolic cost (Byrne and Fitzer, 2019).
278 Marine deoxygenation impacts metabolism, reducing an organism's ability to respond to these increased
279 metabolic requirements of shell generation and tissue buffering under a more acidic environment. Therefore, the
280 increased impact from combining these two stressors confirms our physiological understanding of the organism
281 (Pörtner and Farrell, 2008).

282 Mean effect sizes for each climate stressor differ between families within Bivalvia. Consequently, the effects of
283 climate change on this group will be habitat dependant and alter the taxonomic composition of coastal
284 ecosystems. The four most investigated families in our dataset (Mytilidae, Osteridae, Pectinidae, and Veneridae)
285 exhibit consistent negative growth responses to climate stressors (Fig. 5). Exceptions exist for oxygen and
286 temperature changes for Mytilidae and Veneridae and temperature increase for Veneridae where we find mixed
287 responses which are discussed in more detail below (section 4.3). However, pH causes antagonistic decreases in

288   growth rate across these main families (Fig. 5), suggesting that any temperature-driven growth increases are

289   unlikely to occur under future projected conditions..

290   **4.2 Different bivalve life stages and ecologies show distinct responses to climate stressors**

291   Climate change will be acting on each part of the development of an organism. In bivalves, these different life

292   stages have different habitats and mobility from free swimming larvae to sessile adults. Our results on how

293   different bivalve life stages are affected by a range of climate stressors generally confirm previous meta-

294   analyses across calcifying organisms. Our results suggests early life stages are the most vulnerable to a specific

295   set of stressors and that the threat diminishes as organisms mature, supporting analyses by Sampaio et al. (2021)

296   and Kroeker et al. (2013) which focused on the impacts of ocean acidification. It is important to note, though,

297   that the earlier developmental stages are more mobile and hence able to relocate their niche to track their

298   environmental needs.

299   Combined climate stressors (e.g. pH + temperature, O_2 + pH, salinity + temperature) showed negative responses

300   across all growth stages. Our findings oppose those of Harvey et al. (2013) who suggested limited variation in

301   organism growth responses between life stages exposed to individual and synergistic ocean acidification and

302   warming. In contrast to our analysis, their data were pooled from multiple phyla reiterating the need to avoid

303   too much pooling and averaging in meta-analysis.

304   Most studies in our dataset, especially those on the families that dominate our meta-analysis (Fig. 4), are

305   focused on larval or juvenile stages. This likely explains some of the negative impacts on growth as for example

306   shell mineralogy influences the impact of pH changes. Amorphous calcium carbonate secreted by larval

307   bivalves is 50-times more susceptible to dissolution than either calcite or aragonite (Bressan et al., 2014).

308   Changes to body size or decreased shell thickness could increase vulnerability to predation (Sadler et al., 2018).

309   Non-significant effects of lowered pH alone in adult bivalves likely result from more diverse shell mineralogy

310   (Weiss et al., 2002), the effects of a more robust adult shell (Beadman et al., 2003), or shelf formation of adults

311   from a high pCO$_2$ low pH micro-environment quite different to the surrounding seawater (Thomsen et al., 2010;

312   Hiebenthal et al., 2013). The adult's lifestyle, which includes for some taxa exposure to air and/or closed valves

313   while respiring naturally results in high variability of pH in the calcifying fluid and therefore the pH changes in

314   the experiments may be resulted in relatively less stress compared to earlier developmental stages. Most of the

315   adult experiments included in our meta-analysis were on aragonitic individuals or on mixed aragonitic-calcitic

316   Mytilidae and Pectinidae. Only one study (Lemasson et al., 2018) included two genera of adult oysters (Family

317   Ostreidae) which construct their shells primarily from calcite (Stenzel, 1963), a more stable carbonate

318   polymorph.

319   Our results indicate that adults have an increased susceptibility to salinity changes when compared to juvenile

320   and egg/larval stages, suggesting habitats projected to experience decreased salinity due to increased seasonal

321   runoff or enhanced evaporation in a restricted setting (Robins et al., 2016) may become challenging for adult

322   bivalves. It is important to note though that fewer experiments were conducted exploring salinity, resulting in a

323   low number of experimental studies and a greater need for determining the interaction with other drivers such as

324   pH, temperature, and oxygen. Increased sensitivity to climate stressors at different life stages has implications

325   for bivalve aquaculture and conservation effort (Smaal et al., 2019) with the potential to be disruptive to

lifecycles in some taxa. Decreased growth rates in larval and juvenile stages might impact population recruitment by limiting the number of individuals surviving to adulthood. Settlement efficacy will affect repopulation success, following disturbance (Gagnon, et al., 2021). Aquaculture and fisheries will need to account for these increased vulnerabilities and adapt culturing strategies to compensate for the negative growth impacts of climate change.

Efforts to restore historical bivalve populations such as oysters in Chesapeake Bay (Bersoza Hernández et al., 2018) and Europe (Sas et al., 2020) will need to consider how climate stressors will impact population dynamics. Restoration projects often transplant adult or juvenile species into new environments (Johnson et al., 2019); and our findings suggest transplanting adults might be a preferable strategy given the lower impact of climate stressors at this developmental stage.

4.3 Consideration of habitat and ecology in the context of climate change

Many species belonging to the families Mytilidae, Osteridae, and Veneridae occur in intertidal habitats which experience frequent fluctuations in oxygen, acidity, and temperature and has been hypothesised to provide some species with an innate ability to resist or mitigate the effects of future environmental change (Gazeau et al., 2013; Zhang et al., 2020). Furthermore, this high variability may include environments overlapping with those replicated in some of the experimental setups. Species can in natural environments evade some stressors via behavioural thermoregulation, for example mobile infaunal bivalves have been shown to migrate to more offshore habitats, or burrow deeper into the sediment (Domínguez et al., 2020; Dominguez et al., 2021).

Negative growth responses though generally repeat across the taxa in our dataset irrespective of habitat. An intertidal habitat or preference for marine or brackish water does not appear to alter observed growth responses in the experimental setting to accumulated climate stressors. We e find consistent decreases in growth rates across taxa, with commonly subtidal, epifaunal bivalves (such as many Pectinidae) also exhibiting negative responses (Aguirre-Velarde et al., 2019; Maynou et al., 2020). Interpreting the effects of ecology on our results is complicated by the previously mentioned dominance of studies focused on juvenile and early growth stages; many bivalves feature a veliger or early larval stage that live in and can tolerate quite different environmental conditions to those of later stages of life history (i.e., pelagic, free-swimming larvae vs infaunal or benthic attached lifestyles for juveniles and adults) (Waldbusser et al., 2013).

Examining the effect of other aspects of bivalve mode of life on our results also reveals complexities in response. Negative growth responses generally repeat across taxa irrespective of habitat. Most experiments in our dataset are conducted on suspension feeding taxa with an epifaunal habitat. The investigated bivalves are free swimming (Pectinidae), cemented to substrates or form biogenic reefs (Ostreidae), or use byssal threads to anchor in sediments or attach to hard substrates (Pinnidae, Mytilidae, some Pectinidae). There is much lower representation in our dataset of infaunal or burrowing taxa which may also include deposit feeders (e.g., families Tellinidae, Veneridae). Our data suggest overwhelmingly negative impacts on growth of all stressors for epifaunal or free-swimming suspension feeding taxa (families Mytilidae, Ostreidae, Pectinidae in Fig. 5).

Tellinidae and Veneridae show more varied responses to temperature, pH, and O_2 depletion. These taxa are active infaunal burrowers in soft sediment, which can often be undersaturated with respect to calcium carbonate

363 as well as oxygen-limited (Green et al., 2013; Stevens and Gobler, 2018) suggesting some resilience to these

364 conditions. Both semi-infaunal Pinnidae and infaunal Veneridae also show significant positive effect sizes in

365 response to warming (Fig. 5). It has been hypothesised that an infaunal habitat may reduce immediate

366 susceptibility of bivalves to warming, as the substrate may act as a thermal refugia (Zhou et al., 2022). Taken

367 together, these results suggests that lifestyle and habitat will control the ability of bivalves to evade climate

368 stressors. However, interpreting the general role of ecology in providing resilience is complicated by the

369 currently small number of experiments or observations on infaunal taxa, further highlighting the need for

370 additional data on the effects of environmental stressors on the growth of burrowing bivalves and those from a

371 wider range of specific shallow marine habitats.

372 **4.4 Experimental studies of bivalve response are biased by commercially important taxa, and have**
373 **disparate protocols**

374 Our meta-analysis clearly reveals that available data on bivalve growth responses to climate stressors contain a

375 number of biases, likely due to the commercial importance of certain families (e.g., Mytilidae, Ostreidae,

376 Pectinidae, Veneridae) and individual species within them for aquaculture and common ecosystem services

377 (e.g., van der Schatte Olivier et al., 2020), as well as ease of access to specimens. Many experiments document

378 that bivalve specimens were sourced from commercial aquaculture facilities. A number of families included in

379 our meta-analysis are represented only by individual experiments: for example, Dreissenidae, Hitellidae,

380 Mesodesmatidae, Myidae and Pharidae. Comparison of the number of experiments vs. bivalve phylogeny shows

381 that entire families have no documented experimental or observational work investigating climate stressor

382 impacts on growth (Fig. 2). This confirms our hypothesis that even though bivalves are considered a well-

383 studied group, the signals detected in the literature are often driven by a subset of taxa.

384 While our results are based on studies with varying experimental protocols, our approach is consistent with

385 other meta-analyses (e.g., Hoppit and Schmidt 2022; Harvey et al., 2013; Kroeker et al., 2013; Sampaio et al.,

386 2021). As we are using studies with disparate protocols and experimental measurements, the meta-regression

387 analyses we conducted (Appendix B; Fig. B1) show that effect sizes across studies and experimental setups have

388 not changed across time. This result suggests that variability in research practices does not impact our results.

389 Some stressor combinations have low sample sizes, as multi-factor experiments are notoriously work intensive

390 and difficult to perform. These lower numbers decrease confidence in those specific observations and

391 conclusion, and highlights the importance of considering a wider range of drivers than the most frequently

392 assessed combination of warming and acidification alone.

393 Our findings are also geographically biased towards the global north. Most studies clearly gathered organisms

394 and data from the coasts of the USA, Europe, or China, resulting in important portions of the global ocean like

395 the Caribbean or African coasts being unrepresented in these data. While our meta-analysis focused specifically

396 on bivalve growth, this result emphasizes the unevenness of experimental research into this group. If this

397 disparity of understanding is not rectified then implementing effective climate change adaptation and mitigation

398 strategies and upscaling these results to ecosystem-scale changes are challenging.

399 While our experimental sample is larger than previous meta-analyses, these biases also leave much uncertainty

400 about how responses will scale up from commercially important species to other, rarely studied groups of

bivalves, which while of lesser importance for aquaculture or commercial exploitation, may act as keystone species within fragile marine ecosystems. This further limits the quality and quantity of available information that conservationists and stakeholders need to develop strategies to safeguard marine social-ecological systems. Given our findings overwhelmingly suggest that bivalves as a group (Figs 3, 4) and common, well-studied families (Fig. 5) will likely experience decreased growth rates under protected projected end-of-century conditions, how likely is it that families or species with no current experimental observations will also follow this trend? Additional experimental and observational work on specific bivalve species and families is urgently required which would greatly assist in developing conservation strategies for this important group of marine calcifiers.

5 Conclusions

1. Our results show that growth rates of bivalve molluscs decrease when exposed to climate stressors with synergistic factors (e.g., effects of combined temperature + O_2 + pH change) causing greater reductions in bivalve growth then individual stressors. This result is true for bivalves overall, and when separating out by growth stage in the most commonly studied bivalve families (Ostreidae, Mytilidae, Pectinidae, Veneridae). Reduced growth rates predicted by our meta-analysis have important implications for population stability in these commercially important keystone marine taxa, as well as for guiding future conservation and mitigation efforts.

2. Epifaunal filter feeders, such as Ostreidae and Mytilidae, had mostly negative growth responses to environmental stressors. In contrast, infaunal and semi-infaunal suspension or deposit feeding bivalves, Veneridae, Tellinidae, and Pinnidae showed more mixed or even positive growth response under higher temperatures, suggesting that burrowing or buried taxa may be buffered from or resilient to some predicted changes. However, these data are based on a small number of studies, providing less confidence in the negative growth effects with other stressors and combinations of stressors.

3. By focusing on a few commercially relevant taxa, these commonly studied families are creating a bias in the literature. A large proportion of bivalve families lack any rigorous experimental or observational data resulting in large knowledge gaps hampering conservation efforts. Available data on bivalve response to climate stressors also contain large biases towards early or juvenile growth stages and commercially important species from the global north. Our results should be replicated for other commonly studied marine organisms like seaweeds or echinoderms to assess if taxonomic bias drives commonly assumed physiological responses to climate change.

Appendices

Appendix A

Table A1. Publication bias results of Egger's regression test.

437   For all stressors: df=195

	estimate	se	pval	tval	ci.lb	ci.ub
	estimate	se	pval	tval	ci.lb	ci.ub
sqrt(vi):StressorO$_2$	-5.5054	0.367	<.0001	-15.0026	-6.2292	-4.7816
sqrt(vi):StressorpH	-1.5811	0.3003	<.0001	-5.2654	-2.1733	-0.9888
sqrt(vi):StressorpH and O$_2$	-10.929	0.3705	<.0001	-29.4969	-11.6597	-10.1982
sqrt(vi):StressorpH and temperature	-7.2009	0.3165	<.0001	-22.7541	-7.8251	-6.5767
sqrt(vi):Stressorsalinity	-1.5428	0.7805	0.0495	-1.9765	-3.0823	-0.0033
sqrt(vi):Stressorsalinity and pH	-10.1106	0.9205	<.0001	-10.9841	-11.9261	-8.2951
sqrt(vi):Stressortemperature	-0.8807	0.3563	0.0143	-2.4717	-1.5834	-0.1779
sqrt(vi):Stressortemperature and O$_2$	-1.0071	0.5775	0.0828	-1.7439	-2.1462	0.1319

sqrt(vi):Stressortemperature and pH and O$_2$	-9.7482	0.5994	<.0001	-16.2629	-10.9304	-8.5659
sqrt(vi):Stressortemperature and salinity	-4.2012	0.869	<.0001	-4.8344	-5.9153	-2.4872

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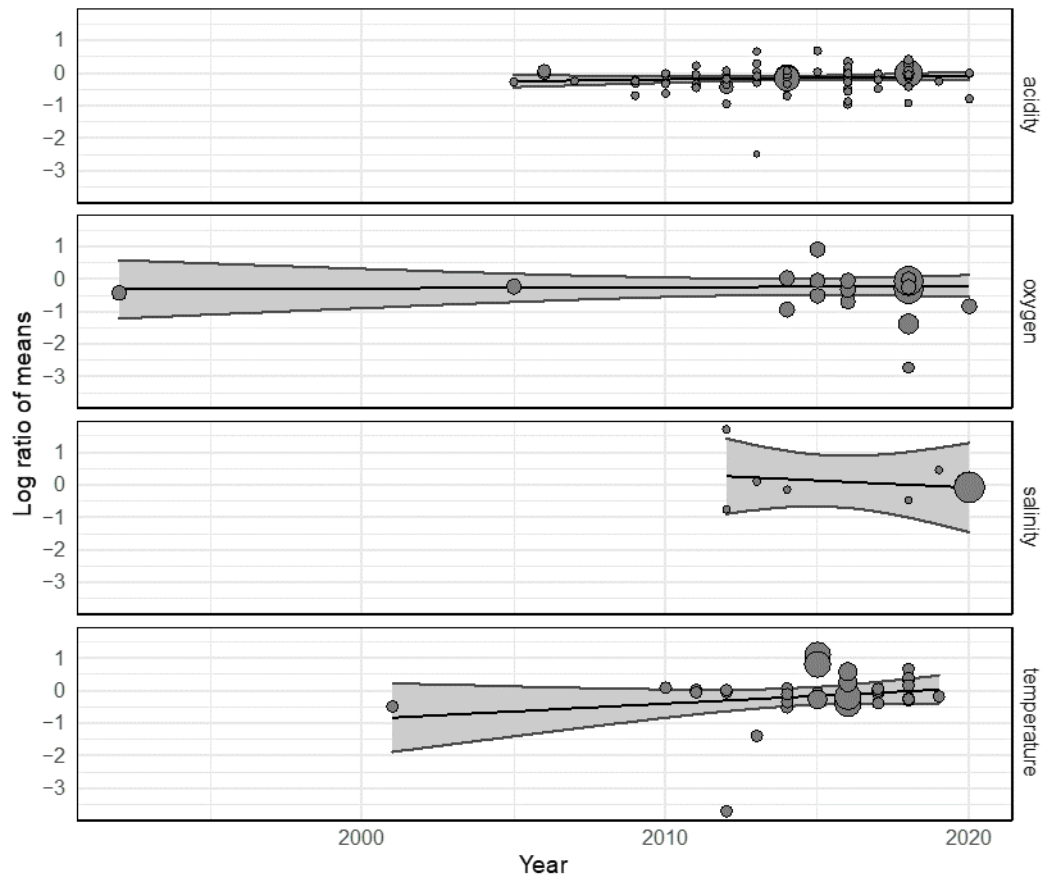
Appendix B.

Fig. B1 Meta-regression change of effect sizes of 203 experimental setups on Bivalvia growth through time from 1997 to 2020. **A**, acidity (pH). **B**, temperature. **C**, deoxygenation. **D**, salinity. Each point shows the effect size against the data set publication year. Point size indicates the experiment contribution weight to the linear model. Each plot shows the regression of effect size against publication year with the 95% confidence interval shaded. All regression analyses show no significant change during this period.

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453 **Table B1.** Regression analysis of publications by stressor per year.

Acid	estimate	se	tval	df	pval	ci.lb	ci.ub
intrcpt	-21.2396	19.6612	-1.0803	88	0.2830	-60.3120	17.8328
Year	0.0105	0.0098	1.0725	88	0.2864	-0.0089	0.0299
Temp							
intrcpt	-96.5465	74.7711	-1.2912	33	0.2056	-248.6695	55.5764
Year	0.0478	0.0371	1.2888	33	0.2064	-0.0277	0.1233
Oxygen							
intrcpt	-7.5967	36.9562	-0.2056	16	0.8397	-85.9404	70.7470
Year	0.0037	0.0183	0.1990	16	0.8447	-0.0352	0.0425
Salinity							
intrcpt	87.7248	203.0242	0.4321	6	0.6808	-409.0574	584.5071
Year	-0.0435	0.1007	-0.4315	6	0.6812	-0.2900	0.2030

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455   Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

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478   **Code availability**

479   Code used for analyses available at https://github.com/georgehoppit/Bivalve-meta-analysis

480   **Data availability**

481   Data used for analyses available at https://github.com/georgehoppit/Bivalve-meta-analysis

Author contributions

Conceptualization: GH, BCM; data curation, formal analysis, investigation, methodology: RKW, GH; resources, software, validation: RKW, GH, BCM, JDW; supervision: GH, JDW, BCM; visualization: RKW, GH, BCM; writing – original draft: RKW; writing – review & editing: RKW, GH, DNS, BCM, JDW. (https://credit.niso.org)

Competing interests

The authors declare that they have no conflict of interest.

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790 **Figure 1.** PRISMA flow diagram of screening process for the present study following recommended
791 guidelines (Page et al., 2021). Relevant articles on Bivalvia growth experiments were identified from
792 the Web of Science Core Collection using a series of keywords (see main text). Screening resulted in
793 the identification of 79 relevant articles with 203 experimental set-ups that were included in our
794 meta-analysis.

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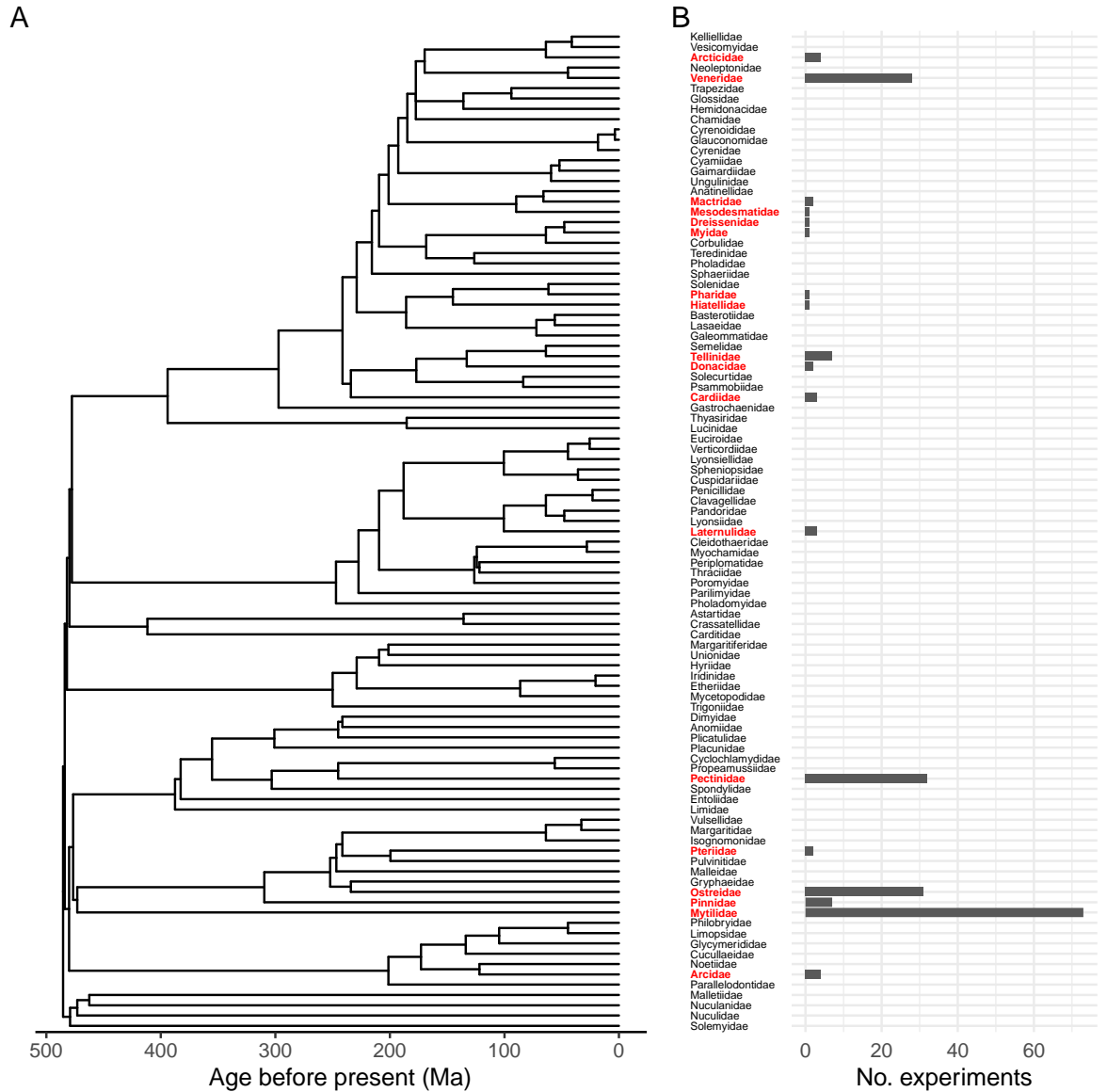
Figure 2. Experimental representation of 18 Bivalvia families in 203 unique experimental setups from 79
relevant articles found in Web of Science Core Collection. **A**, time-scaled 'budding II' phylogeny of
extant Bivalvia from Crouch et al. (2021). The root age is 485.4 Ma. **B**, number of experiments
representing each extant family.

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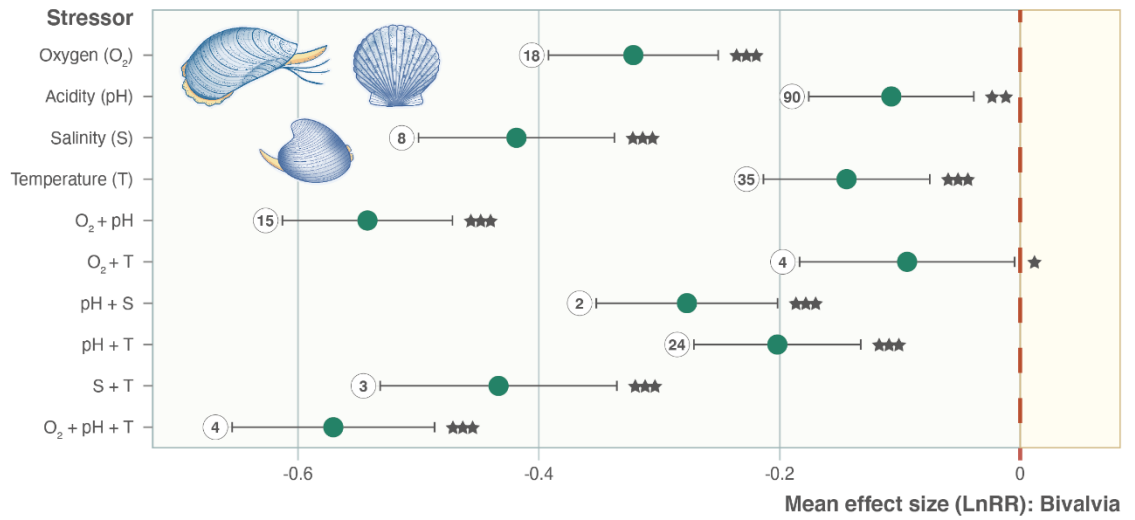
804   **Figure 3.** Effect size (log-response ratio, LnRR) for individual and combined effects of temperature (T),
805   acidity (pH), oxygenation (O₂), and salinity (S) as stressors on bivalve growth rates. **A**, for all
806   Bivalvia. **B**, for Bivalvia excluding Veneridae. Points represent mean effect size with error bars
807   indicating 95% confidence intervals. Numbers indicate number of included experiments.
808   Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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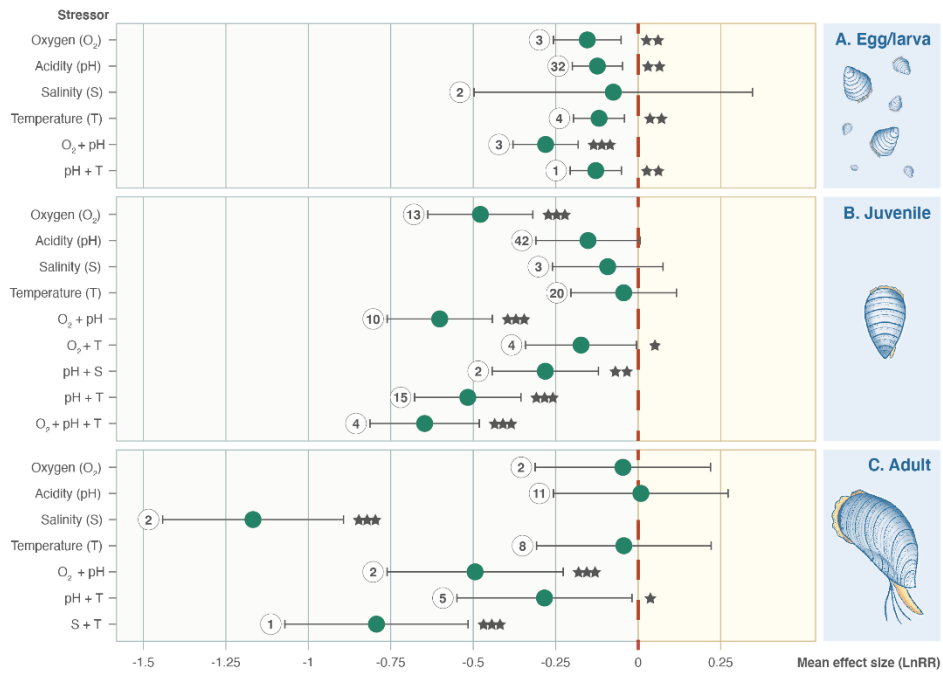
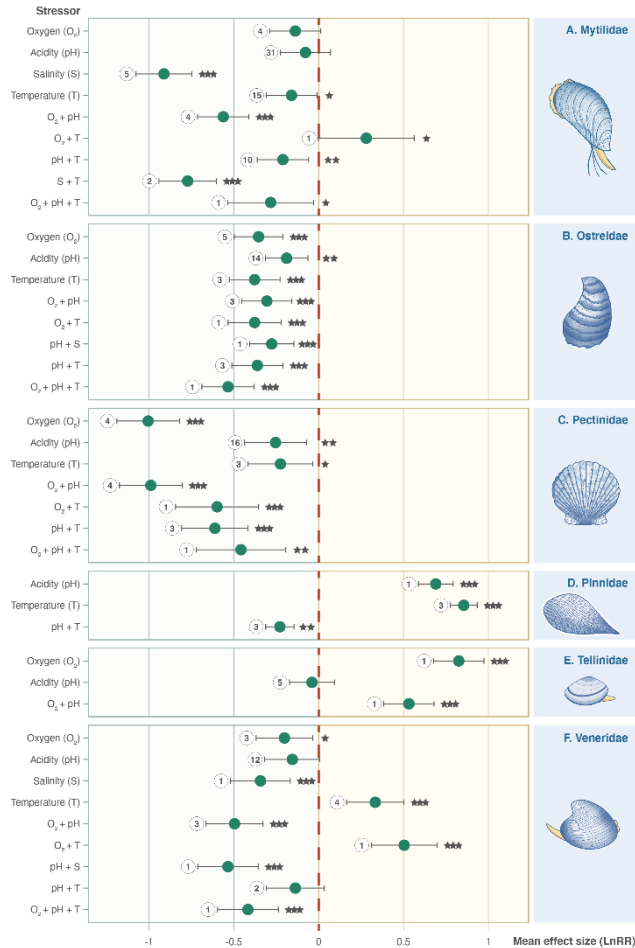
Figure 4. Effect size (log-response ratio, LnRR) for individual and combined effects of oxygenation (O$_2$), acidity (pH), salinity (S), and temperature (T) as stressors on Bivalvia growth rates at different life stages (egg/larval, juvenile, adult). Points represent mean effect size with error bars indicating 95% confidence intervals. Numbers indicate number of included experiments. Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

819   **Figure 5.** Effect size (log-response ratio, LnRR) for individual and combined effects of oxygenation
820   (O_2), acidity (pH), salinity (S), and temperature (T) as stressors on Bivalvia growth rates separated
821   by family. **A**, Mytilidae. **B**, Ostreidae. **C**, Pectinidae. **D**, Pinnidae. **E**, Tellinidae. **F**, Veneridae.
822   Points represent mean effect size with error bars indicating 95% confidence intervals. Numbers
823   indicate number of included experiments. Significance is indicated with asterisks: * $P < 0.05$, ** $P <$
824   0.01, *** $P < 0.001$.

827   **Table 1.** Representation of bivalve families across 203 experimental studies included in this meta-analysis.

Family	Number of experimental set-ups
Arcidae	4
Arcticidae	4
Cardiidae	3
Dinacidae	2
Dreissenidae	1
Hiatellidae	1
Laternulidae	3
Mactridae	2
Mesodesmatidae	1
Myidae	1
Mytilidae	73
Ostreidae	31
Pectinidae	32
Pharidae	1
Pinnidae	7
Pteriidae	2
Tellinidae	7
Veneridae	28

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830   **Table 2.** Single and combined stressor effect sizes from a meta-analysis of 203 experimental set-ups for

831   bivalves (log-response ratio, LnRR). Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** P

832   < 0.001.

Stressor	Sample size	Mean effect size (R)	95% confidence interval		P-value
			lower	upper	
Oxygenation (O_2)	18	-0.3214	-0.3916	-0.2513	<.0001
Acidity (pH)	90	-0.1077	-0.1762	-0.0392	0.0022
Salinity (S)	8	-0.4184	-0.4997	-0.3372	<.0001
Temperature (T)	35	-0.1445	-0.2135	-0.0756	<.0001
O_2 + pH	15	-0.5421	-0.6126	-0.4716	<.0001
O_2 + T	4	-0.0944	-0.1836	-0.0052	0.0382
pH + S	2	-0.2771	-0.3522	-0.2019	<.0001
pH + T	24	-0.2021	-0.2712	-0.1330	<.0001
S + T	3	-0.4335	-0.5316	-0.3354	<.0001
O_2 + pH + T	4	-0.5703	-0.6542	-0.4864	<.0001

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