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 shows 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 motile taxa but this difference between the two taxa 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

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

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

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

77   habitat suitability for other benthos.

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

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

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

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

82   2020), and disrupt larval settlement patterns and spawning (Bascur et al., 2020; Figueirodo et al., 2022). In

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

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

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

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

87   Currently our understanding of how bivalves will respond to various climate change stressors is based on field

88   studies and lab-derived experimental data focused largely on ocean acidification and response to warming,

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

90   Eymann et al., 2020). Synthesis work through meta-analysis supports the notion that bivalves overall will

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

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

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

94   organisms (Kroeker et al., 2010; Maynou et al., 2020; Knights et al., 2020; Sampaio et al., 2021). However,

95   these analyses have been conducted at high taxonomic rankings, e.g., examining changes at phylum level,

96   thereby risking averaging differential outcomes at finer taxonomic resolution. Organisms experience disparate

97   responses to environmental drivers based on local phenotypic expression (Dong et al., 2017) and environmental

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

99   on local microclimates and adaptation (Montalto et al., 2016). 'Clumping' these diverse responses make high

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

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

102   the granularity (the level of detail) and diversity of responses this group exhibits.

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

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

105   explores 10 stressor combinations (found in table 2), greatly expanding earlier work examining only four

106   stressors (Sampaio et al. 2021). For the first time in a meta-analysis of impacts of marine climate change, we

107   explore taxonomic sensitivities within a family and identify large gaps in taxonomic understandings of how

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

109   to climate change is intrinsic to the group or driven by specific taxa. We focused on studies that emphasize

110   bivalve growth rates; a commonly studied trait that offers insight into organism vulnerability to answer how

111   these growth rates are impacted by climate stressors, and whether different families or developmental stages are

112   more sensitive to 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 code is accessible in the Github folder https://github.com/georgehoppit/Bivalve-meta-analysis. Article data can be found at 10.5281/zenodo.10118176.

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. The publication date of 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 (according to what study authors stated were plausible conditions based on study location/ bivalve examined), 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 is often recorded just as a percentage

148   which is not sufficient for this type of analysis, as meta-analysis requires means, standard deviation, and sample

149   size being reported to calculate effect size.

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

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

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

153   directly comparable to absolute measures of growth. Only studies where the bivalves were fed ad libitum and

154   studies on larvae that develop without feeding were included, as nutrient intake has a strong impact on growth

155   (Norkko et al., 2005; Thomsen et al., 2013; Ballesta-Artero et al., 2018). Study sample size, mean growth value

156   of both control and treatment groups, and indication of the variation of growth values (confidence intervals,

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

158   data could not be combined with absolute measurements within the Metafor package. Data were extracted

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

160   WebPlotDigitizer v. 4.4 (Rohatgi, 2022). Control values for climate stressors for each article were based on

161   article author's determination of control conditions for their respective bivalve. Climate stressor values were

162   based on realistic end of century projections based on article author's determination for that experimental setup

163   or study location. The phylogeny and column chart (Fig. 2) were plotted using R v. 4.1.0 (R Core Team, 2021)

164   and the packages ggplot2 v. 3.3.5 (Wickham, 2016), ggtree v. 3.2.1 (Yu et al., 2017), ape v. 5.6.1 (Paradis and

165   Schliep, 2019), and patchwork v. 1.1.1 (Pederson, 2020). The topology is taken from the time-scaled 'budding

166   II' family-level phylogeny of Crouch et al. (2021).

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

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

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

170   extant family.

171   **2.2 Statistical analysis**

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

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

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

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

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

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

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

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

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

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

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

183   corresponds to a statistically insignificant effect. Linear multivariate meta-analytical models (function rma.mv)

184   were used to calculate mean effect sizes of climate stressor impacts on bivalve growth rates for three subsets of

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

186   Significant results were identified when model 95% confidence intervals did not overlap zero effect size.

187   Models used random intercepts for articles and species intercepts for each treatment to compensate for

188   similarities introduced by studies, as data originating from the same experimental setup or from the same species

189   are assumed to be more likely similar than data from different articles or species. Residual heterogeneity (QE),

190   calculated as part of the meta-analytical models, was used to determine whether additional study moderators not

191   considered might be influencing study results (Hedges and Olkin, 1985).

192   Publication bias was tested using Egger's regression test. Following Habeck and Schultz (2015), function

193   rma.mv was extended using the square root of effect size variance in the model moderator variables to conduct a

194   regression test. Egger's regression test looks at the symmetry of the data published and determines whether there

195   are statistically 'missing' studies within the spread of the papers published (Egger et al., 1997). We used meta-

196   regression to determine whether published results had changed over the 25 years from which studies had been

197   collated, using study year as a moderator variable. This would indicate whether increasingly detailed knowledge

198   has altered the overall picture with regards to the effect of each climate change stressor.

3 Results

200   Our literature search produced the most detailed examination of bivalve growth rates under multiple climate

201   stressors to date. We identified 79 studies with 203 unique experiments meeting the criteria, comprising 18

202   families and 37 species (Figs 1, 2; Table 1). Sampling of families was highly uneven: Mytilidae make up 36% of

203   the experiments and 81% of the experiments include just four families: Mytilidae, Ostreidae, Pectinidae, and

204   Veneridae; including Pinnidae and Tellinidae increases the total to 88% (Table 1).

205   We find consistent and significant negative effects of all single stressors and most combinations acting on the

206   entire class Bivalvia, in agreement with previous meta-analyses (Fig. 3; Table 2). At the class level, many

207   combinations of stressors increase the negative effect on growth in a synergistic way (Fig. 3; Table 2). For

208   example, pH and O_2 treatments are greater in combination than either alone, as were salinity + temperature and

209   pH + temperature. The effect of pH + salinity is intermediate between that of the two single stressors, , while

210   O_2 + temperature causes a smaller effect than either single stressor. The combination of three stressors, O_2 +

211   pH + temperature, causes the strongest negative effect size to both individual stressors and any combinations.

212   While low heterogeneity is preferable in terms of data validity it is rarely achievable in environmental meta-

213   analyses. Therefore, the significant heterogeneity in the data is expected given it is drawn from so many

214   disparate studies: QE = 300509.7155, df = 148, $P < 0.0001$.

215   [Figure 3] Effect size (log-response ratio, LnRR) for individual and combined effects of temperature (T), acidity

216   (pH), oxygenation (O_2), and salinity (S) as stressors on bivalve growth rates for all Bivalvia. Points represent

217   mean effect size with error bars indicating 95% confidence intervals. Numbers indicate number of included

218   experiments. Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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

220   [Table 2] Single and combined stressor effect sizes from a meta-analysis of 203 experimental set-ups (log-

221   response ratio, LnRR). Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Thirty-one of the 203 experimental set-ups involve adult Bivalvia, 14 on unspecified ages/stages, 45 on eggs/ larvae, and the remaining 113 focused on juvenile stages. Separating by growth stage shows that the combination of pH and O_2 stressors causes significantly negative effect size at all points in the life cycle (Fig. 4). Salinity is not an important stressor for larval or juvenile bivalves but causes a reduction in growth in adults. Juveniles show responses to most stressors, whereas egg/larvae and adult bivalves have much smaller sample sizes, and do not show significant effect size responses across the stressors.

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

[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: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

[Figure 5] 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 separated by family. **A**, Mytilidae. **B**, Ostreidae. **C**, Pectinidae. **D**, Pinnidae. **E**, Tellinidae. **F**, Veneridae. Points represent mean effect size with error bars indicating 95% confidence intervals. Numbers indicate number of included experiments. Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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

4 Discussion

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

259   bivalve responses to a true global picture. Furthermore, our analysis hopes to move synthesis literature studies

260   towards higher taxonomic understanding of an individual group's responses to future ocean conditions, by

261   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

263   Our findings clearly show that growth rates in Bivalvia are negatively affected by climate stressors (Fig. 3). By

264   exploring responses at family level, we confirm our hypothesis that negative growth responses to climate change

265   are likely inherent to this taxonomic group as a whole, despite the experimental bias in the published literature

266   towards key families. Previous meta-analyses that incorporated bivalves did not focus on the group specifically

267   but include them alongside numerous other taxa (i.e., within phylum Mollusca) (Harvey et al., 2013; Kroeker et

268   al., 2013; Sampaio et al., 2021). These analyses found little evidence for significant effect sizes except in a few

269   single stressors (pH and temperature: Harvey et al., 2013; hypoxia: Sampaio et al., 2021). Unsurprisingly, the

270   effect of temperature on bivalve growth is the most studied stressor in the experiments included in our meta-

271   analysis (35 experiments: Fig. 3) – a feature seen in other studies of the effects of marine climate change

272   (Borges et al., 2022). This bias is likely because temperature-altering experiments require less complex

273   equipment and sensors than pH or oxygen manipulation, have been performed over decades, and target the most

274   obvious effect of climatic change i.e., global warming. Inclusion of a substantially greater number of previous

275   experiments within our meta-analysis (over 200 specific bivalve growth observations versus 45, 46, and 34

276   Mollusca for Kroker et al. (2013), Harvey et al. (2013), and Sampaio et al. (2021) respectively) confirms that all

277   single climate stressors show significant negative effect sizes in bivalves (Fig. 3). Our analysis also shows that

278   in many cases this effect prevails when individual growth stages (Fig. 4) and the families containing the largest

279   number of experiments or observational data (Table 1; Fig. 5) are examined separately.

280   An important result is the identification of synergistic, additive, and antagonistic effects between different

281   stressors which in all cases in our analysis increase the negative response (Gobler et al., 2014; Stevens and

282   Gobler, 2018) (Table 2). For example, we identify significant negative effect sizes for O_2 + pH, and temperature

283   + salinity when analysing overall bivalve responses (Fig. 3). The combination O_2 + pH has a stronger negative

284   synergistic effect size compared to either oxygen or pH individually in all analyses (Figs. 3-5). Decreases in pH

285   restrict growth via restricting availability of CO_3^{2-} and increasing HCO^{3-} ions making shell building more

286   metabolically expensive and increasing shell dissolution (Ivanina et al., 2013; Byrne and Fitzer, 2019). Internal

287   tissues also require buffering against pH changes, incurring a further metabolic cost (Byrne and Fitzer, 2019).

288   Marine deoxygenation impacts metabolism, reducing an organism's ability to respond to these increased

289   metabolic requirements of shell generation and tissue buffering under a more acidic environment. Therefore, the

290   increased impact from combining these two stressors confirms our physiological understanding of the organism

291   (Pörtner and Farrell, 2008).

292   Mean effect sizes for each climate stressor differ between families within Bivalvia. Consequently, the effects of

293   climate change on this group will be habitat dependant and alter the taxonomic composition of coastal

294   ecosystems. The four most investigated families in our dataset (Mytilidae, Osteridae, Pectinidae, and Veneridae)

295   exhibit consistent negative growth responses to climate stressors (Fig. 5). Exceptions exist for oxygen and

296   temperature changes for Mytilidae and Veneridae and temperature increase for Veneridae where we find mixed

297 responses which are discussed in more detail below (section 4.3). However, pH causes antagonistic decreases in
298 growth rate across these main families (Fig. 5), suggesting that any temperature-driven growth increases are
299 unlikely to occur under future projected conditions.

300 Importantly, our examination of publication bias in the experimental literature shows studies finding that
301 statistically significant results are more likely to be published than insignificant results. The likely explanation is
302 there may be a bias in the experimental literature as authors may prioritise the publication of papers with
303 significant results leading to fewer papers, or later published papers, with negative results (Nakagawa et al.,
304 2022). Such a publication bias is well documented across many fields, but hard to explicitly prove (Van Aert et
305 al., 2019). While this bias likely skews our results towards collective negative growth rates, we can still be
306 confident in our conclusions given the consistent decreases in bivalve growth rates across all stressor
307 permutations. Research finding bivalves with neutral responses to climate change should be more readily
308 published, as this will produce a better understanding of future marine ecosystems and allow scientists and
309 conservationists to identify species or areas of resilience.

310 **4.2 Different bivalve life stages and ecologies show distinct responses to climate stressors**

311 Climate change will be acting on each part of the development of an organism. In bivalves, these different life
312 stages have different habitats and mobility from motile larvae to sessile adults. Our results on how different
313 bivalve life stages are affected by a range of climate stressors generally confirm previous meta-analyses across
314 calcifying organisms. Our results suggest early life stages are the most vulnerable to a specific set of stressors
315 and that the threat diminishes as organisms mature, supporting analyses by Sampaio et al. (2021) and Kroeker et
316 al. (2013) which focused on the impacts of ocean acidification. It is important to note, though, that the earlier
317 developmental stages are more mobile and hence able to relocate their niche to track their environmental needs.

318 Combined climate stressors (e.g., pH + temperature, O_2 + pH, salinity + temperature) showed negative
319 responses across all growth stages. Our findings oppose those of Harvey et al. (2013) who suggested limited
320 variation in organism growth responses between life stages exposed to individual and synergistic ocean
321 acidification and warming. In contrast to our analysis, their data were pooled from multiple phyla reiterating the
322 need to avoid too much pooling and averaging in meta-analysis.

323 Most studies in our dataset, especially those on the families that dominate our meta-analysis (Fig. 4), are
324 focused on larval or juvenile stages. This likely explains some of the negative impacts on growth as for example
325 shell mineralogy influences the impact of pH changes. Amorphous calcium carbonate secreted by larval
326 bivalves is 50-times more susceptible to dissolution than either calcite or aragonite (Bressan et al., 2014).
327 Changes to body size or decreased shell thickness could increase vulnerability to predation (Sadler et al., 2018).
328 Non-significant effects of lowered pH alone in adult bivalves likely result from more diverse shell mineralogy
329 (Weiss et al., 2002), or the effects of a more robust adult shell (Beadman et al., 2003, or from individuals found
330 in microhabitats with naturally low water pH where generational acclimation to low pH may have occurred
331 (Thomsen et al., 2010; Hiebenthal et al., 2013).The adult's lifestyle, which includes for some taxa exposure to
332 air and/or closed valves while respiring naturally results in high variability of pH in the calcifying fluid and
333 therefore the pH changes in the experiments maybe resulted in relatively less stress compared to earlier
334 developmental stages. Most of the adult experiments included in our meta-analysis were on aragonitic

individuals or on mixed aragonitic-calcitic Mytilidae and Pectinidae. Only one study (Lemasson et al., 2018) included two genera of adult oysters (Family Ostreidae) which construct their shells primarily from calcite (Stenzel, 1963), a more stable carbonate polymorph.

Our results indicate that adults have an increased susceptibility to salinity changes when compared to juvenile and egg/larval stages, suggesting habitats projected to experience decreased salinity due to increased seasonal runoff or enhanced evaporation in a restricted setting (Robins et al., 2016) may become challenging for adult bivalves. It is important to note though that fewer experiments were conducted exploring salinity (13 experiments tested salinity, out of 203 unique experimental setups), resulting in a low number of experimental studies and a greater need for determining the interaction with other drivers such as pH, temperature, and oxygen. Increased sensitivity to climate stressors at different life stages has implications 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 this 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, motile 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 motile (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 motile 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 as well as oxygen-limited (Green et al., 2013; Stevens and Gobler, 2018) suggesting some resilience to these conditions. Both semi-infaunal Pinnidae and infaunal Veneridae also show significant positive effect sizes in response to warming (Fig. 5). It has been hypothesised that an infaunal habitat may reduce immediate susceptibility of bivalves to warming, as the substrate may act as a thermal refugia (Zhou et al., 2022). Taken together, these results suggests that lifestyle and habitat will control the ability of bivalves to evade climate stressors. However, interpreting the general role of ecology in providing resilience is complicated by the currently small number of experiments or observations on infaunal taxa, further highlighting the need for additional data on the effects of environmental stressors on the growth of burrowing bivalves and those from a wider range of specific shallow marine habitats.

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

Our meta-analysis clearly reveals that available data on bivalve growth responses to climate stressors contain a number of biases, likely due to the commercial importance of certain families (e.g., Mytilidae, Ostreidae, Pectinidae, Veneridae) and individual species within them for aquaculture and common ecosystem services (e.g., van der Schatte Olivier et al., 2020), as well as ease of access to specimens. Many experiments document that bivalve specimens were sourced from commercial aquaculture facilities. A number of families included in our meta-analysis are represented only by individual experiments: for example, Dreissenidae, Hitellidae, Mesodesmatidae, Myidae and Pharidae. Comparison of the number of experiments vs. bivalve phylogeny shows that entire families have no documented experimental or observational work investigating climate stressor impacts on growth (Fig. 2). This confirms our hypothesis that even though bivalves are considered a well-studied group, the signals detected in the literature are often driven by a subset of taxa.

While our results are based on studies with varying experimental protocols, our approach is consistent with other meta-analyses (e.g., Hoppit and Schmidt 2022; Harvey et al., 2013; Kroeker et al., 2013; Sampaio et al., 2021). As we are using studies with disparate protocols and experimental measurements, the meta-regression analyses we conducted (Appendix B; Fig. B1) show that effect sizes across studies and experimental setups have not changed across time. This result suggests that variability in research practices does not impact our results. Some stressor combinations have low sample sizes, as multi-factor experiments are notoriously work intensive and difficult to perform. These lower numbers decrease confidence in those specific observations and

410 conclusion, and highlights the importance of considering a wider range of drivers than the most frequently
411 assessed combination of warming and acidification alone.

412 Our findings are also geographically biased towards the global north. Most studies clearly gathered organisms
413 and data from the coasts of the USA, Europe, or China, resulting in important portions of the global ocean like
414 the Caribbean or African coasts being unrepresented in these data. While our meta-analysis focused specifically
415 on bivalve growth, this result emphasizes the unevenness of experimental research into this group. If this
416 disparity of understanding is not rectified then implementing effective climate change adaptation and mitigation
417 strategies and upscaling these results to ecosystem-scale changes are challenging.

418 While our experimental sample is larger than previous meta-analyses, these biases also leave much uncertainty
419 about how responses will scale up from commercially important species to other, rarely studied groups of
420 bivalves, which while of lesser importance for aquaculture or commercial exploitation, may act as keystone
421 species within fragile marine ecosystems. This further limits the quality and quantity of available information
422 that conservationists and stakeholders need to develop strategies to safeguard marine social-ecological systems.
423 Given our findings overwhelmingly suggest that bivalves as a group (Figs 3, 4) and common, well-studied
424 families (Fig. 5) will likely experience decreased growth rates under protected projected end-of-century
425 conditions, how likely is it that families or species with no current experimental observations will also follow
426 this trend? Additional experimental and observational work on specific bivalve species and families is urgently
427 required which would greatly assist in developing conservation strategies for this important group of marine
428 calcifiers.

5 Conclusions

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

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

443 3. By focusing on a few commercially relevant taxa, these commonly studied families are creating a bias
444   in the literature. A large proportion of bivalve families lack any rigorous experimental or observational
445   data resulting in large knowledge gaps hampering conservation efforts. Available data on bivalve
446   response to climate stressors also contain large biases towards early or juvenile growth stages and
447   commercially important species from the global north. Our results should be replicated for other

| 448 | commonly studied marine organisms like seaweeds or echinoderms to assess if taxonomic bias drives |
| 449 | commonly assumed physiological responses to climate change. |

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453 **Appendices**

454 **Appendix A**

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

456 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.
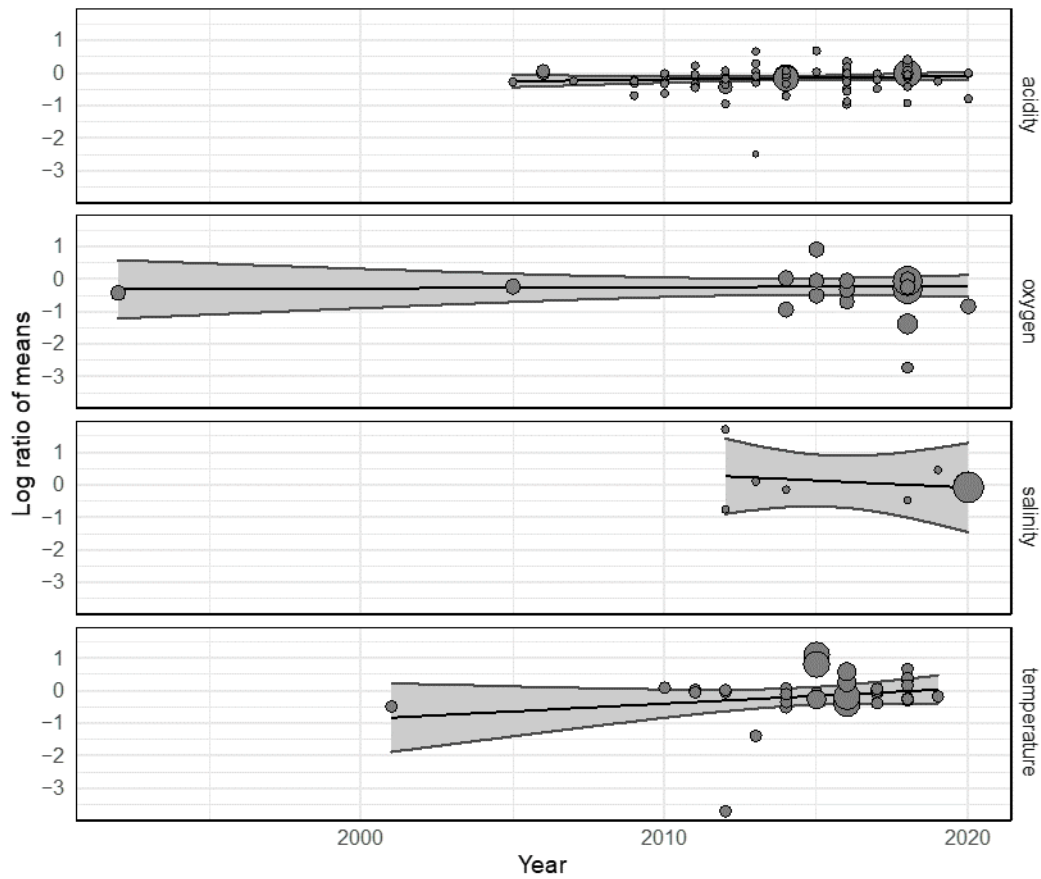
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472 **Table B1.** Regression analysis of publications by stressor per year.

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

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497 **Code availability**

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

499 **Data availability**

500 Data used for analyses available at https://github.com/georgehoppit/Bivalve-meta-analysis OR can be found at
501 10.5281/zenodo.10118176.

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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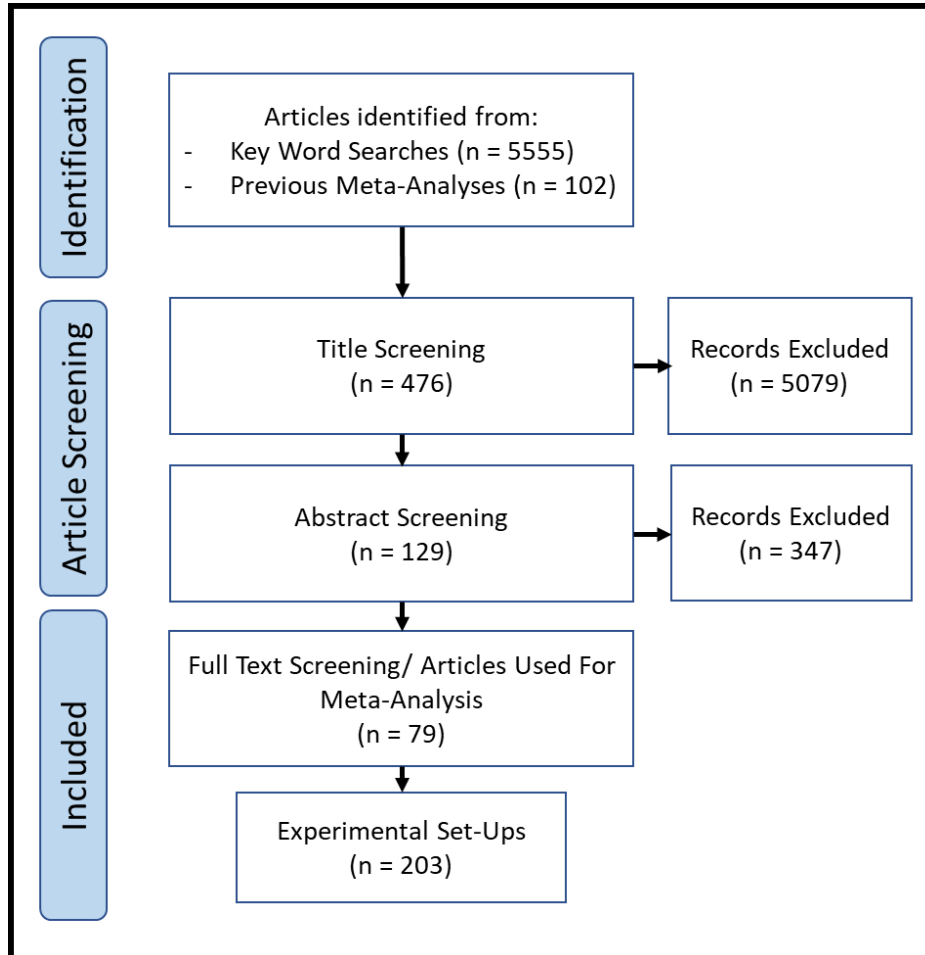807 710, p.136280, https://doi.org/10.1016/j.scitotenv.2019.136280, 2020.

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816 **Figure 1.** PRISMA flow diagram of screening process for the present study following recommended
817   guidelines (Page et al., 2021). Relevant articles on Bivalvia growth experiments were identified from
818   the Web of Science Core Collection using a series of keywords (see main text). Screening resulted in
819   the identification of 79 relevant articles with 203 experimental set-ups that were included in our
820   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
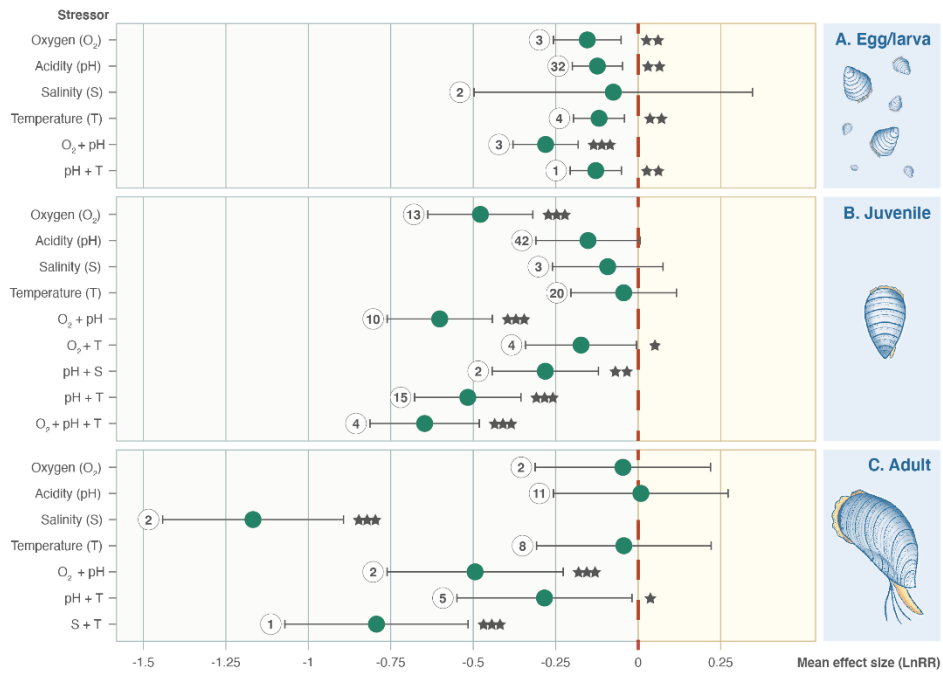representing each extant family.
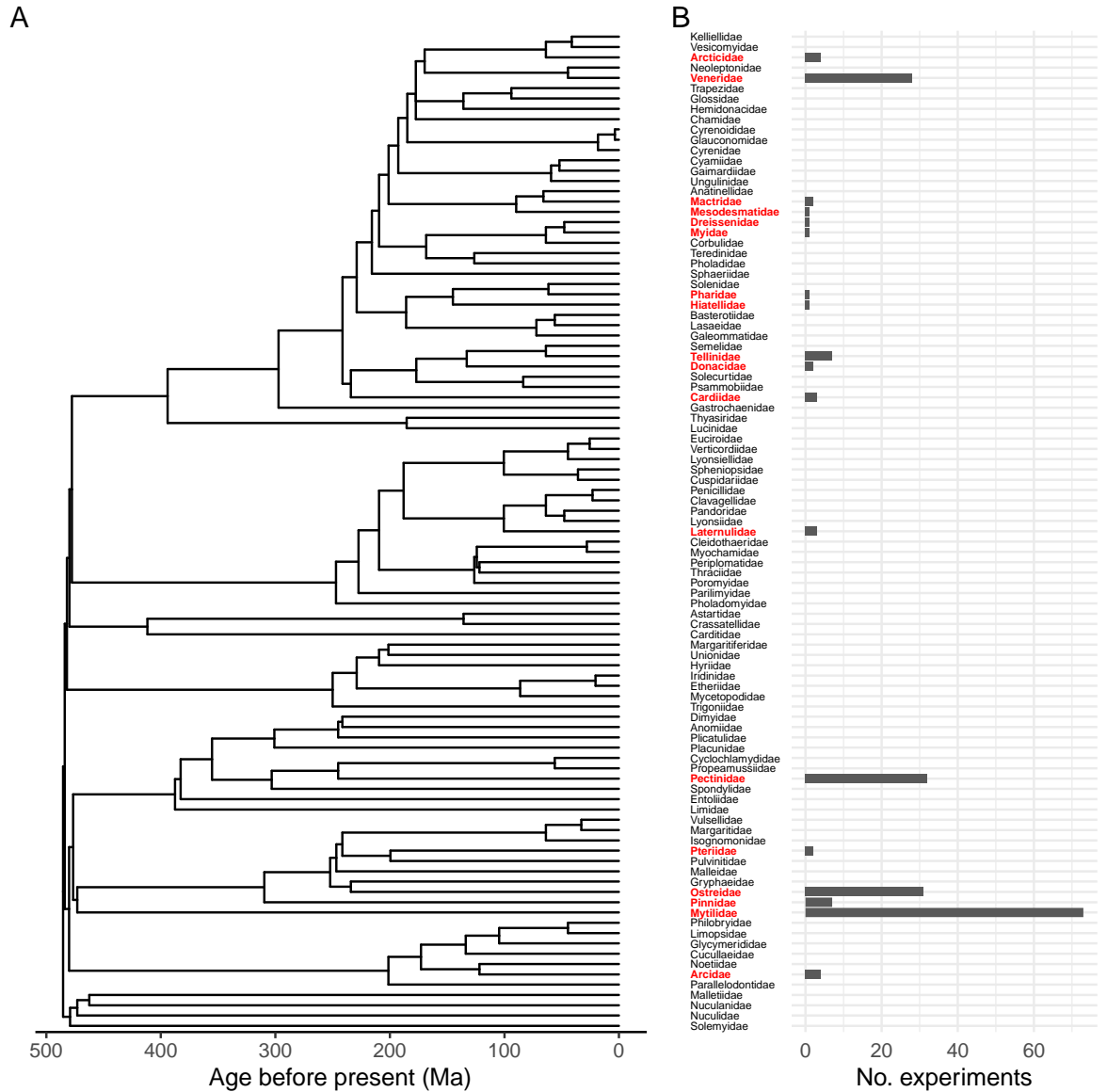
830 **Figure 3.** Effect size (log-response ratio, LnRR) for individual and combined effects of temperature (T),
831 acidity (pH), oxygenation (O_2), and salinity (S) as stressors on bivalve growth rates. **A**, for all
832 Bivalvia. **B**, for Bivalvia excluding Veneridae. Points represent mean effect size with error bars
833 indicating 95% confidence intervals. Numbers indicate number of included experiments.
834 Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
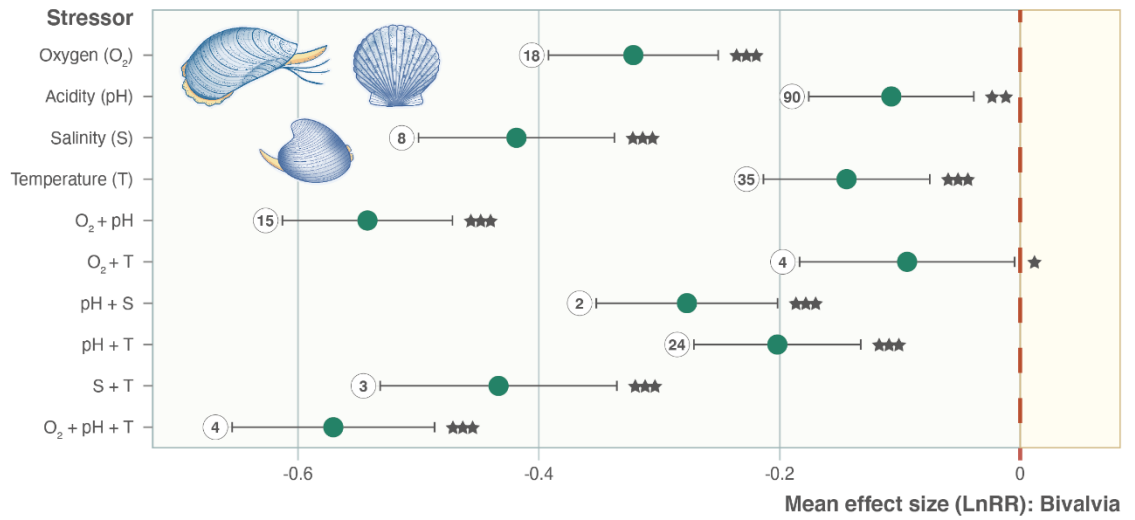

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838   **Figure 4.** Effect size (log-response ratio, LnRR) for individual and combined effects of oxygenation

839   (O_2), acidity (pH), salinity (S), and temperature (T) as stressors on Bivalvia growth rates at different

840   life stages (egg/larval, juvenile, adult). Points represent mean effect size with error bars indicating

841   95% confidence intervals. Numbers indicate number of included experiments. Significance is

842   indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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Figure 5. Effect size (log-response ratio, LnRR) for individual and combined effects of oxygenation (O₂), acidity (pH), salinity (S), and temperature (T) as stressors on Bivalvia growth rates separated by family. **A**, Mytilidae. **B**, Ostreidae. **C**, Pectinidae. **D**, Pinnidae. **E**, Tellinidae. **F**, Veneridae. Points represent mean effect size with error bars indicating 95% confidence intervals. Numbers indicate number of included experiments. Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
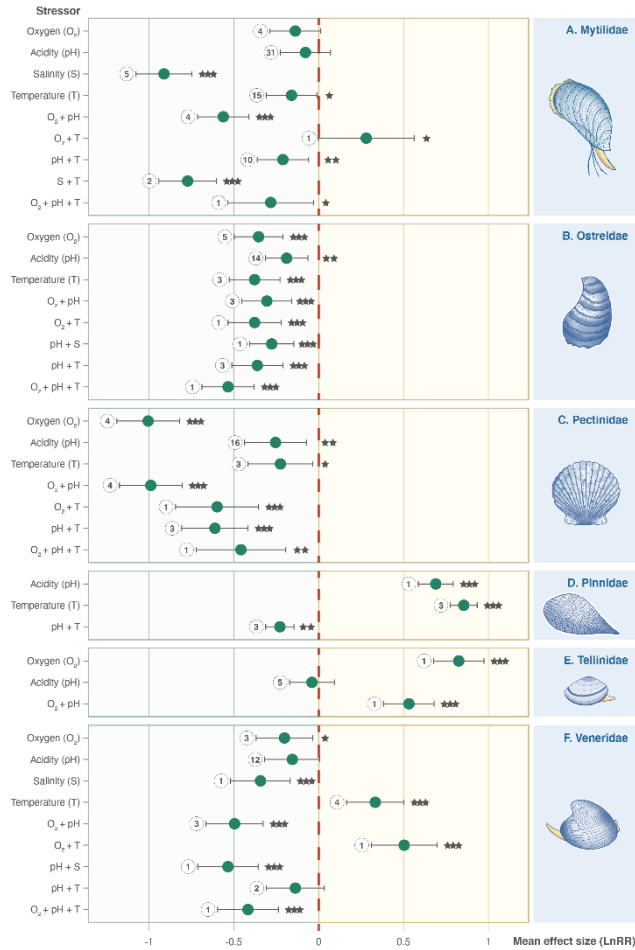
853 **Table 1.** Representation of bivalve families across 203 experimental studies included in this meta-analysis.

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

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

858 < 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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