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 ~~a range of~~ climate change on ~~individual~~ marine ~~organisms~~ organismstaxa ~~have been~~are increasingly ~~being analysed~~documented in laboratory and experimental studies. The use of different taxonomic groupings, and assessment of ~~different~~ a range of processes, though, makes identifying overall trends challenging. Meta-analysis ~~has~~have been used to determine ~~these~~ general trends but ~~their~~ coarse taxonomic granularity, and may mask phylogenetically ~~different~~ specific responses. Bivalve molluscs ~~are~~are a data rich clade of ~~an~~ecologically and economically important calcifying marine ~~important data-rich clade~~taxa, allowing for assessment of ~~individual~~ species--specific vulnerability ~~and~~across developmental stages. Drawing on the large body of available literature, ~~w~~We ~~conduct a~~use meta-analysis of 203 unique experimental setups, ~~and~~to ~~10 climate change stressor combinations, to~~ examine how bivalve growth ~~rates~~ respon~~ds~~sesd to increased water temperature, acidity, deoxygenation, and changes to salinity in 10 climate change stressor combinations. This is the ~~, providing the~~ most complete examination of bivalve ~~s~~responses to date, and~~, and combinations of these drivers. Results~~ show~~s~~ that anthropogenic climate change will disproportionally affect ~~different~~ particularsome families ~~of bivalves disproportionally but almost unanimously negatively,~~ suggesting taxonomic ~~granularity~~differentiation ~~in what is considered a well understood group regarding~~ ~~their~~ climate change response. ~~Specifically~~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. ~~However~~O, ~~o~~ur analysis ~~suggests~~show ~~past work confirming~~that earlier studies showing negative impacts ~~these results~~on bivalves are driven by only 3-4 well studied commercially important ~~bivalve~~ families. Despite the taxonomic differentiation, a~~All~~most all drivers and their combinations have significant negative effects on growth~~, suggesting this is inherent to the group~~. The synergistic impacts of ~~Combined d~~deoxygenation, acidification, and temperature ~~shows~~ results in the largest negative effect size. ~~Eggs/larval bivalves are more vulnerable overall than either juveniles or adults.~~ 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 ~~of habitats~~ creates gaps in understanding of global impacts on these economically important foundation organisms.

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1 Introduction

~~Predictions of R~~Rising levels of atmospheric carbon dioxide ~~indicate~~ will alter ~~that~~ the marine environment ~~will significantly alter~~ 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). ~~The heterogeneric nature of change in each parameter will result in different combinations of stressors and varying extent of the effect of each stressor on communities in different areas. It is increasingly important to identify how stressors work both alone and in different combinations.~~ 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 ~~with shallower waters~~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 heterogene~~ous~~~~eric~~ nature of change in each environmental driver will result in location-specific combinations and extent~~d~~ of stressors ~~.~~. This complexity presents a significant ~~challenging~~ challenge for decision--mak~~ers~~ing ~~in~~for 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~~regions~~. ~~as interaction of stressors, though increasingly recognised in the literature, are still underexplored.~~

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

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74 biodiversity (Fariñas-Franco and Roberts, 2014). Complex reef frameworks and individual bivalve shells in soft-
75 substrate environments can act as microhabitats to other invertebrates through creation of new hard substrates
76 and by altering local flow regimes or even temperature (McAfee et al., 2017). Filter-feeding bivalves can reduce
77 pollution and clear large particulates out of the water column (Smyth et al., 2018). They enhance or change local
78 marine productivity (Donnarumma et al., 2018; Strain et al., 2021) via selective removal of specific species of
79 phytoplankton (Ward and Shumway, 2004). Deposition of bivalve faeces and pseudofaeces, along with
80 burrowing activity of motile infaunal deposit or suspension feeders, can lead to changes in the local flux or
81 enrichment of organic matter into the sediment and biogeochemical cycling (Smyth et al., 2013), and ultimately
82 habitat suitability for other benthos.

83 Anthropogenic pressures including coastal development, overfishing, and pollution have resulted in
84 demonstrable decreases in global bivalve populations (e.g., De Groot, 1984; Baeta et al., 2014). Akin to other
85 calcifying invertebrate organisms, it has been hypothesised that the physiochemical changes resulting from
86 climate change will reduce bivalve growth, impair maintenance of shells (Maynou et al., 2020; Knights et al.,
87 2020), and disrupt larval settlement patterns and spawning (Bascur et al., 2020; Figueirodo et al., 2022). In
88 recognition of the environmental, social, and economic benefits bivalves produce, and the current and future
89 pressures they face, the group is a focus for conservation efforts (zu Ermgassen et al., 2020; Buelow and
90 Waltham, 2020, Gagnon et al*.,* 2020). However, despite extensive study there remain ~~significant~~ important gaps
91 in our understanding of their response to climate change across different bivalve families.

92 Current understanding of how bivalves will respond to various climate change stressors is based on field studies
93 and lab-derived experimental data focused largely on ocean acidification and response to warming, generally
94 observing negative responses (e.g., Beukema et al., 2009; van Colen et al., 2012; Addino et al., 2019; Eymann et
95 al., 2020). Synthesis work through meta-analysis supports the notion that bivalves overall will respond
96 negatively to climate change (Kroeker et al., 2013; Harvey et al., 2013; Sampaio et al., 2021; Hoppit and
97 Schmidt, 2022; Leung et al., 2022). These studies have shown that the synergistic effects of ocean acidification,
98 ocean warming, and an increase in hypoxic events decrease the growth rates of calcifying marine organisms
99 (Kroeker et al., 2010; Maynou et al., 2020; Knights et al., 2020; Sampaio et al., 2021). However, these analyses
100 have been conducted at high taxonomic rankings, e.g., examining changes at phylum level, thereby ~~they~~ risking
101 averaging differential outcomes at finer taxonomic resolution. Organisms experience ~~though~~ disparate responses
102 to environmental drivers based on local phenotypic expression (Dong et al., 2017) and environmental influences
103 (Genner et al., 2010) resulting, for example, in species-specific mortality risk to extreme heat based on local
104 microclimates and adaptation (Montalto et al., 2016). 'Clumping' these diverse responses make hi~~Hi~~gh level
105 analyses and their generalized trends ~~can be~~ difficult to interpret ~~due to clumping diverse responses into~~
106 ~~generalized trends~~ (Helmuth et al., 2005). ~~Organisms experience disparate responses to environmental drivers~~
107 ~~based on local phenotypic expression (Dong et al., 2017) and environmental influences (Genner et al., 2010)~~
108 ~~resulting, for example, in species-specific mortality risk to extreme heat based on local microclimates and~~
109 ~~adaptation (Montalto et al., 2016).~~ Therefore, our current understanding of how bivalves respond to climate
110 change based on broad scale synthesis work might not capture the granularity and diversity of responses this
111 group exhibits.

112 We aimed to fill this gap by employing a meta-analysis methodology to explore the effects of marine climate
113 stressors, and combinations thereof, on bivalve growth at both the whole-group and family levels. Our analysis
114 explores 10 stressor combinations, greatly expanding earlier work examining only four stressors (Sampaio et al.
115 2021). For the first time in a meta-analysis of impacts of marine climate change, we explore taxonomic
116 sensitivities within a family and identify large gaps in taxonomic understandings of how response to climate
117 change in this very well-studied group. We address the question ofOur aim is to determine whether a negative
118 response to climate change is intrinsic to the group or driven by specific taxa. We focused on studies that
119 emphasize bivalve growth rates; a commonly studied trait that offers insight into organism vulnerability to
120 answer how these growth rates are impacted by climate stressors, and whether different families or
121 developmental stages are more sensitive to climate stressors than others. Additionally, we examine the range of
122 experimental work assessing bivalve sensitivity to climate change to understand which families are most
123 representedtaxonomic diversity of the experiments available in the published literature for meta-analysis. We
124 We hypothesise that a focus on commercially important bivalve taxa may be creating a likely bias in current
125 observations. Our findings encourage a new approach to meta-analysis by moving towards more differentiated
126 taxonomic understandings of a group's responses to the future conditions, while still providing a summative
127 response above the individual species level needed for conservation decision making.

129 **2 Methods**

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

131 1.12.1 **Study selection criteria**

132 Primary literature focusing on bivalve growth was identified using Web of Science Core collection. The
133 keywords used were "bivalve", "Bivalvia", "meta-analysis", "acidification", "pH", "hypercapnia", "ocean
134 change" "temperature", "salinity", "oxygen", "deoxygenation", "hypoxia", "anoxia", and combinations thereof.
135 Articles collected ranged from 1997–2020. Articles were screened initially through title relevance, then abstract
136 content, and finally full-text content (Fig. 1), from which individual experimental set-ups were extracted. Article
137 lists from previous meta-analyses with similar scope (Kroeker et al., 2013; Harvey et al., 2013; Sampaio et al.,
138 2021) were additionally consulted to identify material missed from initial search strings. For a list of included
139 articles used for analysis please consult 'Data availability' section.

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

144 When extracting data from papers, we optedselected for experiments that fitted within what the authors of said
145 experiments considered represented plausible climate change values for end-of-century climate conditions
146 conditions or their location/ bivalve examined specific expression, and excluded physiological stress
147 experiments which often subject animals to artificially unnatural conditions. Data were extracted from studies

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

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

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

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

167 larvae that develop without feeding were included, as nutrient intake has a ~~significant~~ strong impact on growth

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

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

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

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

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

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

174 authors' determination of control conditions. Climate stressor values were based on realistic end of century

175 projections based on author's determination for that experimental setup or study location. The phylogeny and

176 column chart (Fig. 2) were plotted using R v. 4.1.0 (R Core Team, 2021) and the packages ggplot2 v. 3.3.5

177 (Wickham, 2016), ggtree v. 3.2.1 (Yu et al., 2017), ape v. 5.6.1 (Paradis and Schliep, 2019), and patchwork v.

178 1.1.1 (Pederson, 2020). The topology is taken from the time-scaled 'budding II' family-level phylogeny of

179 Crouch et al. (2021).

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

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

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

183 extant family.

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184   **1.22.2 Statistical analysis**

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

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

187   experiments are water oxygen depletion (O_2), increased acidity (decreased pH), salinity ~~decrease~~ change (S),

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

189   2). Stressor effects could be synergistic (additive) or antagonistic (~~dampening~~reductive) (*sensu* Harvey et al.,

190   2013), or dominated by one stressor (unaffected by changes in another stressor). Additionally, we separated out

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

192   Bivalvia.

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

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

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

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

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

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

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

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

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

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

203   more likely similar than data from different articles or species. Residual heterogeneity (QE), calculated as part

204   of the meta-analytical models, was used to determine whether additional study moderators not considered might

205   be influencing study results (Hedges and Olkin, 1985).

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

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

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

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

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

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

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

213   **23 Results**

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

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

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

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

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

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

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

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

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

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

224 ~~dampening the salinity effect~~, while O_2 + temperature causes a smaller effect than either single stressor. The

225 combination of three stressors, O_2 + pH + temperature, causes the strongest negative effect size to both

226 individual stressors and any combinations. While low heterogeneity is preferable in terms of data validity it is

227 rarely achievable in environmental meta-analyses. Therefore, the significant heterogeneity in the data is

228 expected given it is drawn from so many disparate studies: QE = 300509.7155, df = 148, $P < 0.0001$.

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

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

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

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

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

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

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

236 Thirty-one of the 203 experimental set-ups involve adult Bivalvia, 14 on unspecified ages/stages, 45 on eggs/

237 larvae, and the remaining 113 focused on juvenile stages. Separating by growth stage shows that the

238 combination of pH and O_2 stressors causes significantly negative effect size at all points in the life cycle (Fig.

239 4). Salinity is not a~~n~~ ~~significant~~ important stressor for larval or juvenile bivalves but causes a ~~significant~~

240 reduction in growth in adults. Juveniles show responses to most stressors, whereas egg/larvae and adult bivalves

241 have much smaller sample sizes, and do not show significant effect size responses across the stressors.

242 Families do not all respond in the same way as the whole class Bivalvia, and stressors affect different families in

243 unexpected ways (Fig. 5). Mytilidae, Ostreidae, and Pectinidae (67% of experiments) respond with negative

244 effect sizes for all individual stressors (Fig. 5A–C). Pinnidae show positive responses for single stressors

245 temperature and pH, but negative when ~~in combination~~combined (Fig. 5D). Tellinidae show positive responses

246 for oxygen and O_2 + pH (Fig. 5E). Veneridae (14% of experiments) show mixed results with significant

247 negative effect sizes of salinity, pH + S, O_2 + pH, and O_2 + pH + T, but strong positive responses to temperature

248 and O_2 + T (Fig. 5F).

249 [Figure 4] Effect size (log-response ratio, LnRR) for individual and combined effects of oxygenation (O_2),

250 acidity (pH), salinity (S), and temperature (T) as stressors on Bivalvia growth rates at different life stages

251 (egg/larval, juvenile, adult). Points represent mean effect size with error bars indicating 95% confidence

252 intervals. Numbers indicate number of included experiments. Significance is indicated with asterisks: * $P <$

253 0.05, ** $P < 0.01$, *** $P < 0.001$.

254 [Figure 5] Effect size (log-response ratio, LnRR) for individual and combined effects of oxygenation (O_2),

255 acidity (pH), salinity (S), and temperature (T) as stressors on Bivalvia growth rates separated by family. **A**,

256 Mytilidae. **B**, Ostreidae. **C**, Pectinidae. **D**, Pinnidae. **E**, Tellinidae. **F**, Veneridae. Points represent mean effect

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257   size with error bars indicating 95% confidence intervals. Numbers indicate number of included experiments.

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

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

267   ~~3~~4 **Discussion**

268   ~~Our analysis explores a much greater combination of climate change stressors then past work, exploring 10~~
269   ~~stressor combinations, while the largest known previous work Sampaio et al. (2021) explored 4. We also present~~
270   ~~the first known meta-analysis for marine climate change which explores a taxon in its entirety and identify that~~
271   ~~even a very well-studied group has large gaps in taxonomic understandings of how its organisms respond to~~
272   ~~climate change.~~ The impact of individual and combined climate stressors on growth rates of all bivalve molluscs
273   in our study concurs with previous meta-analyses on marine calcifying invertebrates. ~~The findings re-iterate that~~
274   ~~as a group, bivalves are highly vulnerable to conditions projected to occur under future climate change.~~ Our
275   analysis demonstrates that increased incidences of deoxygenation, pH decrease, as well as changes to
276   temperature and salinity in nearshore marine environments in the future will inhibit the growth of bivalves.
277   However, by ~~focusing specifically on bivalves and~~ separating out both bivalve family-level response and
278   different life stages, we build upon previous synthesis work by revealing ~~previously to date~~previously
279   unappreciated complexity in responses. Effects of climate change for ~~this group~~bivalves will in addition~~ally~~ to
280   the physico-chemical environment, depend on the varied ecological and taxonomic makeup of specific habitats
281   and will also vary across growth stages which exploit the marine habitat different~~ly as plankton to settling as~~
282   ~~benthos~~. We also ~~also~~ highlight ~~that~~ numerous biases that exist in currently available studies (taxonomic,
283   ecological, geographic) which ~~currently~~ hinder upscaling of individual bivalve responses to a true global picture.
284   Furthermore, our analysis hopes to move synthesis literature studies towards higher taxonomic understandings
285   of an individual group's responses to ~~the~~ future ocean conditions, by showing the level of variability that can be
286   present once taxonomic distinctions within a group are teased out.

287   ~~3.1~~4.1 **Climate change stressors will negatively impact bivalve growth**

288   Our findings clearly show that growth rates in Bivalvia are negatively affected by climate stressors (Fig. 3). By
289   exploring ~~bivalves~~responses at ~~a~~ family level, we confirm our hypothesis that negative growth responses to
290   climate change are likely inherent to this taxonomic group as a whole, despite the experimental bias in the
291   published literature towards key families. Previous meta-analyses that incorporated bivalves did not focus on the
292   group specifically but include them alongside numerous other taxa (i.e., ~~categorizing bivalves~~ within phylum
293   Mollusca~~the group mollusc~~) (Harvey et al., 2013; Kroeker et al., 2013; Sampaio et al., 2021). These analyses

294 ~~which average over a wide range of taxa~~ found little evidence for significant effect sizes except in a few single

295 stressors (pH and temperature: Harvey et al., 2013; hypoxia: Sampaio et al., 2021).

296 Unsurprisingly, the effect of temperature on bivalve growth is the most studied stressor in the experiments

297 included in our meta-analysis (35 experiments: Fig. 3) – a feature seen in other studies of the effects of marine

298 climate change (Borges et al., 2022). This bias is likely because temperature-altering experiments require less

299 complex equipment and sensors than pH or oxygen manipulation, have been performed over decades, and target

300 the most obvious effect of climatic change i.e., global warming. Inclusion of a substantially greater number of

301 previous experiments within our meta-analysis (over 200 specific bivalve growth observations versus 45, 46,

302 and 34 Mollusca for Kroker et al. (2013), Harvey et al. (2013), and Sampaio et al. (2021) respectively) confirms

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

304 shows that in many cases this effect prevails when individual growth stages (Fig. 4) and the families containing

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

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

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

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

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

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

311 in pH restrict growth via restricting availability of CO_3^{2-} and increasing HCO_3^{-} ions making shell building more

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

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

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

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

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

317 (Pörtner and Farrell, 2008).

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

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

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

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

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

323 responses which are discussed in more detail below (section 4.3). However, pH causes antagonistic decreases in

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

325 unlikely to occur under future projected conditions. ~~These bivalve families are largely commercial species,~~

326 ~~suggesting these families create a bias in the wider synthesis literature exploring bivalve response to climate~~

327 ~~change. Additionally, this confirms our hypothesis that even though bivalves are considered a well-studies~~

328 ~~group, the signals detected in the literature are driven by a small subset of the taxa.~~

> **Commented [GH22]:** Deleted because of repetition in the discussion, following rewriting to address reviewer comments

329 **~~3.2~~4.2 Different bivalve life stages and ecologies show distinct responses to climate stressors**

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

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

different bivalve life stages are affected by a range of climate stressors generally confirm previous meta-analyses across calcifying organsimsorganisms. Egg/larval bivalve growth rates display the largest number of negative responses to single climate stressors, followed by juveniles, with adults showing more mixed responses (Fig. 4). ThisOur results suggests early life stages are the most vulnerable to a specific set of stressors and that the threat diminishes as organisms mature, supporting analyses by Sampaio et al. (2021) and Kroeker et al. (2013) which focused primarily on the impacts of ocean acidification. It is important to note, though, that the earlier developmental stages are more mobile and hence more able to relocate their niche to track their environmental needs.

Combined climate stressors (e.g. pH + temperature, O_2 + pH, salinity + temperature) showed negative responses across all growth stages impacts on growth throughout ontogeny and different stages of life history. Our findings oppose those of Harvey et al. (2013) who suggested limited variation in organism growth responses exists between life stages exposed to individual and synergistic ocean acidification and warming. In contrast to our analysis, tTheir data were pooled from multiple phyla not specific taxonomic groups reiterating the need to avoid too much pooling and averaging in meta-analysis.

Most studies in our dataset, especially those on the families that dominate our meta-analysis (Fig. 4), are focused on larval or juvenile stages. This likely explains some of the negative impacts on growth as for example shell mineralogy influences the impact of pH changes. Amorphous calcium carbonate secreted by larval bivalves is 50-times more susceptible to dissolution than either calcite or aragonite (Bressan et al., 2014). Changes to body size or decreased shell thickness could increase vulnerability to predation (Sadler et al., 2018). Non-significant effects of lowered pH alone in adult bivalves likely result from more diverse shell mineralogy (Weiss et al., 2002), the effects of a more robust adult shell (Beadman et al., 2003), or shelf formation of adults from a high pCO_2 low pH micro-environment quite different to the surrounding seawater (Thomsen et al., 2010; Hiebenthal et al., 2013). The adult's lifestyle, which includes for some taxa exposure to air and/or closed valves while respiring naturally results in high variability of pH in the calcifying fluid and therefore the pH changes in the experiments may be resulted in relatively less stress compared to earlier 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 suggest 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) will may become challenging for adult bivalves. It is important to note though that fewer experiments were conducted exploring salinity, resulting in a low number of experimental studies and a greater need for determining the interaction with other drivers such as pH, temperaturetemperature, 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 . Hence an increased frequency of these conditions will be disruptive to lifecycles in some taxa. Decreased growth rates in larval and juvenile stages might impact

370 population recruitment by limiting the number of individuals surviving to adulthood. Settlement efficacy will
371 affect repopulation success, following disturbance (Gagnon, et al., 2021). Aquaculture and fisheries will need to
372 account for these increased vulnerabilities and adapt culturing strategies to compensate for the negative growth
373 impacts of climate change.

374 Efforts to restore historical bivalve populations such as oysters in Chesapeake Bay (Bersoza Hernández et al.,
375 2018) and Europe (Sas et al., 2020) will need to consider how climate stressors will impact population
376 dynamics. Restoration projects often transplant adult or juvenile species into new environments (Johnson et al.,
377 2019); and our findings suggest transplanting adults might be a preferable strategy given the lower impact of
378 climate stressors at this developmental stage.

379 ### 3.34.3 Consideration of habitat and ecology in the context of climate change

380 Many species belonging to the families Mytilidae, Osteridae, and Veneridae occur in intertidal habitats which
381 experience frequent fluctuations in oxygen, acidity, and temperature and has been hypothesised to provide some
382 species with an innate ability to resist or mitigate the effects of future environmental change (Gazeau et al.,
383 2013; Zhang et al., 2020). Furthermore, this high variability may include environments overlapping with those
384 replicated in some of the experimental setups. Species can in natural environments evade some stressors vaia
385 behavioural thermoregulation, for example mobile infaunal bivalves have been shown to migrate to more
386 offshore habitats, or burrowing deeper into the sediment (Domínguez et al., 2020; Dominguez et al., 2021).

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

Commented [JW24]: Broke this sentence up a bit

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

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

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

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

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

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

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

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

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

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

415 wider range of specific shallow marine habitats.

416 **~~3.4~~4.4 Experimental studies of bivalve response are biased by commercially important taxa, ~~and have~~**
417 **~~disparate protocols~~**

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

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

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

421 (e.g., van der Schatte Olivier et al., 2020), as well as ease of access to specimens. ~~Our meta-analysis clearly~~

422 ~~reveals that available data on bivalve growth responses to climate stressors contain a number of biases. The~~

423 ~~majority of experimental set-ups are limited to a few families (e.g. Mytilidae [73], Ostreidae [31], Pectinidae~~

424 ~~[32], Veneridae [28]) (Fig. 2; Table 1), with a focus on epifaunal (Mytilidae, Pectinidae) or reef-building taxa~~

425 ~~(Ostreidae) that inhabit both intertidal and subtidal zones, and limited number of infaunal (Veneridae) or semi-~~

426 ~~infaunal (Pinnidae) taxa. This bias is likely due to the commercial importance of these families and individual~~

427 ~~species within them for aquaculture and common ecosystem services (e.g., van der Schatte Olivier et al., 2020),~~

428 ~~as well as ease of access to specimens.~~ Many experiments document that bivalve specimens were sourced from

429 commercial aquaculture facilities. A number of families included in our meta-analysis are represented only by

430 individual experiments: for example, Dreissenidae, Hitellidae, Mesodesmatidae, Myidae and Pharidae.

431 Comparison of the number of experiments vs. bivalve phylogeny shows that entire families have no documented

432 experimental or observational work investigating climate stressor impacts on growth (Fig. 2). This confirms our

433 hypothesis that even though bivalves are considered a well-studied group, the signals detected in the literature

434 are often driven by a subset of taxa.

435

436 While our results are based on studies with varying experimental protocols, ~~this is unavoidable when conducting~~

437 ~~synthesis analyses due to the vast range of labs and researchers gathering data, and~~ our approach is consistent

438 with other meta-analyses ~~of similar nature~~ (e.g., Hoppit and Schmidt 2022; Harvey et al., 2013; Kroeker et al.,

439 2013; Sampaio et al., 2021). ~~While~~As we are using studies with disparate protocols and experimental

440 measurements ~~(e.g., some studies measuring soft tissue weight and others shell length) can introduce variability,~~

441 the meta-regression analyses we conducted (Appendix B; Fig. B1) ~~shows~~ that effect sizes across studies and

442 experimental setups have not ~~significantly~~ changed across time. This result ~~is, suggesting~~suggests that

443 variability in research practices ~~consistently observes similar results~~does not impact our results. ~~While we~~

444 ~~acknowledge that s~~Some stressor combinations have low sample sizes, as multi-f~~f~~actor experiments are

445 notoriously work intensive and difficult to perform. These lower numbers decreases ~~which lowers~~ confidence in

those specific observations and conclusion, ~~this is a reflection of the available literature for synthesis, and~~ highlight~~ss the stressor combinations in greater need of experimental study~~ the importance of~~to~~ considering a wider range of drivers than the most frequently ~~often~~ assessed~~s~~ combination of warming and acidification alone.

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

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

~~4~~5 Conclusions

1. ~~Regardless of these biasesO~~, our results ~~suggest that climate change will greatly affect marine bivalves, interacting with other stresses these organisms already face.~~show that g~~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. Our meta-analysis concludes that g~~rowth rates of bivalve molluscs ~~significantly~~ decrease when exposed to climate ~~stressors~~stressors ~~by exploring the largest and most diverse grouping of climate stressor impacts on bivalve growth to date. We demonstrate tha~~with~~t~~ synergistic ~~combinations~~ factors ~~of stressors~~ (e.g., effects of combined temperature + O_2 + pH change) caus~~ing~~e 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.

1. ~~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). We show that the signal of negative bivalve growth responses to climate change observed in the wider literature is likely driven by~~

these commonly studied families, confirming our hypothesis that commercial species are creating a bias in the literature, and that most of the taxa has no known experimental observations.

> **Commented [GH32]:** Links back to our hypothesis

2. Eggs/larval stages are significantly more susceptible to reduced growth then other developmental stages. The potential effects on recruitment, as well as settlement and recovery after disturbance. has important implications for conservation or transplant efforts, suggesting a renewed focus on transplanting adult specimens rather than larvae/juveniles should be examined.

3.2. 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, and these families still showedproviding less confidence in the negative growth effects with other stressors and combinations of stressors.

4.3. 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. We highlight thatA available data on bivalve response to climate stressors also containhas large biases towards early or juvenile growth stages and, commercially important species from the global north, and that a large proportion of bivalve families lack any rigorous experimental or observational data. Regardless of these biases, our results suggest that climate change will greatly affect marine bivalves, interacting with other stresses these organisms already face. Further, based on the consistently negative growth responses to different climate stressors we document, it is likely novel experiments on unexplored bivalve species will also experience negative growth responses to climate change. Our results should be replicated for other commonly studied marine organisms like seaweeds or echinoderms to seeassess if taxonomic bias drives commonly assumed physiological responses to climate change.

> **Commented [DS33]:** Deleted to remove repetition from earlier in conclusions

> **Commented [GH34]:** Added this as we think negative growth responses are inherent to the group based on our results

> **Commented [GH35]:** This adds how our work can influence the wider field, not just for bivalves

Appendices

Appendix A

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

For all stressors: df=195

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	estimate	se	pval	tval	ci.lb	ci.ub
sqrt(vi):Stressortemperature and salinity	-4.2042	1.0869	<.0001	-3.8344	-6.3153	-2.0872
sqrt(vi):StressorO$_2$	-5.5054	0.367	<.0001	-15.0026	-6.2292	-4.78
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.
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

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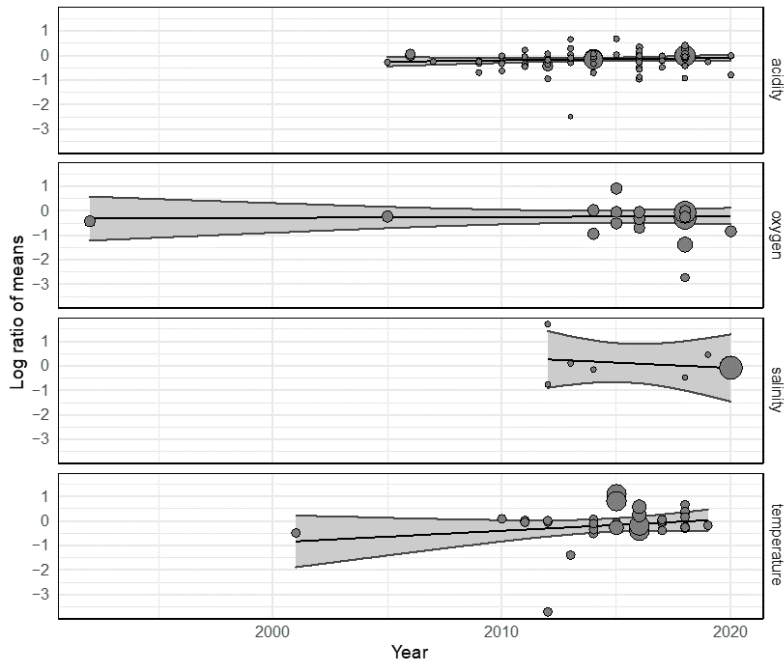
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532　**Table B1.** Regression analysis of publications by stressor per year.

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

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557   **Code availability**

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

559   **Data availability**

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

Commented [DS37]: Can we make the datafile also available via Pangaea to increase visibility? If you give it to me I will also link it at our data archive on data.bris so that people can find it with the paper

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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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870 **Figure 1.** PRISMA flow diagram of screening process for the present study following recommended
871   guidelines (Page et al., 2021). Relevant articles on Bivalvia growth experiments were identified from
872   the Web of Science Core Collection using a series of keywords (see main text). Screening resulted in
873   the identification of 79 relevant articles with 203 experimental set-ups that were included in our
874   meta-analysis.
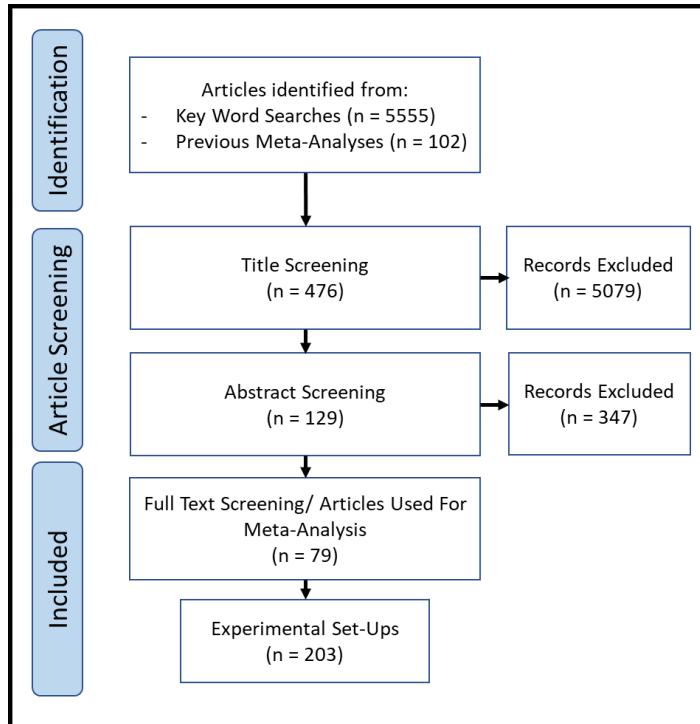
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Figure 2. Experimental representation of 18 Bivalvia families in 203 unique experimental setups from 79 relevant articles found in Web of Science Core Collection. **A**, time-scaled 'budding II' phylogeny of extant Bivalvia from Crouch et al. (2021). The root age is 485.4 Ma. **B**, number of experiments representing each extant family.
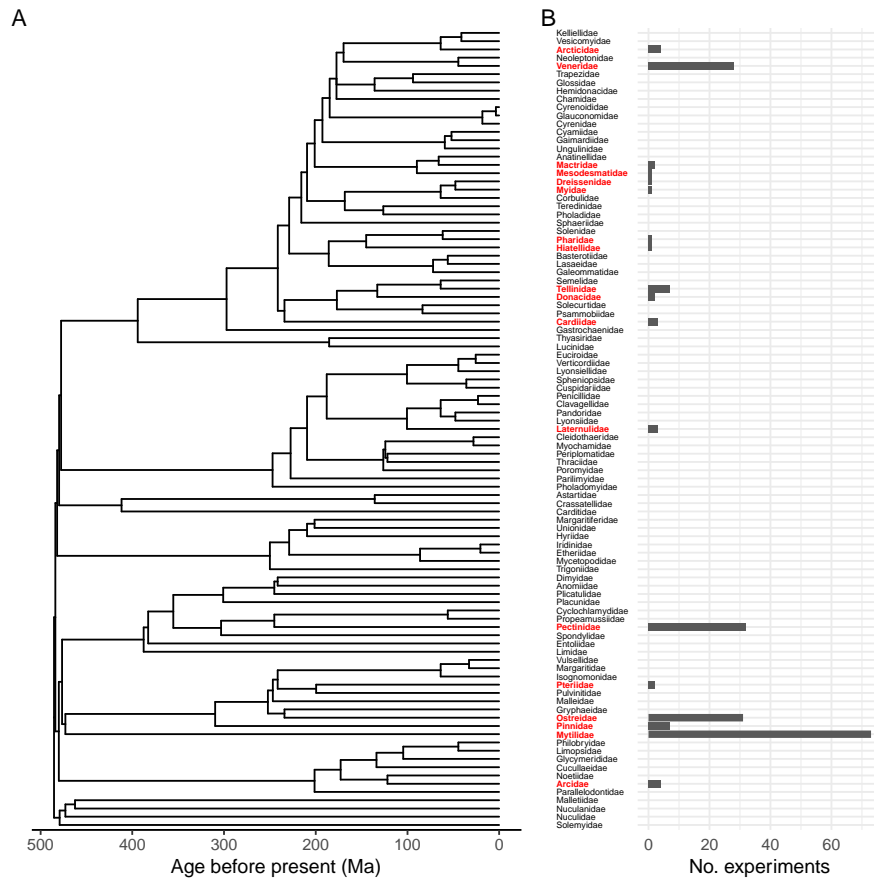
884 **Figure 3.** Effect size (log-response ratio, LnRR) for individual and combined effects of temperature (T),
885   acidity (pH), oxygenation (O_2), and salinity (S) as stressors on bivalve growth rates. **A**, for all
886   Bivalvia. **B**, for Bivalvia excluding Veneridae. Points represent mean effect size with error bars
887   indicating 95% confidence intervals. Numbers indicate number of included experiments.
888   Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
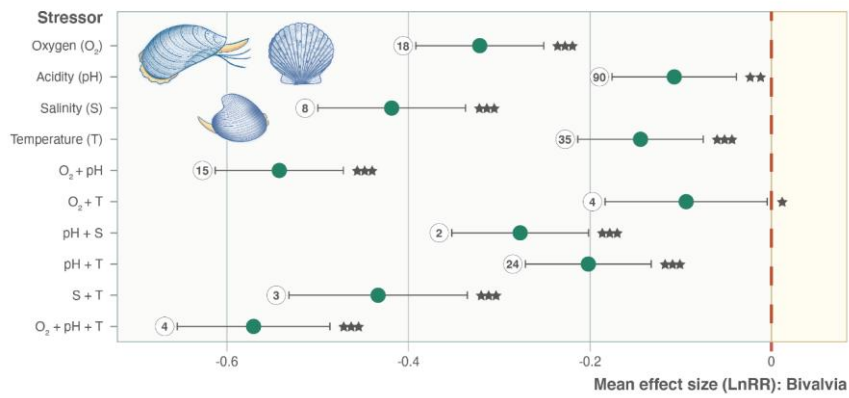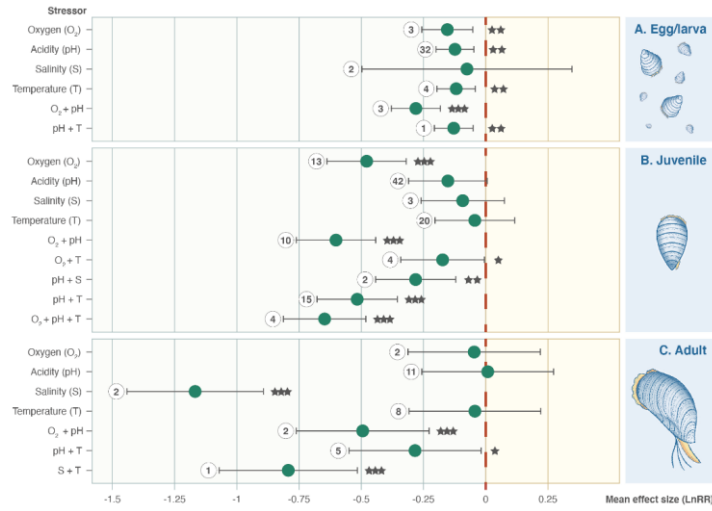

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Figure 4. Effect size (log-response ratio, LnRR) for individual and combined effects of oxygenation
(O_2), acidity (pH), salinity (S), and temperature (T) as stressors on Bivalvia growth rates at different
life stages (egg/larval, juvenile, adult).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

899 **Figure 5.** Effect size (log-response ratio, LnRR) for individual and combined effects of oxygenation
900   (O_2), acidity (pH), salinity (S), and temperature (T) as stressors on Bivalvia growth rates separated
901   by family. **A**, Mytilidae. **B**, Ostreidae. **C**, Pectinidae. **D**, Pinnidae. **E**, Tellinidae. **F**, Veneridae.
902   Points represent mean effect size with error bars indicating 95% confidence intervals. Numbers
903   indicate number of included experiments. Significance is indicated with asterisks: * $P < 0.05$, ** $P <$
904   0.01, *** $P < 0.001$.
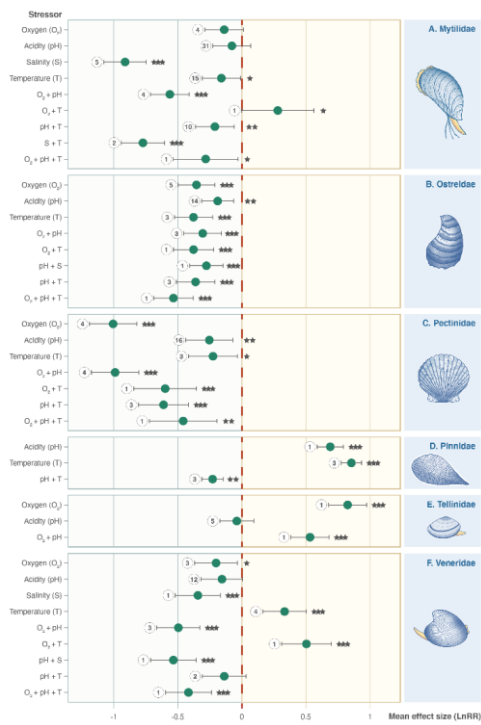
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907   **Table 1.** Representation of bivalve families across 203 experimental studies included in this meta-analysis.

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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910 **Table 2.** Single and combined stressor effect sizes from a meta-analysis of 203 experimental set-ups for
911   bivalves (log-response ratio, LnRR). Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** P
912   < 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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