



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

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7 **Abstract.**

8 Impacts of a range of climate change on marine organisms have been analysed in laboratory and experimental
9 studies. The use of different taxonomic groupings, and assessment of different processes, though, makes
10 identifying overall trends challenging, and may mask phylogenetically different responses. Bivalve molluscs are
11 an ecologically and economically important data-rich clade, allowing for assessment of individual vulnerability
12 and across developmental stages. We use meta-analysis of 203 unique experimental setups to examine how
13 bivalve growth rates respond to increased water temperature, acidity, deoxygenation, changes to salinity, and
14 combinations of these drivers. Results show that anthropogenic climate change will affect different families of
15 bivalves disproportionately but almost unanimously negatively. Almost all drivers and their combinations have
16 significant negative effects on growth. Combined deoxygenation, acidification, and temperature shows the
17 largest negative effect size. Eggs/larval bivalves are more vulnerable overall than either juveniles or adults.
18 Infaunal taxa, including Tellinidae and Veneridae, appear more resistant to warming and oxygen reduction than
19 epifaunal or free-swimming taxa but this assessment is based on a small number of datapoints. The current focus
20 of experimental set-ups on commercially important taxa and families within a small range of habitats creates
21 gaps in understanding of global impacts on these economically important foundation organisms.

22



23 **1 Introduction**

24 Predictions of rising levels of atmospheric carbon dioxide indicate that the marine environment will
25 significantly alter over the coming decades. Sea surface temperatures are projected to rise 2–4°C globally by the
26 end of the century depending on region and emission scenario (IPCC, 2021). Higher latitudes will be exposed to
27 more severe warming than the tropics (Meredith et al., 2019), resulting in sea ice and glacial melting, raising
28 global sea levels, and increasing runoff and freshwater influx into marine settings (Lu et al., 2022). Ocean pH
29 will decline by between 0.3–1 units by the end of the 21st century, with shallower waters expected to experience
30 greater pH decreases than the open ocean (IPCC, 2021). Oxygen levels in the ocean are projected to decrease by
31 up to 7% leading to an expansion of ‘dead zones’ (Breitburg, et al., 2018; Messié and Chavez, 2017; Schmidtke
32 et al., 2017).

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

45 Bivalve molluscs (Class Bivalvia) are cornerstones of coastal and shallow marine ecosystems, with
46 representatives in all marine biomes where they provide provisioning and regulatory services (Olivier et al.,
47 2020; Carss et al., 2020; Vaughn and Hoellein, 2018). Bivalves are a key global food source, with production
48 for human consumption growing from 51 thousand tonnes in 1950 to more than 12.4 million tonnes today
49 (Smaal et al., 2019). As a result, bivalve aquaculture has an estimated global market value of \$17.1 billion (van
50 der Schatte Olivier et al., 2018).

51 Additionally, there is a growing awareness of the wider ecosystem benefits of bivalves as habitat formers. Their
52 biogenic three-dimensional reefs formed by sessile epifaunal taxa such as oysters increase surrounding
53 biodiversity (Fariñas-Franco and Roberts, 2014). Complex reef frameworks and individual bivalve shells in soft-
54 substrate environments can act as microhabitats to other invertebrates through creation of new hard substrates
55 and by altering local flow regimes or even temperature (McAfee et al., 2017). Filter-feeding bivalves can reduce
56 pollution and clear large particulates out of the water column (Smyth et al., 2018). They enhance or change local
57 marine productivity (Donnarumma et al., 2018; Strain et al., 2021) via selective removal of specific species of
58 phytoplankton (Ward and Shumway, 2004). Deposition of bivalve faeces and pseudofaeces, along with
59 burrowing activity of motile infaunal deposit or suspension feeders, can lead to changes in the local flux or
60 enrichment of organic matter into the sediment and biogeochemical cycling (Smyth et al., 2013), and ultimately
61 habitat suitability for other benthos.



62 Anthropogenic pressures including coastal development, overfishing, and pollution have resulted in
63 demonstrable decreases in global bivalve populations (e.g., De Groot, 1984; Baeta et al., 2014). Akin to other
64 calcifying invertebrate organisms, it has been hypothesised that the physiochemical changes resulting from
65 climate change will reduce bivalve growth, impair maintenance of shells (Maynou et al., 2020; Knights et al.,
66 2020), and disrupt larval settlement patterns and spawning (Bascur et al., 2020; Figueirodo et al., 2022). In
67 recognition of the environmental, social, and economic benefits bivalves produce, and the current and future
68 pressures they face, the group is a focus for conservation efforts (zu Ermgassen et al., 2020; Buelow and
69 Waltham, 2020; Gagnon et al., 2020). However, despite extensive study there remain significant gaps in our
70 understanding of their response to climate change across different bivalve families.

71 Current understanding of how bivalves will respond to various climate change stressors is based on field studies
72 and lab-derived experimental data focused largely on ocean acidification and response to warming, generally
73 observing negative responses (e.g., Beukema et al., 2009; van Colen et al., 2012; Addino et al., 2019; Eymann et
74 al., 2020). Synthesis work through meta-analysis supports the notion that bivalves will respond negatively to
75 climate change (Kroeker et al., 2013; Harvey et al., 2013; Sampaio et al., 2021; Hoppit and Schmidt, 2022;
76 Leung et al., 2022). These studies have shown that the synergistic effects of ocean acidification, ocean warming,
77 and an increase in hypoxic events decrease the growth rates of calcifying marine organisms (Kroeker et al.,
78 2010; Maynou et al., 2020; Knights et al., 2020; Sampaio et al., 2021). However, these analyses have been
79 conducted at high taxonomic rankings, e.g., examining changes at phylum level thereby they risk averaging
80 differential outcomes at finer taxonomic resolution. High level analyses can be difficult to interpret due to
81 clumping diverse responses into generalized trends (Helmuth et al., 2005). Organisms experience disparate
82 responses to environmental drivers based on local phenotypic expression (Dong et al., 2017) and environmental
83 influences (Genner et al., 2010) resulting, for example, in species-specific mortality risk to extreme heat based
84 on local microclimates and adaptation (Montalto et al., 2016). Therefore, our current understanding of how
85 bivalves respond to climate change based on broad scale synthesis work might not capture the granularity and
86 diversity of responses this group exhibits.

87 We aimed to fill this gap by employing a meta-analysis methodology to explore the effects of marine climate
88 stressors, and combinations thereof, on bivalve growth at both the whole-group and family levels. We address
89 the question of whether a negative response to climate change is intrinsic to the group or driven by specific taxa.
90 We focused on studies that emphasize bivalve growth rates; a commonly studied trait that offers insight into
91 organism vulnerability to answer how these growth rates are impacted by climate stressors, and whether
92 different families or developmental stages are more sensitive to climate stressors than others. Additionally, we
93 examine the range of experimental work assessing bivalve sensitivity to climate change to understand which
94 families are most represented. We hypothesise that a focus on commercially important bivalve taxa may be
95 creating a likely bias in observations.



96 **2 Methods**

97 **2.1 Study selection criteria**

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

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

110 We included articles with lab-based studies that focused on direct measurements of Bivalvia growth including
111 length, mass, condition index, or shell thickness. Proxies for growth were excluded, such as scope for growth or
112 RNA production, as these introduce additional uncertainties and variability to the growth signal and were not
113 directly comparable to absolute measures of growth. Only studies where the bivalves were fed and studies on
114 larvae that develop without feeding were included, as nutrient intake has a significant impact on growth (Norkko
115 et al., 2005; Thomsen et al., 2013; Ballesta-Artero et al., 2018). Study sample size, mean growth value of both
116 control and treatment groups, and indication of the variation of growth values (confidence intervals, standard
117 error, and standard deviation) were extracted from articles. Absolute values were used, as percentage data could
118 not be combined with absolute measurements within the Metafor package. Data were extracted directly from
119 result text, tables, or supplementary data when possible. Data from figures was collected using WebPlotDigitizer
120 v. 4.4 (Rohatgi, 2022). Control values for climate stressors for each article were based on authors’ determination
121 of control conditions. Climate stressor values were based on realistic end of century projections based on
122 author’s determination for that experimental setup or study location. The phylogeny and column chart (Fig. 2)
123 were plotted using R v. 4.1.0 (R Core Team, 2021) and the packages ggplot2 v. 3.3.5 (Wickham, 2016), ggtree
124 v. 3.2.1 (Yu et al., 2017), ape v. 5.6.1 (Paradis and Schliep, 2019), and patchwork v. 1.1.1 (Pederson, 2020). The
125 topology is taken from the time-scaled ‘budding II’ family-level phylogeny of Crouch et al. (2021).

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

130 **2.2 Statistical analysis**

131 We performed meta-analysis on the impacts of climate stressors on the growth of Bivalvia at whole-class and
132 family levels following methods described in Hoppit and Schmidt (2022). Stressors identified from the included



133 experiments are water oxygen depletion (O_2), increased acidity (decreased pH), salinity decrease (S), and
134 temperature increase (T), and combinations of these stressors (indicated as, e.g., $O_2 + \text{pH}$) (Figs 3–5; Table 2).
135 Stressor effects could be synergistic (additive) or antagonistic (dampening) (*sensu* Harvey et al., 2013), or
136 dominated by one stressor (unaffected by changes in another stressor). Additionally, we separated out the effect
137 sizes of these stressors on different growth stages (egg/larva, juvenile, adult) for the entire class Bivalvia.

138 Analyses used R v. 4.0.3 (R Core Team, 2020) and the package Metafor version 3.0-2 (Viechtbauer, 2010).
139 Metafor function `escalc` was used to calculate effect size and sampling variance. We chose Log Response Ratio
140 (LnRR ; the natural log of the response ratio) as the measure of effect size to measure the proportion of change
141 between the mean of the treatment and control responses to experimental intervention. An effect size of zero
142 corresponds to a statistically insignificant effect. Multivariate meta-analytical models (function `rma.mv`) were
143 used to calculate mean effect sizes of climate stressor impacts on bivalve growth rates for three subsets of data:
144 all bivalves pooled, different developmental stages, and families with sufficient sample sizes ($n \geq 7$). Significant
145 results were identified when model 95% confidence intervals did not overlap zero effect size. Models used
146 random intercepts for articles and species intercepts for each treatment to compensate for similarities introduced
147 by studies, as data originating from the same experimental setup or from the same species are assumed to be
148 more likely similar than data from different articles or species. Residual heterogeneity (QE), calculated as part
149 of the meta-analytical models, was used to determine whether additional study moderators not considered might
150 be influencing study results (Hedges and Olkin, 1985).

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

158 **3 Results**

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

164 We find consistent and significant negative effects of all single stressors and most combinations acting on the
165 entire class Bivalvia, in agreement with previous meta-analyses (Fig. 3; Table 2). At the class level, many
166 combinations of stressors increase the negative effect on growth in a synergistic way (Fig. 3; Table 2). For
167 example, pH and O_2 treatments are greater in combination than either alone, as were salinity + temperature and
168 pH + temperature. The effect of pH + salinity is intermediate between that of the two single stressors,
169 dampening the salinity effect, while O_2 + temperature causes a smaller effect than either single stressor. The



170 combination of three stressors, O₂ + pH + temperature, causes the strongest negative effect size to both
171 individual stressors and any combinations. While low heterogeneity is preferable in terms of data validity it is
172 rarely achievable in environmental meta-analyses. Therefore, the significant heterogeneity in the data is
173 expected given it is drawn from so many disparate studies: QE = 300509.7155, df = 148, $P < 0.0001$.

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

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

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

181 Thirty-one of the 203 experimental set-ups involve adult Bivalvia, 14 on unspecified ages/stages, 45 on eggs/
182 larvae, and the remaining 113 focused on juvenile stages. Separating by growth stage shows that the
183 combination of pH and O₂ stressors causes significantly negative effect size at all points in the life cycle (Fig.
184 4). Salinity is not a significant stressor for larval or juvenile bivalves but causes a significant reduction in growth
185 in adults. Juveniles show responses to most stressors, whereas egg/larvae and adult bivalves have much smaller
186 sample sizes, and do not show significant effect size responses across the stressors.

187 Families do not all respond in the same way as the whole class Bivalvia, and stressors affect different families in
188 unexpected ways (Fig. 5). Mytilidae, Ostreidae, and Pectinidae (67% of experiments) respond with negative
189 effect sizes for all individual stressors (Fig. 5A–C). Pinnidae show positive responses for single stressors
190 temperature and pH, but negative when in combination (Fig. 5D). Tellinidae show positive responses for oxygen
191 and O₂ + pH (Fig. 5E). Veneridae (14% of experiments) show mixed results with significant negative effect
192 sizes of salinity, pH + S, O₂ + pH, and O₂ + pH + T, but strong positive responses to temperature and O₂ + T
193 (Fig. 5F).

194 [Figure 4] Effect size (log-response ratio, LnRR) for individual and combined effects of oxygenation (O₂),
195 acidity (pH), salinity (S), and temperature (T) as stressors on Bivalvia growth rates at different life stages
196 (egg/larval, juvenile, adult). Points represent mean effect size with error bars indicating 95% confidence
197 intervals. Numbers indicate number of included experiments. Significance is indicated with asterisks: * $P <$
198 0.05, ** $P < 0.01$, *** $P < 0.001$.

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

204 Egger's regression test showed highly significant ($P < 0.001$) results for every stressor, indicating publications
205 with significant results are published more often than would be expected by chance, suggesting negative



206 observations are less frequently reported (see Appendix A; Table A1). Meta-regression analysis of publication
207 by year and stressor showed that no individual stressor is changing in effect size signal through time, showing
208 consistency in publication findings over the years (see Appendix B; Fig. B1 and Table B1).

209 **4 Discussion**

210 The impact of individual and combined climate stressors on growth rates of bivalve molluscs in our study
211 concurs with previous meta-analyses on marine calcifying invertebrates. The findings re-iterate that as a group,
212 bivalves are highly vulnerable to conditions projected to occur under future climate change. Our analysis
213 demonstrates that increased incidences of deoxygenation, pH decrease, as well as changes to temperature and
214 salinity in nearshore marine environments in the future will inhibit the growth of bivalves. However, by
215 focusing specifically on bivalves and separating out both family-level response and different life stages, we
216 build upon previous synthesis work by revealing previously unappreciated complexity in responses. Effects of
217 climate change for this group will additionally to the physico-chemical environment depend on the varied
218 ecological and taxonomic makeup of specific habitats and will vary across growth stages which exploit the
219 habitat differently as plankton to settling as benthos. We also highlight that numerous biases exist in currently
220 available studies (taxonomic, ecological, geographic) which currently hinder upscaling of individual bivalve
221 responses to a true global picture.

222 **4.1 Climate change stressors will negatively impact bivalve growth**

223 Our findings clearly show that growth rates in *Bivalvia* are negatively affected by climate stressors (Fig. 3).
224 Previous meta-analyses that incorporated bivalves did not focus on the group specifically but include them
225 alongside numerous other taxa (Harvey et al., 2013; Kroeker et al., 2013; Sampaio et al., 2021). These analyses
226 which average over a wide range of taxa found little evidence for significant effect sizes except in a few single
227 stressors (pH and temperature: Harvey et al., 2013; hypoxia: Sampaio et al., 2021). Unsurprisingly, the effect of
228 temperature on bivalve growth is the most studied stressor in the experiments included in our meta-analysis (35
229 experiments: Fig. 3). This bias is likely because temperature-altering experiments require less complex
230 equipment and sensors than pH or oxygen manipulation, have been performed over decades, and target the most
231 obvious effect of climatic change i.e., global warming. Inclusion of a substantially greater number of previous
232 experiments within our meta-analysis (over 200 specific bivalve growth observations versus 45, 46, and 34
233 Mollusca for Kroeker et al. (2013), Harvey et al. (2013), and Sampaio et al. (2021) respectively) confirms that all
234 single climate stressors show significant negative effect sizes in bivalves (Fig. 3). Our analysis also shows that
235 in many cases this effect prevails when individual growth stages (Fig. 4) and the families containing the largest
236 number of experiments or observational data (Table 1; Fig. 5) are examined separately.

237 An important result is the identification of synergistic, additive, and antagonistic effects between different
238 stressors which in all cases in our analysis increase the negative response (Gobler et al., 2014; Stevens and
239 Gobler, 2018) (Table 2). For example, we identify significant negative effect sizes for O₂ + pH, and temperature
240 + salinity when analysing overall bivalve responses (Fig. 3). The combination O₂ + pH has a stronger negative
241 effect size than either oxygen or pH individually in all analyses (Figs. 3-5). Decreases in pH restrict growth via
242 restricting availability of CO₃²⁻ and increasing HCO₃⁻ ions making shell building more metabolically expensive



243 and increasing shell dissolution (Ivanina et al., 2013; Byrne and Fitzer, 2019). Internal tissues also require
244 buffering against pH changes, incurring a further metabolic cost (Byrne and Fitzer, 2019). Marine
245 deoxygenation impacts metabolism, reducing an organism's ability to respond to these increased metabolic
246 requirements of shell generation and tissue buffering under a more acidic environment. Therefore, the increased
247 impact from combining these two stressors confirms our physiological understanding of the organism (Pörtner
248 and Farrell, 2008).

249 Mean effect sizes for each climate stressor differ between families within Bivalvia. Consequently, the effects of
250 climate change on this group will be habitat dependant and alter the taxonomic composition of coastal
251 ecosystems. The four most investigated families in our dataset (Mytilidae, Ostreidae, Pectinidae, and Veneridae)
252 exhibit consistent negative growth responses to climate stressors (Fig. 5). Exceptions exist for oxygen and
253 temperature changes for Mytilidae and Veneridae and temperature increase for Veneridae where we find mixed
254 responses. However, pH causes antagonistic decreases in growth rate across these main families (Fig. 5),
255 suggesting that any temperature-driven growth increases are unlikely to occur under future projected conditions.

256 **4.2 Different bivalve life stages and ecologies show distinct responses to climate stressors**

257 Climate change will be acting on each part of the development of an organism. In bivalves, these different life
258 stages have different habitats and mobility from free swimming larvae to sessile adults. Our results on how
259 different bivalve life stages are affected by a range of climate stressors generally confirm previous meta-
260 analyses. Egg/larval bivalve growth rates display the largest number of negative responses to single climate
261 stressors, followed by juveniles, with adults showing more mixed responses (Fig. 4). This suggests early life
262 stages are the most vulnerable to a specific set of stressors and that the threat diminishes as organisms mature,
263 supporting analyses by Sampaio et al. (2021) and Kroeker et al. (2013) which focused primarily on the impacts
264 of ocean acidification. It is important to note though that the earlier developmental stages are more mobile and
265 hence more able to relocate their niche to track their environmental needs.

266 Combined climate stressors (e.g. pH + temperature, O₂ + pH, salinity + temperature) showed negative responses
267 across all growth stages impacts on growth throughout ontogeny and different stages of life history. Our
268 findings oppose those of Harvey et al. (2013) who suggested limited variation in organism growth responses
269 exists between life stages exposed to individual and synergistic ocean acidification and warming. Their data
270 were pooled from multiple phyla not specific taxonomic groups reiterating the need to avoid too much pooling
271 and averaging in meta-analysis.

272 Most studies in our dataset, especially those on the families that dominate our meta-analysis (Fig. 4), are
273 focused on larval or juvenile stages. This likely explains some of the negative impacts on growth as for example
274 shell mineralogy influences the impact of pH changes. Amorphous calcium carbonate secreted by larval
275 bivalves is 50-times more susceptible to dissolution than either calcite or aragonite (Bressan et al., 2014).
276 Changes to body size or decreased shell thickness could increase vulnerability to predation (Sadler et al., 2018).
277 Non-significant effects of lowered pH alone in adult bivalves likely result from more diverse shell mineralogy
278 (Weiss et al., 2002), the effects of a more robust adult shell (Beadman et al., 2003), or shelf formation of adults
279 from a high pCO₂ low pH micro-environment quite different to the surrounding seawater (Thomsen et al., 2010;
280 Hiebenthal et al., 2013). The adult's lifestyle, which includes for some taxa exposure to air and/or closed valves



281 while respiring naturally results in high variability of pH in the calcifying fluid and therefore the pH changes in
282 the experiments may be resulted in relatively less stress compared to earlier developmental stages. Most of the
283 adult experiments included in our meta-analysis were on aragonitic individuals or on mixed aragonitic-calcitic
284 Mytilidae and Pectinidae. Only one study (Lemasson et al., 2018) included two genera of adult oysters (Family
285 Ostreidae) which construct their shells primarily from calcite (Stenzel, 1963), a more stable carbonate
286 polymorph. Our results suggest adults have an increased susceptibility to salinity changes when compared to
287 juvenile and egg/larval stages, suggesting habitats projected to experience decreased salinity due to increased
288 seasonal runoff or enhanced evaporation in a restricted setting (Robins et al., 2016) will become challenging for
289 adult bivalves.

290 Increased sensitivity to climate stressors at different life stages has implications for bivalve aquaculture and
291 conservation effort (Smaal et al., 2019). Hence an increased frequency of these conditions will be disruptive to
292 lifecycles in some taxa. Decreased growth rates in larval and juvenile stages might impact population
293 recruitment by limiting the number of individuals surviving to adulthood. Settlement efficacy will affect
294 repopulation success, following disturbance (Gagnon, et al., 2021). Aquaculture and fisheries will need to
295 account for these increased vulnerabilities and adapt culturing strategies to compensate for the negative growth
296 impacts of climate change.

297 Efforts to restore historical bivalve populations such as oysters in Chesapeake Bay (Bersosa Hernández et al.,
298 2018) and Europe (Sas et al., 2020) will need to consider how climate stressors will impact population
299 dynamics. Restoration projects often transplant adult or juvenile species into new environments (Johnson et al.,
300 2019); and our findings suggest transplanting adults might be a preferable strategy given the lower impact of
301 climate stressors at this developmental stage.

302 **4.3 Consideration of habitat and ecology in the context of climate change**

303 Many species belonging to the families Mytilidae, Ostreidae, and Veneridae occur in intertidal habitats which
304 experience frequent fluctuations in oxygen, acidity, and temperature and has been hypothesised to provide some
305 species with an innate ability to resist or mitigate the effects of future environmental change (Gazeau et al.,
306 2013; Zhang et al., 2020). Furthermore, this high variability may include environments overlapping with those
307 replicated in some of the experimental setups. Species can in natural environments evade some stressors via
308 behavioural thermoregulation, for example mobile infaunal bivalves have been shown to migrate to more
309 offshore habitats, or burrowing deeper into the sediment (Domínguez et al., 2020; Dominguez et al., 2021).

310 Negative growth responses though generally repeat across the taxa in our dataset irrespective of habitat. An
311 intertidal habitat or preference for marine or brackish water does not appear to alter observed growth responses
312 in the experimental setting to accumulated climate stressors, as we find consistent decreases in growth rates, and
313 commonly subtidal, epifaunal bivalves (such as many Pectinidae) also exhibiting significant negative responses
314 (Aguirre-Velarde et al., 2019; Maynou et al., 2020). Interpreting the effects of ecology on our results is
315 complicated by the previously mentioned dominance of studies focused on juvenile and early growth stages;
316 many bivalves feature a veliger or early larval stage that live in and can tolerate quite different environmental



317 conditions to those of later stages of life history (i.e., pelagic, free-swimming larvae vs infaunal or benthic
318 attached lifestyles for juveniles and adults) (Waldbusser et al., 2013).

319 The ability to evade will depend on the lifestyle and habitat. Most experiments in our dataset are suspension
320 feeding taxa with an epifaunal habitat. The investigated bivalves are free swimming (Pectinidae), cemented to
321 substrates or form biogenic reefs (Ostreidae), or use byssal threads to anchor in sediments or attach to hard
322 substrates (Pinnidae, Mytilidae, some Pectinidae). There is much lower representation in our dataset of infaunal
323 or burrowing taxa which may also include deposit feeders (e.g., families Tellinidae, Veneridae). Our data
324 suggest overwhelmingly negative impacts on growth of all stressors for epifaunal or free-swimming suspension
325 feeding taxa (families Mytilidae, Ostreidae, Pectinidae in Fig. 5).

326 Tellinidae and Veneridae show more varied responses to temperature, pH, and O₂ depletion. These taxa are
327 active infaunal burrowers in soft sediment, which can often be undersaturated with respect to calcium carbonate
328 as well as oxygen-limited (Green et al., 2013; Stevens and Gobler, 2018) suggesting some resilience to these
329 conditions. Both semi-infaunal Pinnidae and infaunal Veneridae also show significant positive effect sizes in
330 response to warming (Fig. 5). It has been hypothesised that an infaunal habitat may reduce immediate
331 susceptibility of bivalves to warming, as the substrate may act as a thermal refugia (Zhou et al., 2022). However,
332 interpreting the general role of tiering is complicated by the currently small number of experiments or
333 observations on infaunal taxa, further highlighting the need for additional data on the effects of environmental
334 stressors on the growth of burrowing bivalves and those from a wider range of specific shallow marine habitats.

335 **4.4 Experimental studies of bivalve response are biased by commercially important taxa**

336 Our meta-analysis clearly reveals that available data on bivalve growth responses to climate stressors contain a
337 number of biases. The majority of experimental set-ups are limited to a few families (e.g. Mytilidae [73],
338 Ostreidae [31], Pectinidae [32], Veneridae [28]) (Fig. 2; Table 1), with a focus on epifaunal (Mytilidae,
339 Pectinidae) or reef-building taxa (Ostreidae) that inhabit both intertidal and subtidal zones, and limited number
340 of infaunal (Veneridae) or semi-infaunal (Pinnidae) taxa. This bias is likely due to the commercial importance of
341 these families and individual species within them for aquaculture and common ecosystem services (e.g., van der
342 Schatte Olivier et al., 2020), as well as ease of access specimens. Many bivalve specimens were sourced from
343 commercial aquaculture facilities. A number of families included in our meta-analysis are represented only by
344 individual experiments: for example, Dreissenidae, Hitellidae, Mesodesmatidae, Myidae and Pharidae.
345 Comparison of the number of experiments vs. bivalve phylogeny shows that entire families have no documented
346 experimental or observational work investigating climate stressor impacts on growth (Fig. 2).

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



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

363 5 Conclusions

364 Reduced growth rates predicted by our meta-analysis have important implications for population stability in
365 these commercially important keystone marine taxa, as well as for guiding future conservation and mitigation
366 efforts. Our meta-analysis concludes that growth rates of bivalve molluscs significantly decrease when exposed
367 to climate stressors. We demonstrate that synergistic combinations of stressors (e.g., effects of combined
368 temperature + O₂ + pH change) cause greater reductions in bivalve growth than individual stressors. This result
369 is true for bivalves overall, and when separating out by growth stage in the most commonly studied bivalve
370 families (Ostreidae, Mytilidae, Pectinidae, Veneridae).

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

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

381 We highlight that available data on bivalve response to climate stressors has large biases towards early or
382 juvenile growth stages, commercially important species from the global north, and that a large proportion of
383 bivalve families lack any rigorous experimental or observational data. Regardless of these biases, our results
384 suggest that climate change will greatly affect marine bivalves, interacting with other stresses these organisms
385 already face.

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389 **Appendices**

390 **Appendix A**

391 **Table A1.** Publication bias results of Egger’s regression test.

392 For all stressors: df=195

	estimate	se	pval	tval	ci.lb	ci.ub
sqrt(vi):StressorO2	-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 O2	-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 O2	-1.0071	0.5775	0.0828	-1.7439	-2.1462	0.1319
sqrt(vi):Stressortemperature and pH and O2	-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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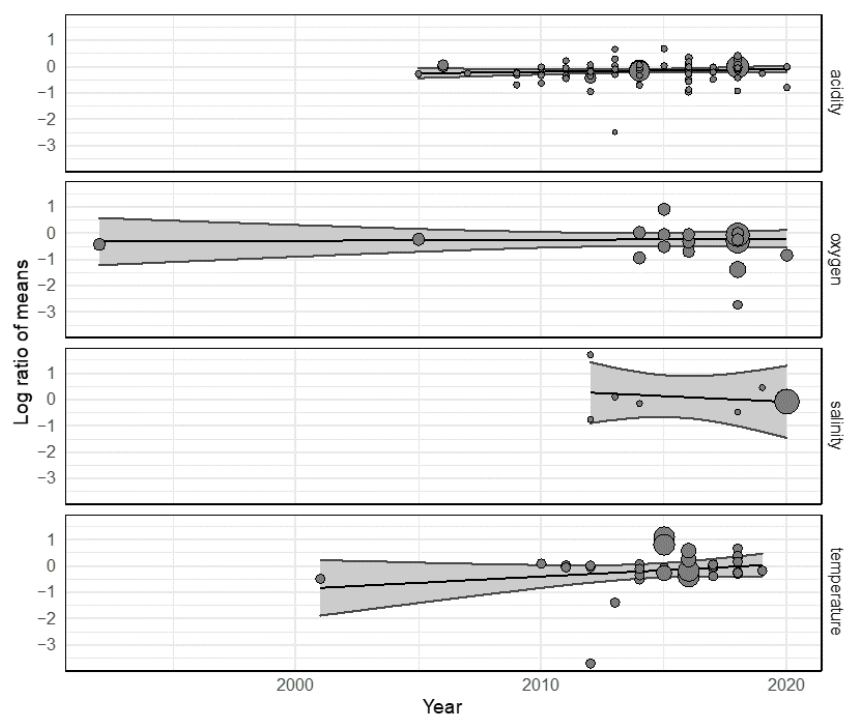
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400 **Appendix B.**

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



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408 **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							



intcpt	-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							
intcpt	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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410 Signif. codes: 0 '****' 0.001 '***' 0.01 '**' 0.05 '.' 0.1 ' ' 1

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433 **Code availability**

434 Code used for analyses available at <https://github.com/georgehopit/Bivalve-meta-analysis>

435 **Data availability**

436 Data used for analyses available at <https://github.com/georgehopit/Bivalve-meta-analysis>

437 **Author contributions**

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

442

443 **Competing interests**

444 The authors declare that they have no conflict of interest.

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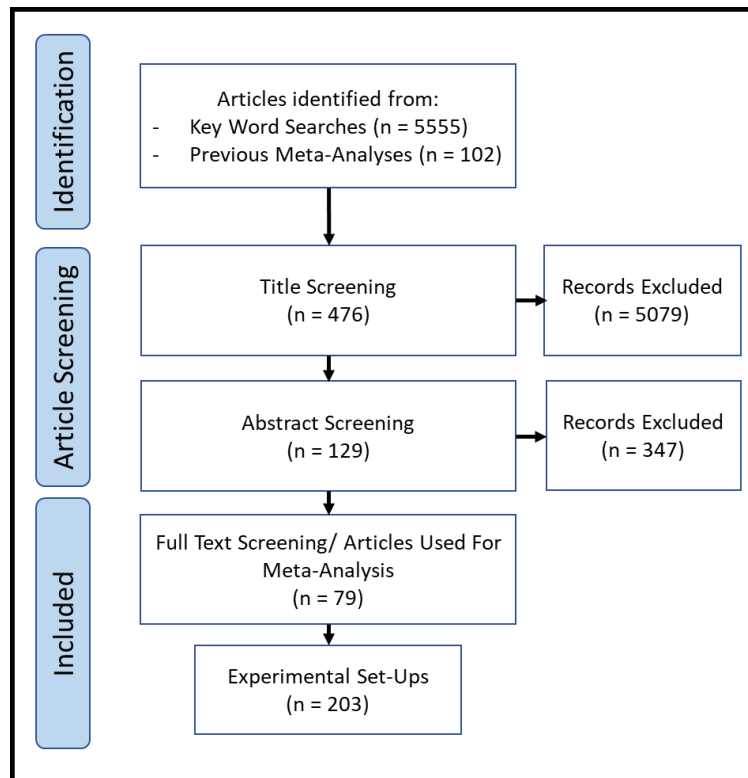
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743 **Figure 1.** PRISMA flow diagram of screening process for the present study following recommended
744 guidelines (Page et al., 2021). Relevant articles on Bivalvia growth experiments were identified from
745 the Web of Science Core Collection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



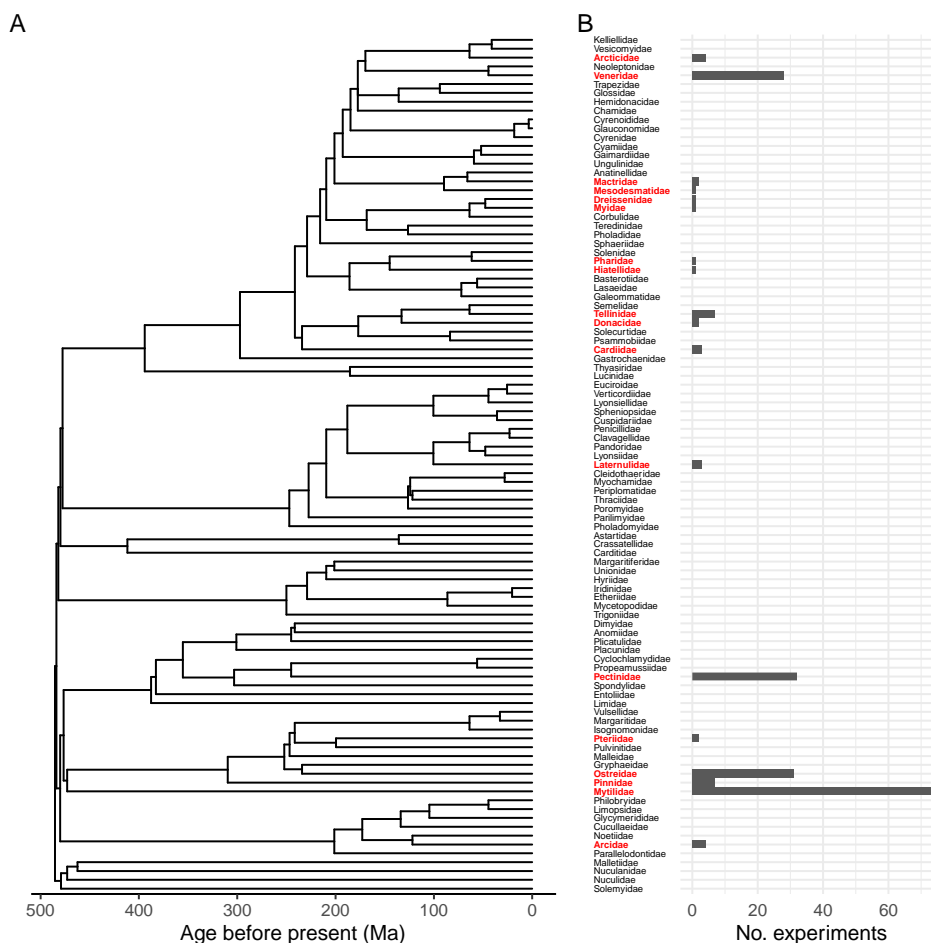
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751 **Figure 2.** Experimental representation of 18 Bivalvia families in 203 unique experimental setups from 79
 752 relevant articles found in Web of Science Core Collection. **A,** time-scaled ‘budding II’ phylogeny of
 753 extant Bivalvia from Crouch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

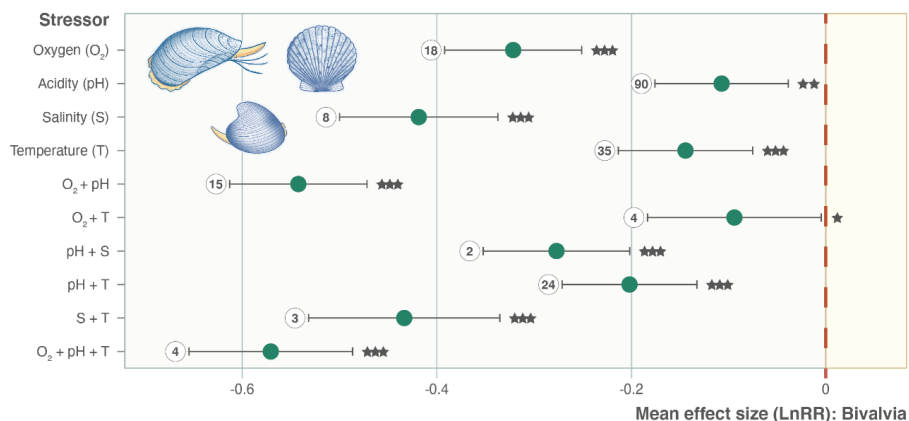


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757 **Figure 3.** Effect size (log-response ratio, LnRR) for individual and combined effects of temperature (T),
 758 acidity (pH), oxygenation (O₂), and salinity (S) as stressors on bivalve growth rates. **A**, for all
 759 Bivalvia. **B**, for Bivalvia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



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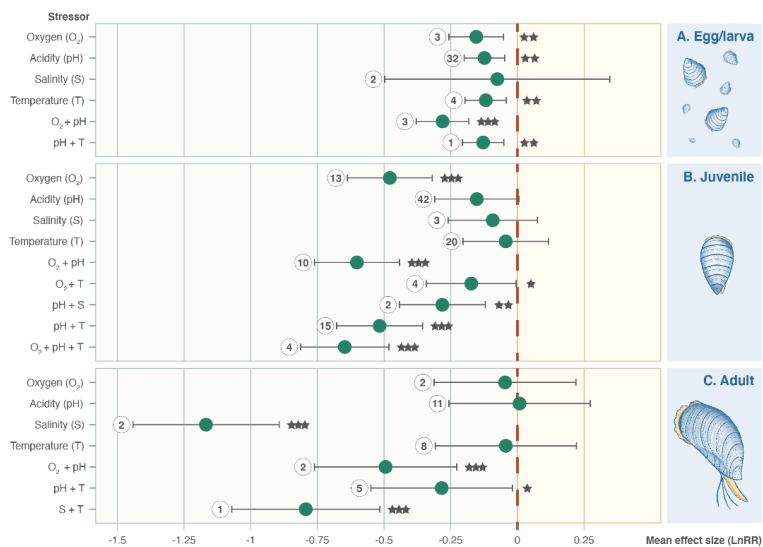
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766 **Figure 4.** Effect size (log-response ratio, LnRR) for individual and combined effects of oxygenation
 767 (O₂), acidity (pH), salinity (S), and temperature (T) as stressors on *Bivalvia* growth rates at different
 768 life stages (egg/larval, juvenile, adult). Points represent mean effect size with error bars indicating
 769 95% confidence intervals. Numbers indicate number of included experiments. Significance is
 770 indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

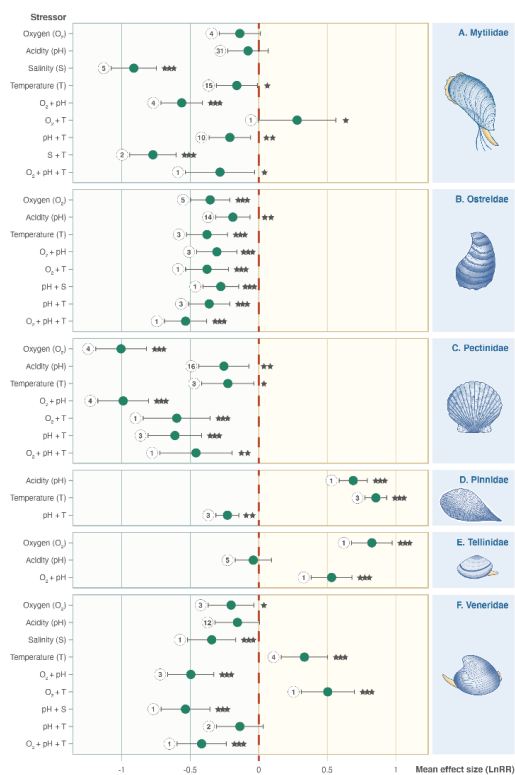


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773 **Figure 5.** Effect size (log-response ratio, LnRR) for individual and combined effects of oxygenation
 774 (O_2), acidity (pH), salinity (S), and temperature (T) as stressors on *Bivalvia* growth rates separated
 775 by family. **A.** Mytilidae. **B.** Ostreidae. **C.** Pectinidae. **D.** Pinnidae. **E.** Tellinidae. **F.** Veneridae.
 776 Points represent mean effect size with error bars indicating 95% confidence intervals. Numbers
 777 indicate number of included experiments. Significance is indicated with asterisks: * $P < 0.05$, ** $P <$
 778 0.01 , *** $P < 0.001$.



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783 **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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786 **Table 2.** Single and combined stressor effect sizes from a meta-analysis of 203 experimental set-ups (log-
787 response ratio, LnRR). Significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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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