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1 **Hidden impacts of ocean warming and acidification on biological responses of marine animals**
2 **revealed through meta-analysis**

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35

36 **ABSTRACT**

37 Conflicting results remain on the impacts of climate change on marine organisms, hindering our capacity
38 to predict the future state of marine ecosystems. To account for species-specific responses and for the
39 ambiguous relation of most metrics to fitness, we developed a meta-analytical approach based on the
40 deviation of responses from reference values (absolute change) to complement meta-analyses of
41 directional (relative) changes in responses. Using this approach, we evaluate responses of fish and
42 invertebrates to warming and acidification. We find that climate drivers induce directional changes in
43 calcification, survival, and metabolism, and significant deviations in twice as many biological responses,
44 including physiology, reproduction, behavior, and development. Widespread deviations of responses are
45 detected even under moderate intensity levels of warming and acidification, while directional changes
46 are mostly limited to more severe intensity levels. Because such deviations may result in ecological shifts
47 impacting ecosystem structures and processes, our results suggest that climate change will likely have
48 stronger impacts than those previously predicted based on directional changes alone.

49

50 **Keywords** Global warming, acidification, invertebrates, fish, meta-analysis, climate stressors

51

52 **INTRODUCTION**

53 The rapid increase in atmospheric carbon dioxide is changing our climate at a pace never observed before,
54 with consequences on global biodiversity and ultimately human well-being¹. Ocean warming (OW), ocean
55 acidification (OA), caused by the increased partial pressure of carbon dioxide ($p\text{CO}_2$) in seawater, and
56 deoxygenation represent the three greatest climatic threats to marine life². Dramatic effects of these
57 three drivers have already been observed not only at the organism level but also at the scale of entire
58 ecosystems³. Examining the impacts of climate change on marine life has been one of the most rapidly
59 growing fields of research⁴. Research shows that OW increases energetic costs and decreases the survival
60 of marine organisms and that OA impacts invertebrates more than fish through adverse effects on
61 survival, calcification, growth and development⁵⁻¹¹. Additional factors such as life-stage, taxa and
62 acclimation time have been demonstrated to significantly alter the sensitivity of marine organisms to
63 climate change drivers^{5,7-8,12-14}. Recently, experimental designs have increased in complexity and realism
64 to account for the interaction of simultaneous climate change drivers although the combined effect of
65 deoxygenation with OW or OA remains understudied^{11,15}.

66 An inherent challenge to the richness of the published literature documenting effects of climate drivers is
67 to design quantitative syntheses that summarize results while accounting for the diversity of systems
68 tested. Previous meta-analyses testing effects on similar taxa and biological responses have found varying
69 magnitudes of climate driver effects and even different directions of changes (Fig. 1). While publication
70 biases and decline effects (i.e., decreasing effect of a driver over time) may contribute to this
71 heterogeneity¹⁶⁻²², conflicting results also arise from differences in methods used to pool data since meta-
72 analyses have either been performed on metrics individually (e.g., “growth rate”, “size”, “weight”²⁰),
73 grouped by category (e.g., “growth”^{11,14}) or all pooled together (e.g., “overall sensitivity”¹³). While testing
74 effects on categories of biological responses rather than on individual metrics increases the statistical
75 power of meta-analyses, this approach requires to attribute a direction to each metric, i.e., whether an
76 increase of the metric is beneficial or detrimental to fitness, so that metrics of opposite directions (e.g.,
77 mortality and survival) do not cancel out when aggregated. However, in most cases, the effect of a metric’s
78 increase on fitness remains uncertain or is context-dependent. For example, an increase in boldness is
79 linked to longer exploration periods which might result in more success in foraging for food but also may
80 increase mortality due to increased exposure to predators²³⁻²⁵. Similarly, although increases in respiration
81 rates are generally considered to be positively linked to fitness in meta-analyses, such increases can also
82 indicate higher metabolic needs that come at the expense of growth and reproduction²⁶⁻²⁷. Hence,
83 changes in metrics may result in trade-offs rather than in unequivocal benefits or costs to fitness and, for
84 most metrics, it remains challenging to confidently determine their relation to fitness.

85 Many meta-analyses have dealt with the ambiguous relation of metrics to fitness by assuming a positive
86 effect in all cases except when a negative effect on fitness is clearly established (e.g., mortality, shell
87 damage)^{5,7,11}. However, this assumption may result in mislabeling the direction of more ambiguous
88 metrics, ultimately leading to meaningful but opposite changes in metrics canceling out when averaged
89 and underestimating climate impacts²⁸. This risk is amplified when results are pooled across species,
90 ecosystems, and climates because of the importance of species-specific traits in mediating responses to
91 climate change drivers^{13,29} and because benefits provided by traits are context-dependent. Some analyses
92 have taken these specificities into account by summarizing results at the taxa level⁷, for given species
93 traits¹⁴, life-stages¹¹, or by presenting individual effect sizes in addition to means⁸. However,
94 disaggregating data comes with the trade-off of lower statistical robustness and generates multiple
95 heterogeneous results that obscure overall trends.

96 A different approach is therefore needed to overcome our limited understanding of the effect of metrics'
97 changes on fitness and to mitigate the risks of underestimating effects when pooling data. We propose
98 that testing for deviations of biological responses, i.e., absolute distance to reference value, can be used
99 to complement the traditional directional change approach, i.e., relative distance to reference value, to
100 detect impacts of climate drivers on marine life (Fig. 2). We argue that testing for deviations of biological
101 response to climate drivers is meaningful because any significant deviation from the reference state of a
102 metric value, whether “positive” or “negative”, can cause cascading changes up to community and
103 ecosystem levels³⁰⁻³². Testing for deviation of metrics rather than for directional changes is a widespread
104 approach in medical fields such as human physiology and cognition³³⁻³⁴ and has recently been applied to
105 test the effects of environmental drivers on the abundance of fish species³⁵.
106 Here, we conduct a meta-analysis testing for deviations in biological responses under climate change
107 drivers to complement the directional meta-analytical approach that has so far dominated this field. We
108 first review metrics measured in the literature and evaluate which ones can confidently be linked to either
109 adverse or positive effects on fitness, which is necessary to interpret results from directional meta-
110 analyses. Then, we test the effects of OW, OA, and their combination on marine organisms by evaluating
111 both directional changes and deviations in ten categories of biological responses. We analyze impacts of
112 climate drivers for invertebrates and fish separately and for three intensity levels of OW and OA: levels
113 predicted for 2100 under IPCC Representative Concentration Pathways 6.0 and 8.5 (RCP 6 and RCP 8.5),
114 and levels exceeding RCP 8.5 (hereafter “extreme level”). Finally, we compare significant effects detected
115 when testing for directional changes with those detected when testing for deviations. We found
116 significant deviational effects of climate drivers in twice as many biological responses of fish and
117 invertebrates than when testing for directional effects. Widespread deviations of responses were
118 detected even under moderate intensity levels (IPCC RCP 6) of OW and OA for 2100 while directional
119 changes were mostly limited to higher intensity levels (RCP 8.5 and extreme). Our results highlight the
120 risks of underestimating the impacts of climate change on biological response and reveal impacts of
121 climate change that were until now hidden by counterbalancing effects.

122

123 **RESULTS AND DISCUSSION**

124 Relation of metrics to fitness

125 We identified 217 studies that investigated the combined effect of OA and OW on marine organisms,
126 yielding 3,162 control-treatment comparisons testing different species, climate driver levels, or metrics.
127 We grouped metrics into ten categories of biological responses, and restricted data extraction to two
128 metrics per biological response per study, selecting the metrics most frequently measured in the literature
129 (see Methods and Supplementary Data 2 for details on metric selection). This resulted in the extraction
130 of data documenting 110 metrics, which were evaluated by experts’ judgment for their effect on fitness
131 (Supplementary Data 4). Five out of the ten biological response categories included over ten metrics (Fig.
132 3), with physiology and behavior being measured through the broadest range of metrics (n = 34 and n =
133 20 respectively). Only four biological responses (biodiversity, biomechanics, reproduction, and survival)
134 were entirely measured by metrics for which an increase is associated with a non-ambiguous (i.e., positive
135 or negative) effect on fitness (Fig. 3). By contrast, 50 to 80% of metrics used to measure the six other
136 biological responses (behavior, calcification, development, growth, metabolism, physiology) have an
137 ambiguous relation to fitness either because of lack of knowledge or because of context-dependent
138 effects.

139

140 Directional effects of climate drivers

141 Following the approach used in previous meta-analyses^{5-11,14}, we first tested for directional effects of
142 climate drivers on biological responses using logarithm response ratios (lnRR). Due to recent research
143 efforts focusing on previously understudied biological responses, we also synthesized the effect of OA and

144 OW on a community-level response, i.e., invertebrate biodiversity, and increased the number of
145 organism-level responses evaluated for fish and invertebrates in comparison to previous meta-analyses
146 (Fig. 1). However, we did not find any study investigating the effects of combined OA and OW on fish
147 biomechanics or biodiversity. We found that most biological responses (seven out of ten for invertebrates
148 and five out of eight for fish) were significantly affected by OW or OA (Fig. 4). OA negatively impacted
149 most biological responses of invertebrates (behavior, biomechanics, calcification, development, growth,
150 reproduction, survival) but only affected one of eight biological responses of fish (decrease in growth).
151 These results are consistent with previous meta-analyses^{6-7,10,16} and reflect the reliance of invertebrates
152 on the availability of carbonate ions, which decreases under OA³⁷⁻³⁸, to build their shells and skeletons^{7,36}.
153 By contrast, fish can tolerate higher OA levels than invertebrates³⁹ due to their elaborate acid-base
154 regulation system⁴⁰ and to their bony skeleton composed of calcium phosphate rather than calcium
155 carbonate⁴¹. We did not find any directional effect of OA on fish behavior, although this could be due to
156 the diversity of fish species pooled or to the diversity of behavioral metrics considered jointly and should
157 be interpreted with caution. The effect of OA on fish behavior is presently a matter of debate^{19,21,28,42-44}.
158 OW had more effects on the biological responses of fish than invertebrates (Fig. 4). Stimulation of
159 metabolism and inhibition of survival were observed for both fish and invertebrates, but decrease in
160 development and reproduction were only observed for fish. Larger impacts of OW on fish compared to
161 invertebrates have been hypothesized to derive from greater increases in metabolic costs for this taxa⁴⁵.
162 In comparison to previous meta-analyses, we found similar directional effects of responses to OW on
163 invertebrates but fewer effects of OA on fish (Fig. 1). The combination of OW and OA (OW + OA) resulted
164 in fewer and smaller effects than OA alone on invertebrates, or OW alone on fish (Fig. 4). These results
165 suggest antagonistic effects of OW and OA, which support findings from previous studies^{7,11}, although
166 context-dependent synergistic and additive effects have also been reported⁶. When significant, responses
167 of invertebrates to OW + OA mostly mirrored responses to OA while for fish they mostly mirrored
168 responses to OW (Fig. 4), reflecting the climate driver most impactful to these respective taxa.

169

170 Impact of climate driver level

171 The number of biological responses affected by OW and OA, as well as the magnitude of these responses,
172 increased with the intensity level of climate drivers (Fig. 5, Supplementary Table 1). For invertebrates,
173 exposure to RCP 6 levels of climate drivers did not induce any directional response. Yet, under RCP 8.5
174 levels, OW increased metabolism, OA decreased survival, reproduction, growth, development,
175 calcification and biomechanics, and their combination increased metabolism and decreased calcification.
176 Similarly, we found only two significant effects of RCP 6 level drivers on fish directional responses:
177 inhibition of growth under OW and increases of behavioral responses under OW + OA. Effects on fish were
178 more pronounced under RCP 8.5 levels: OW decreased survival and development and enhanced
179 metabolism while OA reduced growth and their combination inhibited development. More directional
180 responses were affected under extreme levels of drivers (exceeding RCP 8.5) for both invertebrates and
181 fish (Fig. 5). These trends are consistent with previous results on OW or OA individually^{13-14,46} and
182 document, for the first time, this pattern for the combination of these drivers. Currently, RCP 8.5 levels of
183 climate drivers have been tested six-fold more often than RCP 6 levels. The underrepresentation of less
184 severe levels of climate drivers hinders our ability to evaluate the ecological outcomes associated with
185 achieving different RCP trajectories and limits our capacity to predict and manage for near-term impacts
186 of OW and OA. The smaller sample size associated with RCP 6 levels might also contribute to the limited
187 effects detected in this study and calls for further research effort.

188 The intensity level of an experiment depends on the choice of its control value, which should account for
189 the mean local environmental conditions but also for the variability and extreme conditions that
190 organisms experienced during their development. However, $p\text{CO}_2$ control values used in studies are
191 sometimes based on $p\text{CO}_2$ values for the open ocean, which can strongly differ from local coastal $p\text{CO}_2$

192 conditions⁴⁷⁻⁴⁸. For this reason, it has been suggested to measure intensity levels of experimental OA using
193 a $\Delta p\text{CO}_2$ exposure index based on local $p\text{CO}_2$ upper conditions rather than on control values provided by
194 studies⁴⁶. Applying this approach, we found a significant correlation between the $\Delta p\text{CO}_2$ exposure index
195 and the magnitude of both directional and deviational responses, yet the data fit was similar to that based
196 on $\Delta p\text{CO}_2$ as provided in studies (Supplementary Fig. 2). Similarly, responses of invertebrates to RCP 6,
197 RCP 8.5, and extreme levels of OA were stable using either study-based or exposure index $\Delta p\text{CO}_2$, i.e., 75%
198 and 79% of significant responses were shared using both approaches for directional and deviational effect
199 sizes, respectively (Supplementary Fig. 3-4). While the exposure index approach is currently restricted to
200 sessile organisms and $p\text{CO}_2$ treatments, adapting this methodology to accommodate the study of
201 additional climate drivers and their combination, as well as mobile organisms, could provide further
202 insights to elucidate drivers of organisms' response to climate change.

203 204 Deviations of biological responses

205 Because of the diversity of species, experimental designs, and metrics tested in the literature, and because
206 of the predominance of metrics with ambiguous relation to fitness, we posit that restricting analyses of
207 climate impacts to mean directional changes across studies can be misleading. When pooling different
208 species and metrics, changes of opposite direction can cancel out, masking individually significant changes
209 (Fig. 2). This is problematic as the deviation of any response from its reference state holds biological
210 significance by altering the balance at the cellular, organism, or ecosystem scale. Deviation of responses
211 requires thorough consideration and testing when evaluating climate change impacts and cannot be
212 captured by meta-analyses based on relative effect size. For this reason, we converted relative effect size
213 into absolute effect size ($|\ln\text{RR}|$) to calculate the average deviation in biological responses across studies.
214 By mathematical construction, all significant directional changes translate into significant deviations, but
215 significant deviations can be found in the absence of significant directional change, because unlike relative
216 effect sizes, absolute effect sizes do not cancel out when averaged (Fig. 2).

217 We found that OW, OA, and their combination caused significant deviations in all biological responses of
218 invertebrates and fish, except for fish calcification and fish reproduction under OA (Fig. 6). For a given
219 climate driver, significant effects were detected in up to eight times more responses when testing for
220 absolute deviations than for directional changes (Fig. 7). This was especially true for biological responses
221 described through numerous metrics with ambiguous effects on fitness, such as behavior and physiology
222 (Fig. 3), which supports our hypothesis that antagonistic effects might be hidden when testing for
223 directional changes in such responses. We also found significant deviations of most biological responses
224 of invertebrates under OW and of fish under OA, for which we had detected limited directional changes
225 (Fig. 7). Similarly, we found significant deviations in the behavior and physiology of fish and invertebrates
226 under OW + OA whereas no directional change was detected. This is in line with the finding that a number
227 of behavioral effects in fishes can be mediated by neurophysiological or sensory mechanisms²², the effects
228 of which may be revealed only when deviations rather than directional changes are taken into account.
229 Moreover, we observed significant deviations in the responses of invertebrates to RCP 6 levels, whereas
230 no directional changes were detected. In contrast, we found no additional effect of RCP 6 level drivers on
231 fish responses when testing for absolute deviations compared to testing for directional changes. The
232 deviation of responses under OW + OA closely mirrored that of responses under OW or OA alone,
233 depending on taxa and response, and globally followed a trend of antagonistic effect of OW + OA.
234 Although the challenge of including ambiguous metrics in meta-analyses has been previously
235 recognized¹⁶, the most common approach has been to exclude them from analyses or to assign them a
236 positive direction as a default before pooling them⁵⁻⁷. Our results suggest that these approaches
237 underestimate the effects of climate change because ambiguous metrics that are pooled can be
238 antagonistic and cancel out in the overall average effect size. The only alternative approach has been to

239 report metrics separately²⁰ or to analyze metrics that have opposite directionalities in independent
240 categories (e.g., boldness being assessed separately from other behavioral metrics¹⁴).

241

242 Effect of life stage and acclimation time

243 Organisms' life stage (embryo, larvae, juvenile, or adult) had a significant effect on responses to climate
244 drivers. In both fish and invertebrates, early life stages (embryo, larvae, juveniles) displayed more
245 significant directional responses than adults (Supplementary Fig. 5-6, Supplementary Table 2). Early life
246 stage invertebrates predominantly displayed significant decreases in responses (Supplementary Fig. 5)
247 while early life stage fish displayed both significant increases and decreases. Under OW and OA + OW but
248 not OA alone, biological responses of fish embryos were decreased and those of juveniles were increased.
249 Biological responses of fish larvae were decreased under OA and increased under OW. For both
250 invertebrates and fish, deviations of responses were significant and similar in magnitude across life stages
251 and climate drivers, with the exception of embryos' responses that were lower in magnitude. Lower
252 magnitude of deviations, but higher magnitude of directional response of embryos compared to more
253 advanced life stages, could be due to the less ambiguous and less diverse metrics measured on embryos,
254 typically related to survival and "normality" of developmental processes, leading to fewer
255 counterbalancing effects when computing overall relative effect size. The higher sensitivity of early life
256 stages to climate drivers has been found in some, but not all, previous meta-analyses and has been
257 attributed to their lack of regulation and protection mechanisms to cope with environmental changes
258 (Sampaio et al.¹¹ vs. Cattano et al.¹⁴). Conversely, acclimation time had limited to no effect on directional
259 and deviational responses of organisms (Supplementary Fig. 7-8). This is consistent with previous meta-
260 analyses that did not find a clear effect of acclimation time on organisms' response⁷, and suggest that the
261 influence of acclimation time is likely overshadowed by stronger drivers of responses at the meta-
262 analytical scale, such as life stage, metric category, or intensity of climate driver level.

263

264 From deviations in the responses of organisms to ecological shifts

265 The relevance of examining deviational effects of climate drivers is linked to characteristics of biological
266 processes from the cellular to the ecosystem level. Over evolutionary time scales, organisms have
267 adjusted their metabolic machinery to achieve physiological homeostasis at the lowest metabolic cost
268 possible within the range of conditions of their local environment⁴⁹. Any deviation from an optimal
269 setpoint of homeostasis, whether originating from a metric increase or decrease, is energetically costly as
270 it induces metabolic regulation and, in some cases, compensatory responses⁵⁰. If abiotic conditions vary
271 within the evolutionarily experienced maxima and minima, physiological regulation will ensure
272 homeostasis, yet regulatory metabolic costs will usually rise with increasing deviation from the setpoint⁵¹.
273 As such, deviation in physiological responses might provide a valuable indicator of the level of stress that
274 organisms are experiencing.

275 At the population and ecosystem scales, antagonistic responses of different species to climate drivers are
276 unlikely to result in a net absence of change as reflected by directional effect sizes, but rather in a shift of
277 community composition and ecosystem structure⁵²⁻⁵³. Indeed, an increase in the growth rate of a given
278 species will induce cascading effects to predators and prey through trophic interactions, and to
279 competitors because of finite resource availability, resulting in significant shifts in the ecosystem
280 structure. For example, OA has been observed to decrease the relative feeding performance of bivalves
281 and sea urchins in comparison to gastropods^{20,54}, and to increase the relative growth of turf algae in
282 comparison to kelp⁵⁴. Taken together, these changes induced a shift in the habitat-forming species of this
283 ecosystem from kelp to turf algae⁵⁴. Similarly, studies investigating the effects of climate change on marine
284 biodiversity have reported reshuffling of species rather than a net loss^{53,55}. None of these shifts can be
285 detected at the meta-analytical level by averaging relative distances to reference states but can be
286 detected by averaging absolute distances, i.e., deviations in responses. However, we acknowledge that

287 testing for deviation is less conservative than testing for directional effects because the former decreases
288 the variability of results thereby increasing the magnitude or significance of climate effects. Therefore, we
289 suggest that deviation and directional analyses should be performed jointly.

290

291 Perspective and future directions

292 Although experimental designs have increased in complexity to better reflect real-life systems, several
293 knowledge gaps and limitations remain and hinder our understanding of current and future impacts of
294 climate change on marine life. Most studies we reviewed relied on short exposure times to test impacts
295 of climate drivers (51 ± 7 days; mean \pm SE), which cannot account for long-term adaptive responses
296 through phenotypic plasticity or adaptation across generations. Conversely, the effects of short, acute
297 climate drivers, such as heat waves or extreme OA events, remain paradoxically understudied in
298 comparison to the gradual effects of OA and OW¹¹. This limits our capacity to predict near-term impacts
299 of climate change, characterized by increased frequency and intensity of extreme events and milder
300 average increases in OW, OA, and other climate drivers⁵⁶. This represents a problematic mismatch with
301 the timescale of information needed to inform present-day adaptive management interventions
302 attempting to limit impacts and enhance the resilience of socio-ecological systems within the upcoming
303 decade rather than at the end-of-the century. Another important consideration is the role played by
304 environmental variability in the adaptive capacity of organisms. Most studies investigating biological
305 effects of climate drivers have been conducted by exposing organisms to stable experimental conditions
306 even though environmental variability is the norm in nature⁴⁶. While evidence remains scarce, recent
307 studies have shown that organisms tend to be more tolerant to climate change drivers when exposed to
308 fluctuating conditions^{47,57}.

309 Finally, more knowledge on the mechanisms that link biological changes to ecosystem structure is needed
310 to predict how deviations or directional changes of responses at the organism level translate into
311 ecosystem-level shifts. This involves conducting experiments investigating multi-species systems and
312 biotic interactions, measuring community-level indicators such as species richness, evenness, functional
313 redundancy or trophic structure, as well as conducting in-situ experiments. While designing empirical
314 studies that test for community-level shifts is challenging, models can provide valuable insight on this
315 matter (e.g., ecosystem-level impacts from changes in fish boldness⁵⁸).

316

317 Our study constitutes an important step forward in documenting the impacts of ocean warming, ocean
318 acidification, and their combination on marine life by assessing the broadest range of biological responses
319 to date and by testing both directional changes and deviations of these responses. We argue that metrics
320 commonly pooled in meta-analyses have predominantly ambiguous or context-dependent effects on
321 fitness, which results in mean effect sizes that are difficult to interpret and that likely underestimate
322 climate impacts. We found that many biological responses that appear unaffected when testing for
323 directional effects are, in fact, significantly deviated from their reference state, suggesting more pervasive
324 effects of climate change than previously thought. While more work is needed to ascertain the impact of
325 deviations in organism level responses at the ecosystem level, accounting for counterbalancing effects
326 when averaging responses across metrics and species is a fundamental step towards precautionary
327 assessments of climate change impacts on organisms.

328

329 **METHODS**

330 Literature search and data collection

331 Systematic literature search strategy. We performed our systematic literature search on Google Scholar
332 and ISI Web of Science following the PRISMA methodology⁵⁹ (Supplementary Fig. 1). The following search
333 string was used for ISI Web of Science: (ocean acidification OR carbon dioxide OR CO₂) AND (warming OR
334 temperature) AND (fish OR invertebrate* OR mollusk* OR echinoderm* OR crustacean* OR cnidaria OR

335 bryozoan* OR marine organism*). For Google Scholar we searched the following combination of words:
336 ocean acidification, carbon dioxide, CO₂, warming, temperature, ocean warming, fish, invertebrate for
337 each year between 2008 and 2022 and limited the search results to 100 per year. All papers published
338 before January 2022 were included in our systematic review. In addition, the reference lists from the
339 retrieved publications, as well as those from previously published meta-analyses on effects of OA or OW
340 on marine life^{11,19}, were cross-checked to find publications containing relevant data.

341
342 Screening criteria. We retained studies that tested the combined effects of OA and OW on marine
343 ectotherms, i.e. fish (teleosts, elasmobranchs) or invertebrates (annelida, arthropoda, bryozoa, cnidaria,
344 echinodermata, mollusca, nematoda, platyhelminthes, porifera). To be considered in the analysis,
345 publications had to include at least two *p*CO₂ and two temperatures in a full factorial design and include
346 information on control and treatment values of *p*CO₂ and temperature. This was done so that
347 antagonistic, synergistic or additive effects of OA and OW could be evaluated. Only studies that used CO₂
348 or CO₂-enriched gas to manipulate *p*CO₂ were kept, those using acid addition were excluded. We counted
349 studies as testing for OA or OW effects if this was the explicit goal of the experiment. For example, we
350 excluded a study that registered an increase of *p*CO₂ of 86 µatm because this was only an undesired
351 parameter change that occurred during a temperature experiment⁶⁰. We excluded all studies that did not
352 report mean values, sample size or one of the following error types: variance, standard error, standard
353 deviation or 95% confidence interval.

354
355 Data extraction. We extracted quantitative data from the text, tables, and graphs of publications using
356 the software GetData, Graph Digitizer and WebPlotDigitizer. For each study, we extracted information on
357 the biology and ecology of the studied organism (phylum, family, species, life-stage, climatic zone, habitat)
358 as well as information on the experimental design of the study (climate driver tested, climate driver level
359 and biological metric measured). For each tested driver in a study, we recorded control and treatment
360 values (temperature in °C, *p*CO₂ in µatm), and the associated biological response variables (mean, error
361 and sample size). Control conditions for *p*CO₂ and temperature were chosen based on the conditions at
362 which the organism was sampled in the wild and acclimated, or in the case of laboratory-raised organisms,
363 the conditions stated in the paper as representing the common biotic range for that organism.
364 Experiments that tested temperature or *p*CO₂ conditions that were lower than the control conditions
365 were not extracted. In the case of studies testing for more factors than OA and OW (e.g., oxygen, salinity,
366 food level), we only extracted data from experiments in which those factors had control values. Data from
367 trans-generational studies were kept only for the parent generation, i.e., the generation that was exposed
368 to control levels of the climate change driver before experiencing OW and OA.

369
370 Classification of metrics. We grouped metrics among ten biological responses: behavior, biodiversity,
371 biomechanics, calcification, development, growth, physiology, reproduction, metabolism and survival
372 (Supplementary Data 3). Then, we attributed a direction (positive, negative or ambiguous) to each metric
373 according to whether an increase in that metrics' value was considered beneficial, detrimental or
374 ambiguous (and/or unknown) to the organism, species or community. The scores were given based on
375 the expertise of five of the co-authors (KA, PD, MM, CC, FCM), who reviewed metrics and assigned them
376 a direction independently (Supplementary Data 4). We adopted the most conservative approach, i.e., we
377 only assigned a positive or negative direction to a metric if all five co-authors unanimously agreed on that
378 direction. We classified all other metrics as having an ambiguous direction (Supplementary Data 4). When
379 two metrics measuring the same phenomenon were measured in opposite ways across studies (e.g.,
380 mortality rate and survival rate, morphological normality (%) and abnormality (%)), we converted all

381 metrics to their positive measurement (e.g., survival rate and morphological normality) to increase the
382 statistical power of our analysis.

383
384 Climate scenarios. We attributed one of three climate scenarios (RCP 6, RCP 8.5 or extreme) to
385 experiments based on the difference of $p\text{CO}_2$ and temperature (T) between control and treatment values.
386 The attribution of climate scenarios followed projections from IPCC 2022¹: RCP 6 scenario for experiments
387 with $\Delta p\text{CO}_2 < 350 \mu\text{atm}$ or $\Delta T < 2 \text{ }^\circ\text{C}$; RCP 8.5 scenario for experiments with $350 < \Delta p\text{CO}_2 < 750 \mu\text{atm}$ or 2
388 $^\circ\text{C} < \Delta T < 4 \text{ }^\circ\text{C}$, and extreme climate scenario when $\Delta p\text{CO}_2 > 750 \mu\text{atm}$ or $\Delta T > 4 \text{ }^\circ\text{C}$. For experiments
389 combining $p\text{CO}_2$ and temperature treatments, an RCP scenario was only attributed if $\Delta p\text{CO}_2$ and ΔT
390 corresponded to the same scenario. The $\Delta p\text{CO}_2$ treatments in the selected studies ranged from $78 \mu\text{atm}$ ⁶¹
391 to $7894 \mu\text{atm}$ ⁶² and the ΔT ranged from $0.9 \text{ }^\circ\text{C}$ ⁶³ to $12.8 \text{ }^\circ\text{C}$ ⁶⁴.

392
393 Number of data points extracted per study. Multiple data points were extracted from the same study
394 when they corresponded to different drivers, RCP scenarios, species, life-stages, geographic locations,
395 habitats, or biological responses (e.g., a survival metric and a reproduction metric). For biodiversity
396 metrics, the least taxa-aggregated values were extracted because we considered biodiversity at the
397 community level. When a study reported results on different ontogeny (e.g., number of days since
398 hatching) within one life-stage (e.g., juvenile), data corresponding to the most advanced time point within
399 that life-stage was extracted. When experiments were repeated in summer and winter, we kept the data
400 from the summer experiment as this was the season most commonly investigated. When data were
401 collected from several spawning periods, we kept data from the main spawning event. In all other cases
402 (e.g., several clones measured, different time of the day investigated, several body sizes used), values
403 provided in the article were averaged. The variance of the averaged values $s_{\text{aggregated}}^2$ was calculated
404 using equation 1:

$$405 \quad s_{\text{aggregated}}^2 = \frac{1}{k^2} \cdot \sum_i s_i^2 \quad (1)$$

406 where s_i is the variance associated with the averaged value i and k is the total number of values being
407 averaged.

408
409 Number of metrics extracted per study. When several metrics from the same category were reported in
410 one paper (e.g., the activity of three different enzymes, that all fall within the physiology category), we
411 selected a maximum of two metrics to avoid the over-representation of any given study in our dataset.
412 The selected metrics were chosen based on a priority ranking. First, we assigned priority to metrics
413 classified as positive or negative over those classified as ambiguous. Then we inspected if metrics were
414 correlated and only kept the most inclusive one. For example, if condition index, shell length and shell
415 weight were measured, we kept only condition index to avoid codependency of metrics within the data
416 set. When metrics were correlated and equally inclusive, we kept the metric most commonly measured
417 across studies. For example, activities of the two enzymes superoxide dismutase (SOD) and glutathione S-
418 transferase were considered to be correlated because they are both proxies for antioxidant capacity, but
419 SOD was kept because it was measured in more studies. If metrics from the same category were as
420 commonly measured across studies, we chose one randomly. Our choices of selected metrics from studies
421 that reported several metrics from the same category are listed in Supplementary Data 2.

422
423 Data analysis

424 For each treatment i , a relative effect size was calculated as the natural logarithm response ratio of the
425 mean response in treatment i over the mean response in control i (equation 2):

$$426 \quad \ln \text{RR}_i = \ln \left(\frac{\bar{x}_{\text{treatment},i}}{\bar{x}_{\text{control},i}} \right) \quad (2)$$

427 In the case of metrics for which an increase is detrimental to fitness (i.e., negative direction,
428 Supplementary Data 3), the log of the inverse (i.e., control/treatment) was calculated, so that an increase
429 would result in a negative effect size. This formula was also applied in the case of metrics of positive
430 direction but with negative values, because an increase of a negative value corresponds to a negative
431 outcome. If an experiment reported a mean value of zero for its treatment or control, or if an experiment
432 reported values of opposite sign (one positive and one negative) for its control and treatment, the
433 experiment was not included in the analysis because they do not allow to calculate log ratios.

434
435 Additionally, for each experiment i , an absolute effect size $|\ln RR_i|$ was calculated as follow (equation 3):

$$436 \quad \ln RR_i = \left| \ln \left(\frac{\bar{x}_{\text{treatment},i}}{\bar{x}_{\text{control},i}} \right) \right| \quad (3)$$

437 Variance, standard deviations and confidence intervals associated with control and treatment mean
438 values were converted into standard errors ($SE_{\text{treatment},i}$ and $SE_{\text{control},i}$ respectively). The within-
439 experiment variance v_i associated the experiment i was then calculated for both relative and absolute
440 effect size as (equation 4):

$$441 \quad v_i = \frac{SE_{\text{treatment},i}^2}{\bar{x}_{\text{treatment},i}^2} + \frac{SE_{\text{control},i}^2}{\bar{x}_{\text{control},i}^2} \quad (4)$$

442 Experiments measuring survival, morphological abnormalities or fertilization success sometimes had null
443 or extremely low within-study variance, e.g., as a result of all individuals surviving. Because the `rma()`
444 function of the `{metafor}` package has a within-study variance threshold of 0.0001, we attributed the fixed
445 value of 0.0001 to $n=24$ experiments (from a total of 3,162 experiments) for which variance fell under that
446 threshold. We verified that this did not result in a disproportionate weight given to these data points by
447 checking the weights attributed by models to these studies, as detailed in Supplementary Data 1.

448
449 Random-effect model. We performed all the parametric data analyses using the `{metafor}` package⁶⁵⁻⁶⁶.
450 We used a weighted random-effects model to quantify the effect of treatments on variables. Effect sizes
451 were weighted accounting for both the within- and among-study variance components. We conducted a
452 meta-analysis for each combination of taxa (2 levels: invertebrate or fish), climate driver (3 levels: OW,
453 OA and their combination); climate driver level (RCP 6, RCP 8.5 and extreme); and category of biological
454 response (ten levels, see above), which led to 54 models. Model heterogeneity, residual heterogeneity,
455 degrees of freedom and p-values associated with the 54 models tested are detailed in Supplementary
456 Data 5 and 6 (deviation and directional meta-analyses, respectively). We also carried out meta-analyses
457 across these same categories but grouping climate scenarios together (Supplementary Table 3-4). A
458 treatment was considered to have a significant effect on a variable when the 95% confidence interval
459 calculated by the model did not overlap zero.

460
461 Covariates. The influence of the driver intensity (RCP 6, RCP 8.5 and extreme) on both relative and
462 absolute effect sizes was investigated at the taxa x biological response x driver level when the dataset had
463 $n \geq$ ten data points and featured at least two different scenarios populated by at least two data points.
464 The model heterogeneity and residual heterogeneity associated with these models are shown in
465 Supplementary Table 1 and 5 (directional and deviation meta-analyses, respectively).

466 The influence of life stage (embryo, larvae, juveniles or adults) and acclimation time (number of days of
467 acclimation, square-root transformed) on both relative and absolute effect sizes was investigated at the
468 taxa x driver level. Model heterogeneity, residual heterogeneity, and associated p-values are provided in
469 Supplementary Table 2.

470
471 Sensitivity analyses. To test the robustness of our meta-analysis results, we carried out several sensitivity
472 analyses¹⁸ to detect: (1) the presence of a publication bias and of outliers using visual observation of

473 funnel plots (Supplementary Data 1); (2) the sensitivity of our results to publication bias using the
474 Rosenthal's fail-safe number (N_{fs}); (3) whether a different outcome could be obtained when correcting for
475 publication bias using Duval and Tweedie's Trim and Fill test⁶⁷⁻⁶⁸. The Rosenthal's fail-safe number is an
476 estimation of the number of additional non-significant effect sizes required for a significant meta-analysis
477 result to become non-significant. This allowed us to check the sensitivity of results to uncaptured studies.
478 This risk is estimated to be high if N_{fs} is below $5n+10$, with n the number of data points in the meta-
479 analysis. This was not the case for any of our results (Supplementary Table 6). Duval and Tweedie's Trim
480 and Fill test could only be applied to our relative meta-analyses, which were all found to be robust to
481 potential publication bias under this test (Supplementary Table 6).

482 Outlying effect sizes were identified through the visual observation of funnel plots (Supplementary Data
483 1). Additionally, their associated weight was checked using forest plots (Supplementary Data 1) to make
484 sure that no unique value was overwhelmingly influencing the overall effect size¹⁸. The studies
485 corresponding to outlying points were scrutinized for factors that could explain the extreme values found.
486 Because no flaws or marked differences in experimental design of these studies were found, no points
487 were excluded from our meta-analyses.

488
489 Effect of upper environmental conditions. We tested the effect of local upper environmental conditions,
490 as a proxy for local variability, on the biological responses of organisms. We limited this analysis to OA
491 following a detailed methodology developed to test the effects of local pCO_2 extremes on organisms'
492 responses to OA⁴⁶. This methodology can only be applied under a certain number of conditions, i.e., when
493 studied organisms are sessile or have low-vagility and when pCO_2 data from sampling sites are available.
494 Furthermore, it has not yet been extended to evaluate the effects of local temperature extremes. This
495 would require a novel approach that takes into account other bioclimatic metrics such as diurnal
496 temperature ranges, isothermality, temperature seasonality and range, microclimate as well as thermal
497 acclimation capacity. In addition, many studies do not report the date of animal collection, the start date
498 of experiments, and thermal conditions in the laboratory before commencement of experiments, which
499 would be crucial information for such an approach. This adds to the difficulties associated with developing
500 this approach, which is outside the scope of this study. We checked studies included in our meta-analysis
501 against the selection criteria given in Vargas et al.⁴⁶. We retained species selected in Vargas et al.⁴⁶ and
502 included 24 additional sessile and gregarious or low-vagility benthic species (Supplementary Table 7). Out
503 of the 217 studies used in our meta-analyses, 62 met all selection criteria, including 25 studies that were
504 already included in Vargas et al.⁴⁶ and 37 additional studies (Supplementary Fig. 9).

505 Upper environmental conditions at the sampling sites of these 62 studies originated from global database
506 and local buoys deployments, and were extracted from the supplementary information in Vargas et al.⁴⁶.
507 We then calculated (1) a study-based ΔpCO_2 and (2) a ΔpCO_2 exposure index by calculating the difference
508 between the pCO_2 treatment value and (1) the pCO_2 control value as given in studies, or (2) upper local
509 environmental conditions, respectively.

510 We tested the relation between study-based ΔpCO_2 and ΔpCO_2 exposure index and the response of
511 organisms using linear regression models. We attributed climate scenarios to each data point following
512 the same procedure as described in the "Climate scenario" section but using the ΔpCO_2 exposure index
513 instead of the study-based ΔpCO_2 . Because studies that met the criteria necessary to calculate a ΔpCO_2
514 exposure index were much fewer than our initial study pool, we performed tests at the biological response
515 x intensity level regardless of sample sizes. Results from linear regressions are shown in Supplementary
516 Figure 2 and directional and deviational responses by biological response and by intensity level using both
517 ΔpCO_2 approaches in Supplementary Figure 3 and 4, respectively. The model heterogeneity and residual
518 heterogeneity associated with these models are shown in Supplementary Table 8.

519

520 **DATA AVAILABILITY**

521 The data used and generated in this study have been deposited in the Zenodo database under accession
522 code 10223034 [[Hidden impacts of climate change on biological responses of marine life](https://doi.org/10.10223034)
523 (zenodo.org)]⁶⁹. Source data are provided with this paper.

524

525 **CODE AVAILABILITY**

526 The codes used to perform this study are publicly available in the Zenodo database under accession code
527 10223034 [[Hidden impacts of climate change on biological responses of marine life](https://doi.org/10.10223034)
528 (zenodo.org)]⁶⁹.

529

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756
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771 Lars Meiertoberens and Qolbin Saliim, respectively, from the Noun Project (CC BY 3.0).

772

773 **AUTHOR CONTRIBUTIONS STATEMENT**

774 P. D. initiated the study. K. A. led the data compilation to which P. H. M., C. P. G., M. E. L., M. E. B., S. M.,
775 D. A. F., M. M., C. C. contributed. K. A., M. M., C. C., F. C. M., P. D. assigned directions to metrics. J. J.
776 performed with assistance of J. C. the meta-analyses. K. A., J. J., P. H. M., F. C. M., J. C., P. D. interpreted
777 and discussed the results. K. A. and J. J. wrote the first draft with support of P. H. M., F. C. M., M. A. P. and
778 P. D. All co-authors contributed to the final version.

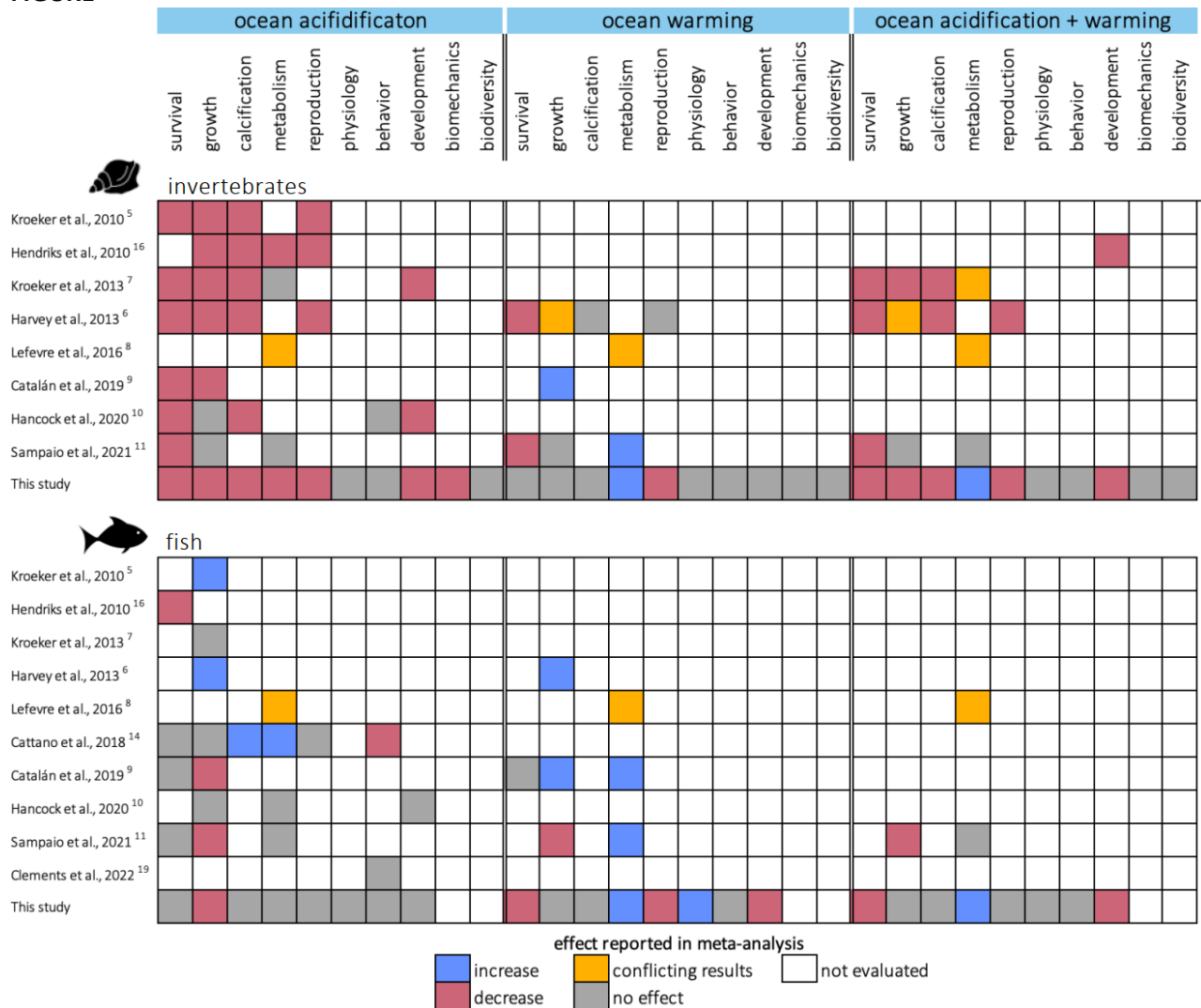
779

780 **COMPETING INTERESTS STATEMENT**

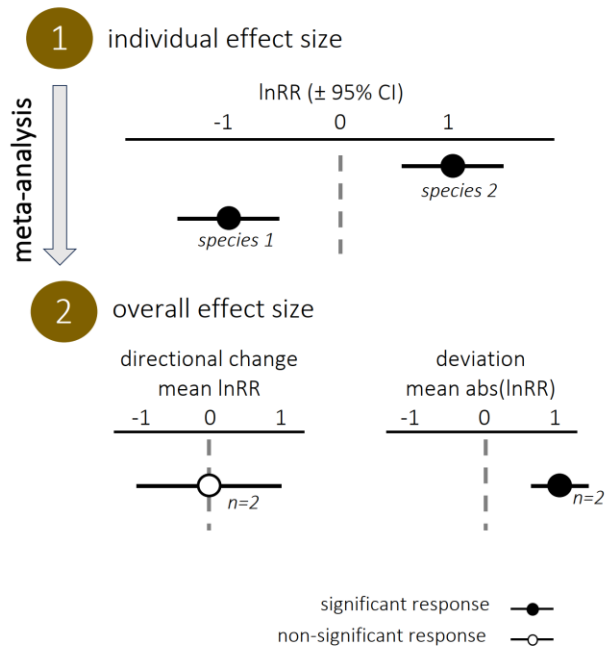
781 The authors declare no competing interests.

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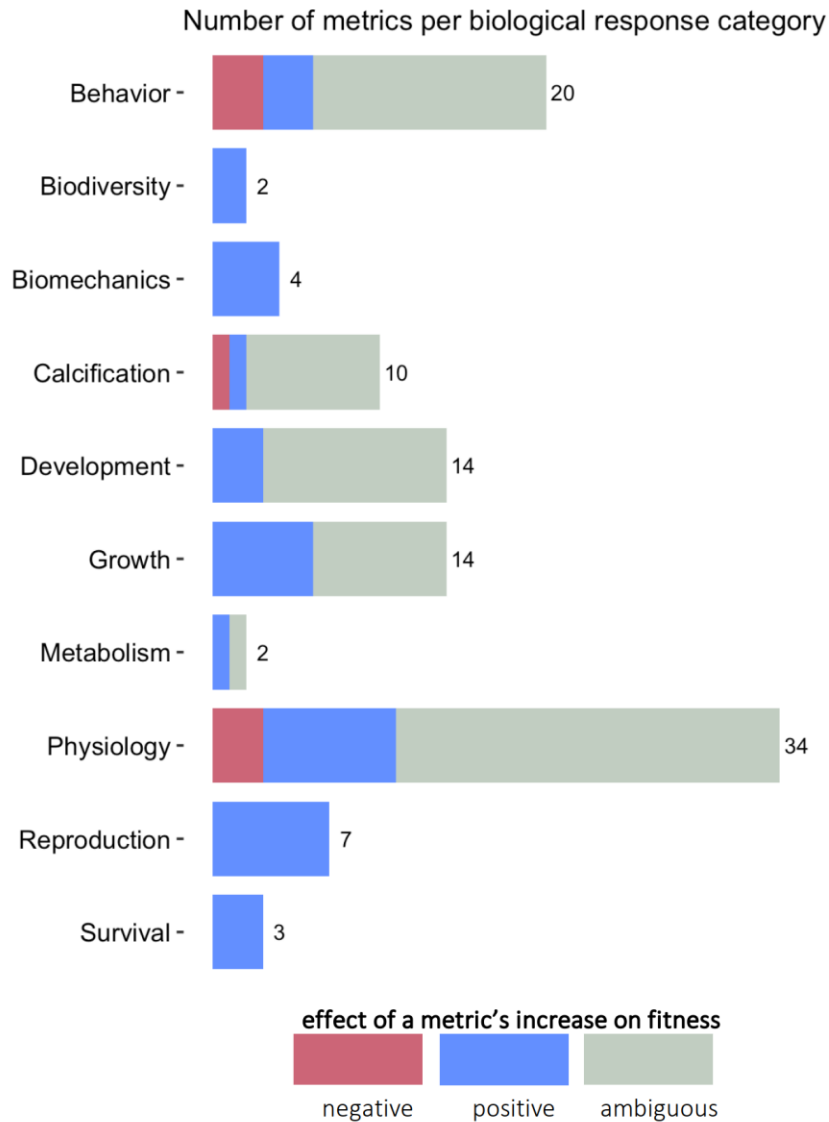
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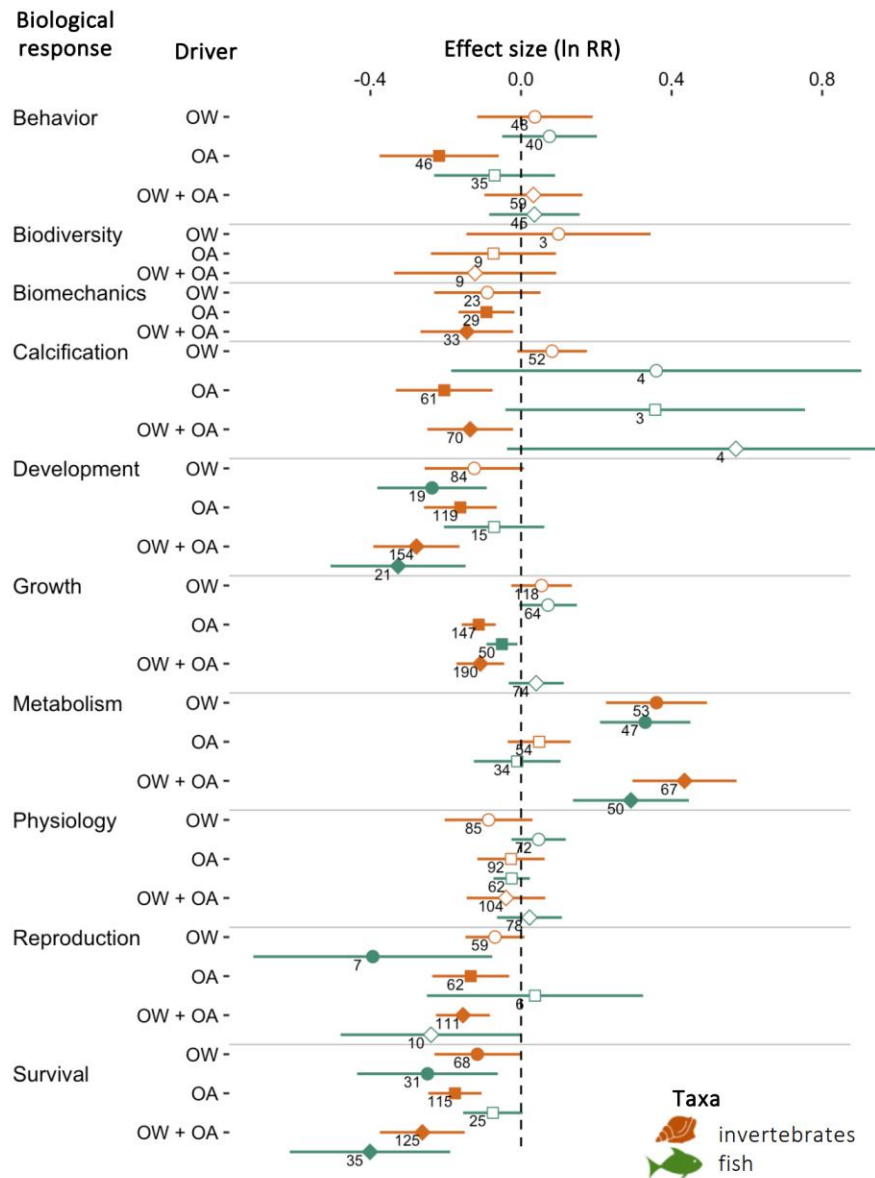
785
 786 Figure 1: Results of previous meta-analyses on the effects of climate drivers on biological responses of
 787 marine animals. Different colored tiles indicate that a given meta-analysis reported increases (blue),
 788 decreases (magenta), conflicting results (i.e., different effects depending on variables tested that were
 789 not pooled in the study; orange), no effect (gray) or did not evaluate (white) a given biological response
 790 of invertebrates and fish to ocean acidification, ocean warming and their combination. Data was assessed
 791 at the 95% confidence interval level. Fish and mollusc icons are available at on the noun project website:
 792 <https://thenounproject.com/icon/fish-1464319/> and [https://thenounproject.com/icon/mollusk-](https://thenounproject.com/icon/mollusk-5552214)
 793 [5552214](https://thenounproject.com/icon/mollusk-5552214), respectively.
 794
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796
 797 Figure 2: Diagram showcasing differences between directional changes and deviations. Antagonistic
 798 responses at the experiment level can cancel out when computing a mean directional change (InRR). By
 799 contrast, significant responses are revealed when computing mean deviation (abs(InRR)). CI = Confidence
 800 interval, n = sample size
 801
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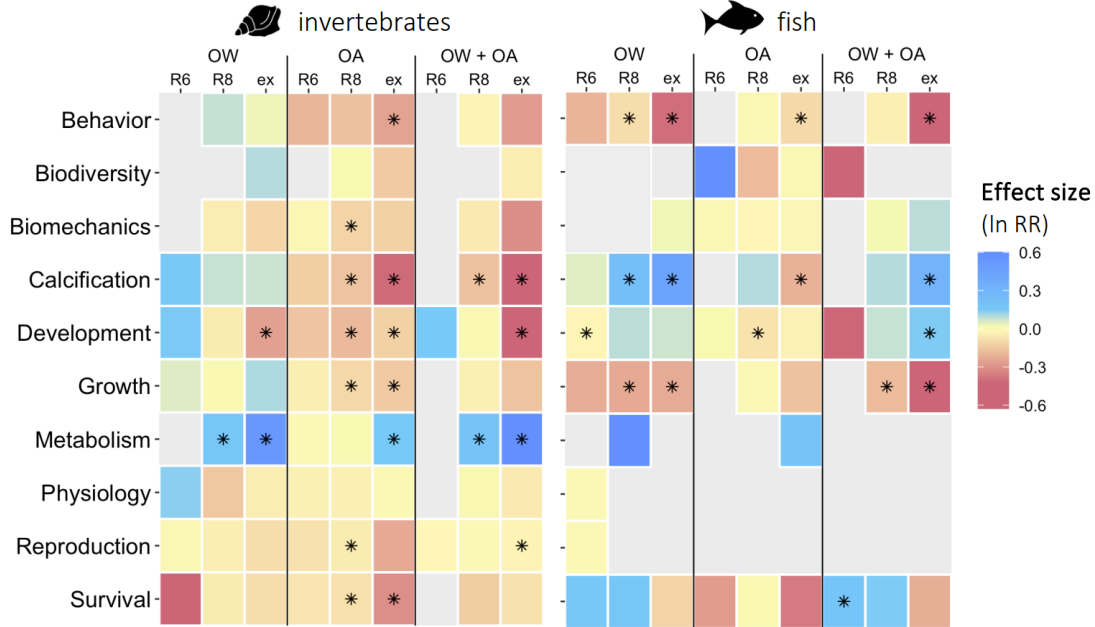


803
 804 Figure 3: Effect of metric's increase on fitness and number of metrics per biological response category.
 805 Magenta, blue and gray fillings indicate metrics for which an increase leads to a negative, positive, or
 806 ambiguous effect on fitness, respectively. The number of metrics per biological response category
 807 included in our analysis is indicated next to each bar. Source data are provided as a Source Data file
 808
 809

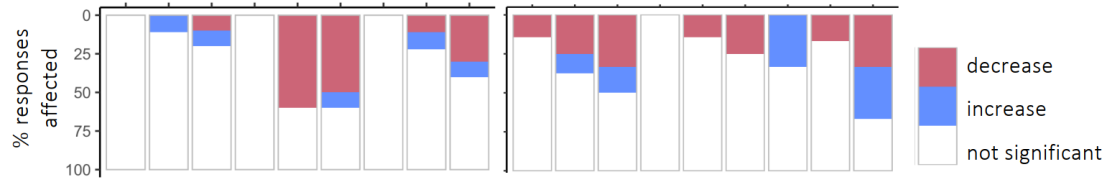


810
811 Figure 4: Directional effects of climate drivers on biological responses of marine animals. Directional effect
812 (lnRR) of ocean warming (OW, circles), ocean acidification (OA, pCO₂, squares) and their combination (OW
813 + OA, diamonds) on the biological responses of invertebrates (orange) and fish (green). Significant
814 deviations are denoted by filled symbols (resp., open symbols for non-significant symbols). Error bars
815 represent 95% confidence intervals associated with the mean effect size and numbers indicate sample
816 sizes. Source data are provided as a Source Data file. Fish and mollusc icons are available at on the noun
817 project website: <https://thenounproject.com/icon/fish-1464319/> and
818 <https://thenounproject.com/icon/mollusk-5552214/>, respectively.
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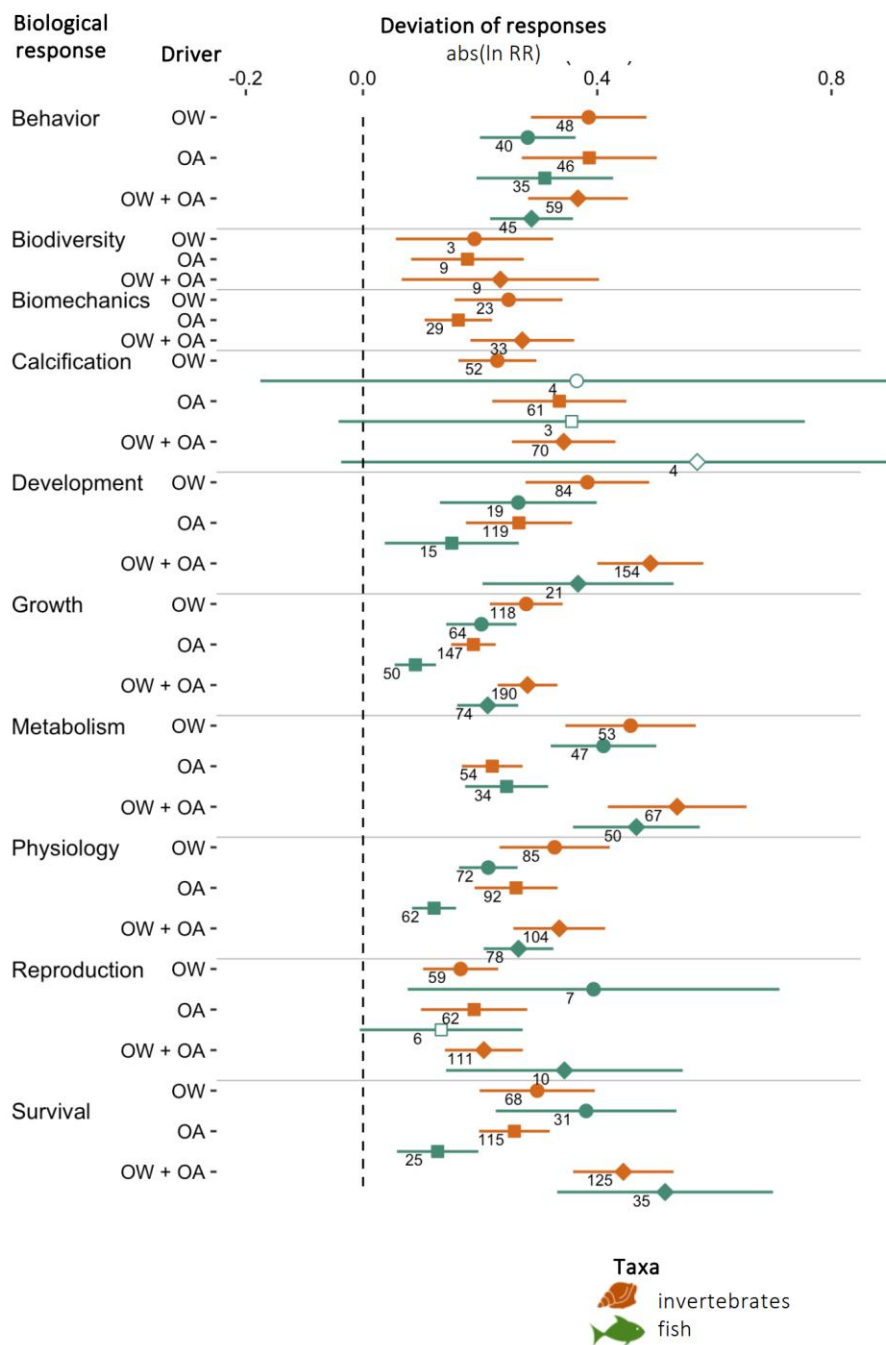
a. Directional effect of climate drivers by intensity level



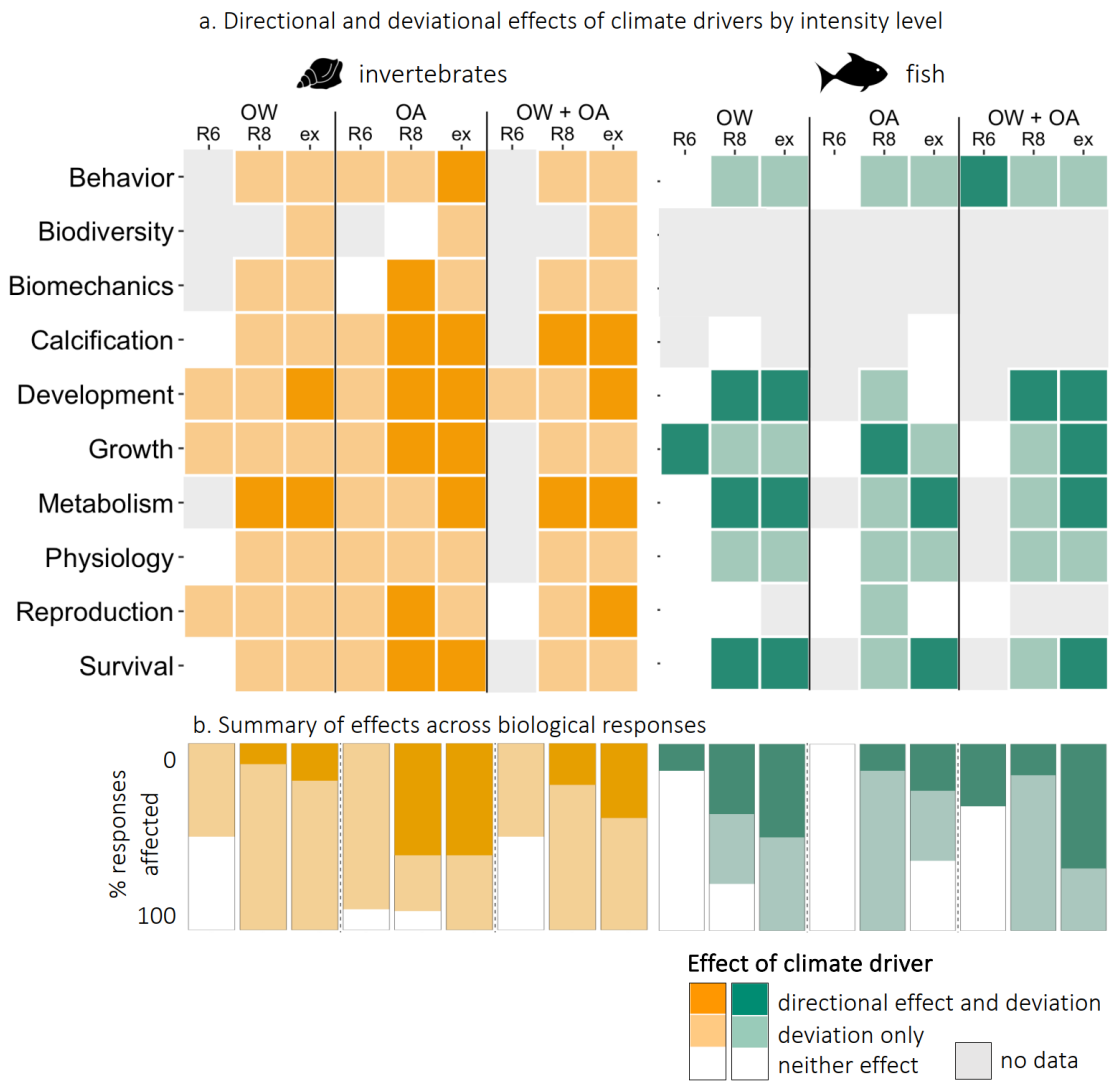
b. Summary of directional effects across biological responses



821
 822 Figure 5: Directional effects of climate drivers by intensity level. (a) Directional effects (lnRR) of ocean
 823 warming (OW), ocean acidification (OA) and their combination (OW + OA) on biological responses of
 824 invertebrates (left) and fish (right) according to the intensity level considered (representative
 825 concentration pathway (RCP) 6 (R6), RCP 8.5 (R8), and extreme (ex)). The magnitude of effects is
 826 represented by a blue (increase) to magenta (decrease) color scale. Light gray tiles indicate an absence of
 827 data. Asterisks indicate significant effects. (b) Proportion of biological responses for which a significant
 828 increase (blue) or decrease (magenta) was found for each climate driver and intensity level. Source data
 829 are provided as a Source Data file. Fish and mollusc icons are available at on the noun project website:
 830 <https://thenounproject.com/icon/fish-1464319/> and [https://thenounproject.com/icon/mollusk-](https://thenounproject.com/icon/mollusk-5552214)
 831 5552214, respectively.
 832
 833



834
 835 Figure 6: Deviation effects of climate drivers on biological responses of marine animals. Deviation
 836 (abs(lnRR)) of biological responses of invertebrates (orange) and fish (green) to ocean warming (OW,
 837 circles), ocean acidification (OA, squares) and their combination (OW + OA, diamonds). Significant
 838 deviations are denoted by filled symbols (resp., open symbols for non-significant symbols). Error bars
 839 represent 95% confidence intervals associated with the mean effect size and numbers indicate sample
 840 sizes. Source data are provided as a Source Data file. Fish and mollusc icons are available at on the noun
 841 project website: <https://thenounproject.com/icon/fish-1464319/> and
 842 <https://thenounproject.com/icon/mollusk-5552214/>, respectively.



844
 845 Figure 7: Directional and deviational effects of climate drivers. (a) Effects of ocean warming (OW), ocean
 846 acidification (OA), and their combination (OW + OA), on biological responses of invertebrates (left, orange)
 847 and fish (right, green) according to the intensity level considered (representative concentration pathway
 848 (RCP) 6 (R6), RCP 8.5 (R8) or extreme (ex)). Colors indicate significant directional and deviational effects
 849 (darkest colored tiles), significant deviational effects only (light colored tiles), or no significant effects
 850 (white tiles). Absence of data is indicated by gray tiles. (b) Proportion of biological responses (%) for which
 851 significant directional and deviational effects (darkest colored tiles), significant deviational effects only
 852 (light colored tiles), or no significant effects (white tiles) were found under each intensity level for
 853 invertebrates (left, orange) and fish (right, green). Note that all significant directional effects imply
 854 significant deviations. Source data are provided as a Source Data file. Fish and mollusc icons are available
 855 at on the noun project website: <https://thenounproject.com/icon/fish-1464319/> and
 856 <https://thenounproject.com/icon/mollusk-5552214/>, respectively.

