

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

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- 1 Hidden impacts of ocean warming and acidification on biological responses of marine animals
- 2 3

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revealed through meta-analysis

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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
- calcification, survival, and metabolism, and significant deviations in twice as many biological responses,
 including physiology, reproduction, behavior, and development. Widespread deviations of responses are
- 44 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 (pCO_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 survival, calcification, growth and development⁵⁻¹¹. Additional factors such as life-stage, taxa and 61 62 acclimation time have been demonstrated to significantly alter the sensitivity of marine organisms to climate change drivers^{5,7-8,12-14}. Recently, experimental designs have increased in complexity and realism 63 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 biases and decline effects (i.e., decreasing effect of a driver over time) may contribute to this 70 71 heterogeneity¹⁶⁻²², conflicting results also arise from differences in methods used to pool data since metaanalyses have either been performed on metrics individually (e.g., "growth rate", "size", "weight"²⁰), 72 grouped by category (e.g., "growth"^{11,14}) or all pooled together (e.g., "overall sensitivity"¹³). While testing 73 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 increase mortality due to increased exposure to predators²³⁻²⁵. Similarly, although increases in respiration 80 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
- that testing for deviations of biological responses, i.e., absolute distance to reference value, can be used
- 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
- 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
- approach in medical fields such as human physiology and cognition³³⁻³⁴ and has recently been applied to
 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 climate change that were until now hidden by counterbalancing effects.
- 121 122

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.
- 130

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 (InRR). 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 on the availability of carbonate ions, which decreases under OA³⁷⁻³⁸, to build their shells and skeletons^{7,36}. 152 153 By contrast, fish can tolerate higher OA levels than invertebrates³⁹ due to their elaborate acid-base regulation system⁴⁰ and to their bony skeleton composed of calcium phosphate rather than calcium 154 carbonate⁴¹. We did not find any directional effect of OA on fish behavior, although this could be due to 155 156 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}. OW had more effects on the biological responses of fish than invertebrates (Fig. 4). Stimulation of 158 159 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 context-dependent synergistic and additive effects have also been reported⁶. When significant, responses 166 167 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 fish (Fig. 5). These trends are consistent with previous results on OW or OA individually^{13-14,46} and 181 182 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.

The intensity level of an experiment depends on the choice of its control value, which should account for the mean local environmental conditions but also for the variability and extreme conditions that organisms experienced during their development. However, pCO_2 control values used in studies are sometimes based on pCO_2 values for the open ocean, which can strongly differ from local coastal pCO_2

conditions⁴⁷⁻⁴⁸. For this reason, it has been suggested to measure intensity levels of experimental OA using 192 193 a ΔpCO_2 exposure index based on local pCO_2 upper conditions rather than on control values provided by 194 studies⁴⁶. Applying this approach, we found a significant correlation between the $\Delta p CO_2$ exposure index 195 and the magnitude of both directional and deviational responses, yet the data fit was similar to that based 196 on ΔpCO_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 Δp CO₂, 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 pCO₂ 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 (|InRR|) 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.

Although the challenge of including ambiguous metrics in meta-analyses has been previously recognized¹⁶, the most common approach has been to exclude them from analyses or to assign them a positive direction as a default before pooling them⁵⁻⁷. Our results suggest that these approaches underestimate the effects of climate change because ambiguous metrics that are pooled can be antagonistic and cancel out in the overall average effect size. The only alternative approach has been to report metrics separately²⁰ or to analyze metrics that have opposite directionalities in independent
 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 possible within the range of conditions of their local environment⁴⁹. Any deviation from an optimal 268 269 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 though 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
- the variability of results thereby increasing the magnitude or significance of climate effects. Therefore, we
- 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 \pm 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}.

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

329 **METHODS**

328

- 330 Literature search and data collection
- 331 Systematic literature search strategy. We performed our systematic literature search on Google Scholar
- 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
- temperature) AND (fish OR invertebrate* OR mollusk* OR echinoderm* OR crustacean* OR cnidaria OR

bryozoan* OR marine organism*). For Google Scholar we searched the following combination of words: ocean acidification, carbon dioxide, CO₂, warming, temperature, ocean warming, fish, invertebrate for each year between 2008 and 2022 and limited the search results to 100 per year. All papers published before January 2022 were included in our systematic review. In addition, the reference lists from the retrieved publications, as well as those from previously published meta-analyses on effects of OA or OW 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 pCO_2 and two temperatures in a full factorial design and include 346 information on control and treatment values of pCO2 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 CO_2 -enriched gas to manipulate pCO_2 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 pCO_2 of 86 μ atm because this was only an undesired parameter change that occurred during a temperature experiment⁶⁰. We excluded all studies that did not 351 352 report mean values, sample size or one of the following error types: variance, standard error, standard 353 deviation or 95% confidence interval.

354

Data extraction. We extracted quantitative data from the text, tables, and graphs of publications using 355 356 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, pCO₂ in µatm), and the associated biological response variables (mean, error 361 and sample size). Control conditions for pCO_2 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 pCO_2 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

metrics to their positive measurement (e.g., survival rate and morphological normality) to increase thestatistical 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 pCO_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 $\Delta pCO_2 < 350 \mu atm$ or $\Delta T < 2$ °C; RCP 8.5 scenario for experiments with 350 < $\Delta pCO_2 < 750 \mu atm$ or 2 388 $^{\circ}C < \Delta T < 4 \,^{\circ}C$, and extreme climate scenario when $\Delta pCO_2 > 750 \,\mu$ atm or $\Delta T > 4 \,^{\circ}C$. For experiments 389 combining pCO_2 and temperature treatments, an RCP scenario was only attributed if ΔpCO_2 and ΔT 390 corresponded to the same scenario. The $\Delta p CO_2$ treatments in the selected studies ranged from 78 μ atm⁶¹ 391 to 7894 μ atm⁶² and the Δ T ranged from 0.9 °C⁶³ to 12.8 °C⁶⁴.

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 provided in the article were averaged. The variance of the averaged values $s_{aggregated}^2$ was calculated 403 404 using equation 1:

405

$$s_{\text{aggregated}}^2 = \frac{1}{\nu^2} \cdot \sum_i s_i^2$$
 (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
$$\ln \operatorname{RR}_{i} = \ln \left(\frac{\bar{x}_{\operatorname{treatment},i}}{\bar{x}_{\operatorname{control},i}} \right)$$
(2)

In the case of metrics for which an increase is detrimental to fitness (i.e., negative direction, Supplementary Data 3), the log of the inverse (i.e., control/treatment) was calculated, so that an increase would result in a negative effect size. This formula was also applied in the case of metrics of positive direction but with negative values, because an increase of a negative value corresponds to a negative outcome. If an experiment reported a mean value of zero for its treatment or control, or if an experiment reported values of opposite sign (one positive and one negative) for its control and treatment, the 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 |In RR_i| was calculated as follow (equation 3):

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

437 Variance, standard deviations and confidence intervals associated with control and treatment mean 438 values were converted into standard errors ($SE_{treatment,i}$ and $SE_{control,i}$ 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
$$v_i = \frac{SE_{\text{treatment},i}^2}{\bar{x}_{\text{treatment},i}^2} + \frac{SE_{\text{control},i}^2}{\bar{x}_{\text{control},i}^2} \qquad (4)$$

Experiments measuring survival, morphological abnormalities or fertilization success sometimes had null or extremely low within-study variance, e.g., as a result of all individuals surviving. Because the rma() function of the {metafor} package has a within-study variance threshold of 0.0001, we attributed the fixed value of 0.0001 to n=24 experiments (from a total of 3,162 experiments) for which variance fell under that threshold. We verified that this did not result in a disproportionate weight given to these data points by 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 $n \ge ten data$ 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 Conducated at the taxa scenarios populated by at least two data points.

- 465 Supplementary Table 1 and 5 (directional and deviation meta-analyses, respectively).
- The influence of life stage (embryo, larvae, juveniles or adults) and acclimation time (number of days of acclimation, square-root transformed) on both relative and absolute effect sizes was investigated at the taxa x driver level. Model heterogeneity, residual heterogeneity, and associated p-values are provided in 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 Rosenthal's fail-safe number (N_{fs}); (3) whether a different outcome could be obtained when correcting for 474 publication bias using Duval and Tweedie's Trim and Fill test⁶⁷⁻⁶⁸. The Rosenthal's fail-safe number is an 475 estimation of the number of additional non-significant effect sizes required for a significant meta-analysis 476 477 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).

Outlying effect sizes were identified through the visual observation of funnel plots (Supplementary Data
Additionally, their associated weight was checked using forest plots (Supplementary Data 1) to make
sure that no unique value was overwhelmingly influencing the overall effect size¹⁸. The studies
corresponding to outlying points were scrutinized for factors that could explain the extreme values found.
Because no flaws or marked differences in experimental design of these studies were found, no points
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
- and local buoys deployments, and were extracted from the supplementary information in Vargas et al.⁴⁶. We then calculated (1) a study-based ΔpCO_2 and (2) a ΔpCO_2 exposure index by calculating the difference between the *p*CO₂ treatment value and (1) the *p*CO₂ control value as given in studies, or (2) upper local 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 $\Delta p CO_2$. Because studies that met the criteria necessary to calculate a $\Delta p CO_2$
- 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 $\Delta p CO_2$ 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
- 523 (zenodo.org)]⁶⁹. Source data are provided with this paper.

524 525 CODE AVAILABILITY

The codes used to perform this study are publicly available in the Zenodo database under accession code
 10223034 [Hidden impacts of climate change on biological responses of marine life

- 528 <u>(zenodo.org)</u>]⁶⁹.
- 529

530 **REFERENCES**

531 1. Pörtner, H. O., Roberts, D. C., Tignor, M., Poloczanska, E. S., Mintenbeck, K., Algería, A., Craig, M.,
532 Langsdorf, S., Löschke, S., Möller, V., Okem, A. & Rama, B. Climate change 2022: Impacts, adaptation and
533 vulnerability (Cambridge University Press, Cambridge, UK and New York, NY, USA, 2022)
534 https://doi.org/10.1017/9781009325844

- 2. Hoegh-Guldberg, O., Jacob, D., Taylor, M., Bindi, M., Brown, S., Camilloni, I., Diedhiou, A., Djalante, R.,
- 536 Ebi, K.L., Engelbrecht, F., Guiot, J., Hijioka, Y., Mehrotra, S., Payne, A., Seneviratne, S. I., Thomas, A.,
- 537 Warren, R. & Zhou, G. Impacts of 1.5°C Global Warming on Natural and human systems. In: Global
- 538 Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial
- 539 levels and related global greenhouse gas emission pathways, in the context of strengthening the global 540 response to the threat of climate change, sustainable development, and efforts to eradicate poverty
- 541 [Masson-Delmotte, V., Zhai, P., Pörtner, H. -O., Roberts, D., Skea, J., Shukla, P. R., Pirani, A., Moufouma-
- 542 Okia, W., Péan, C., Pidcock, R., Connors, S., Matthews, J. B. R., Chen, Y., Zhou, X., Gomis, M. I., Lonnoy, E.,
- 543 Maycock, T., Tignor, M. & Waterfield, T. (eds.)] (Cambridge University Press, Cambridge, UK and New York, 544 NY, USA, 2018). https://doi.org/10.1017/9781009157940.005
- 545 3. Weiskopf, S. R., Rubenstein, M. A., Crozier, L. G., Gaichas, S., Griffis, R., Halofsky, J. E., Hyde, K. J. W., 546 Morelli, T. L., Morisette, J. T., Muñoz, R. C., Pershing, A. J., Peterson, D. L., Poudel, R., Staudinger, M. D., 547 Sutton-Grier, A. E., Thompson, L., Vose, J., Weltzin, J. F. & Whyte, K. P. Climate change effects on 548 biodiversity, ecosystems, ecosystem services, and natural resource management in the United 549 States. Science of the Total Environment 733, 137782 (2020). https://doi.org/ 550 10.1016/j.scitotenv.2020.137782
- 4. Riebesell, U. & Gattuso, J. -P. Lessons learned from ocean acidification research. Nature Climate Change
- 552 5, 12-14 (2015). https://doi.org/10.1038/nclimate2456
- 553 5. Kroeker, K. J., Kordas, R. L., Crim, R. N. & Singh, G. G. Meta-analysis reveals negative yet variable effects
- 554
 of
 ocean
 acidification
 on
 marine
 organisms.
 Ecology
 Letters
 13,
 1419-1434
 (2010).

 555
 https://doi.org/10.1111/j.1461-0248.2010.01518.x
- 6. Harvey, B. P., Gwynn-Jones, D. & Moore, P. J. Meta-analysis reveals complex marine biological
 responses to the interactive effects of ocean acidification and warming. Ecology and Evolution 3, 10161030 (2013). https://doi.org/10.1002/ece3.516
- 559 7. Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S., Duarte, C. M. & Gattuso, J. 560 -P. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with 561 warming. Clobal Change Biology 10, 1884, 1806 (2012). https://doi.org/10.1111/cpb.12170
- 561 warming. Global Change Biology 19, 1884-1896 (2013). https://doi.org/10.1111/gcb.12179
- 562 8. Lefevre, S. Are global warming and ocean acidification conspiring against marine ectotherms? A meta563 analysis of the respiratory effects of elevated temperature, high CO₂ and their interaction. Conservation
 564 Physiology 4(1), cow009 (2016). https://doi.org/10.1093/conphys/cow009
- 565 9. Catalán, I. A., Auch, D., Kamermans, P., Morales-Nin, B., Angelopoulos, N. V., Reglero, P., Sandersfeld,
- 566 T. & Peck, M. A. Critically examining the knowledge base required to mechanistically project climate
- 567 impacts: A case study of Europe's fish and shellfish. Fish and Fisheries 20, 501-517 (2019).

- 568 https://doi.org/10.1111/faf.12359
- 569 10. Hancock, A. M., King, C. K., Stark, J. S., McMinn, A. & Davidson, A. T. Effects of ocean acidification on 570 Antarctic marine organisms: A meta-analysis. Ecology and Evolution 10, 4495-4514 (2020).
- 571 https://doi.org/10.1002/ece3.6205
- 572 11. Sampaio, E., Santos, C., Rosa, I. C., Ferreira, V., Pörtner, H. -O., Duarte, C. M., Levin, L. A. & Rosa, R.
- 573 Impacts of hypoxic events surpass those of future ocean warming and acidification. Nature Ecology and Evolution E 211 221 (2021) https://doi.org/10.1028/c41550.020.01270.2
- 574 Evolution 5, 311-321 (2021). https://doi.org/10.1038/s41559-020-01370-3
- 575 12. Byrne, M. Impact of ocean warming and ocean acidification on marine invertebrate life history stages:
 576 vulnerabilities and potential for persistence in a changing ocean. Oceanography and Marine Biology (CRC
 577 Press : Boca Raton, FL, USA, 2011).
- 578 13. Wittmann, A. C. & Pörtner, H. -O.. Sensitivities of extant animal taxa to ocean acidification. Nature
 579 Climate Change 3, 995-1001 (2013). https://doi.org/10.1038/nclimate1982
- 580 14. Cattano, C., Claudet, J., Domenici, P. & Milazzo, M. Living in a high CO₂ world: a global meta-analysis
 581 shows multiple trait-mediated fish responses to ocean acidification. Ecological Monographs 88, 320-335
 582 (2018). https://doi.org/10.1002/ecm.1297
- 583 15. Boyd, P. W., Collins, S., Dupont, S., Fabricisus, K., Gattuso, J. P., Havenhand, J., Hutchins, D. A.,
- 584 Riebesell, U., Rintoul, M. S., Vichi, M., Biswas, H., Ciotti, A., Gao, K., Gehlen, M., Hurd, C. L., Kurihara, H.,
- 585 McGraw, C. M., Navarro, J. M., Nilsson, G. E., Passow, U. & Pörtner, H. -O. Experimental strategies to assess 586 the biological ramifications of multiple drivers of global ocean change - A review. Global Change Biology
- 587 24, 2239-2261 (2018). https://doi.org/10.1111/gcb.14102
- 16. Hendriks, I. E., Duarte, C. M. & Álvarez, M. Vulnerability of marine biodiversity to ocean acidification:
 A meta-analysis. Estuarine, Coastal and Shelf Science 86, 157-164 (2010).
 https://doi.org/10.1016/j.ecss.2009.11.022
- 591 17. Schooler, J. Unpublished results hide the decline effect. Nature 470, 437-437 (2011). 592 https://doi.org/10.1038/470437a
- 18. Page, M. J., Sterne, J. A. C., Higgins, J. P. T. & Egger, M. Investigating and dealing with publication bias
 and other reporting biases in meta-analyses of health research: A review. Research Synthesis Methods
 12, 248-259 (2021). https://doi.org/10.1002/jrsm.1468
- 19. Clements, J. C., Sundin, J., Clark, T. D. & Jutfelt, F. Meta-analysis reveals an extreme "decline effect" in
 the impacts of ocean acidification on fish behavior. PLOS Biology 20, e3001511 (2022).
 https://doi.org/10.1371/journal.pbio.3001511
- 599 20. Leung, J. Y. S., Zhang, S. & Connell, S. D. Is ocean acidification really a threat to marine calcifiers? A
- systematic review and meta-analysis of 980+ studies spanning two decades. Small 18, 2107407 (2022).
 https://doi.org/10.1002/smll.202107407
- 602 21. Munday, P. L. Reanalysis shows there is not an extreme decline effect in fish ocean acidification
 603 studies. PLoS Biology 20(11), e3001809 (2022). https://doi.org/10.1371/journal.pbio.3001809
- 604 22. Esbaugh, A. J. Recalibrating the significance of the decline effect in fish ocean acidification research.
 605 PLoS Biology 21(5), e3002113 (2023). https://doi.org/10.1371/journal.pbio.3002113
- Ward, A. J., Thomas, P., Hart, P. J. & Krause, J. Correlates of boldness in three-spined sticklebacks
 (Gasterosteus aculeatus). Behavioral Ecology and Sociobiology 55, 561-568 (2004).
 https://doi.org/10.1007/s00265-003-0751-8
- 609 24. Nannini, M. A., Parkos, J. & Wahl, D. H. Do behavioral syndromes affect foraging strategy and risk-
- taking in a juvenile fish predator? Transactions of the American Fisheries Society 141, 26-33 (2012).
 https://doi.org/10.1080/00028487.2011.639268
- 612 25. Mamuneas, D., Spence, A. J., Manica, A. & King, A.J. Bolder stickleback fish make faster decisions, but
- 613 they are not less accurate. Behavioral Ecology 26, 91-96 (2015). https://doi.org/10.1093/beheco/aru160
- 614 26. Ishimatsu, A., Hayashi, M. & Kikkawa, T. Fishes in high-CO₂, acidified oceans. Marine Ecology Progress
- 615 Series 373, 295-302 (2008). https://doi.org/10.3354/meps07823

- 616 27. Lemoine, N. P., & Burkepile, D. E. Temperature-induced mismatches between consumption and
- 617 metabolism reduce consumer fitness. Ecology 93, 2483-2489 (2012). https://doi.org/10.1890/12-0375.1
- 618 28. Esbaugh, A. J. Physiological implications of ocean acidification for marine fish: emerging patterns and 619 new insights. Journal of Comparative Physiology, Part B 188, 1-13 (2018).
- 620 https://doi.org/10.1007/s00360-017-1105-6
- 621 29. Estrada, A., Morales-Castilla, I., Caplat, P. & Early, R. Usefulness of species traits in predicting range 622 shifts. Trends in Ecology and Evolution 31, 190-203 (2016). https://doi.org/10.1016/j.tree.2015.12.014
- 623 30. Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W.,
- 624 Schreiber, S. J., Urban, M. C. & Vasseur, D. A. Why intraspecific trait variation matters in community
- 625 ecology. Trends in Ecology and Evolution 26, 183-192 (2011). https://doi.org/10.1016/j.tree.2011.01.009
- 626 31. Nagelkerken, I. & Munday, P. L. Animal behaviour shapes the ecological effects of ocean acidification
- and warming: moving from individual to community-level responses. Global Change Biology 22, 974-989
 (2016). https://doi.org/10.1111/gcb.13167
- 32. Sih, A., Cote, J., Evans, M., Fogarty, S. & Pruitt, J. Ecological implications of behavioural syndromes.
 Ecology Letters 15(3), 278-289 (2012). https://doi.org/10.1111/j.1461-0248.2011.01731.x
- 631 33. Alexander-Bloch, A., Huguet, G., Schultz, L. M., Huffnagle, N., Jacquemont, S., Seidlitz, J., Saci, Z.,
- Moore, T. M., Bethlehem, R. A. I., Mollon, J., Knowles, E. K., Raznahan, A., Merikangas, A., Chaiyachati, B.
- H., Raman, H., Schmitt, J. E., Barzilay, R., Calkins, M. E., Shinohara, R. T., Satterthwaite, T. D., Gur, R. C.,
 Glahn, D. C., Almasy, L., Gur, R. E., Hakonarson, H. & Glessner, J. Copy number variant risk scores
 associated with cognition, psychopathology, and brain structure in youths in the Philadelphia
- 636NeurodevelopmentalCohort.JAMAPsychiatry79,699-709(2022).637https://doi.org/10.1001/jamapsychiatry.2022.1017537537537537537
- 638 34. Ecker, C., Pretzsch, C. M., Bletsch, A., Mann, C., Schaefer, T., Ambrosino, S., Tillmann, J., Yousaf, A.,
- 639 Chiocchetti, A., Lombardo, M. V., Warrier, V., Bast, N., Moessnang, C., Baumeister, S., Dell'Acqua, F., Floris,
- D.L., Zabihi, M., Marquand, A., Cliquet, F., Leblond, C., Moreau, C., Puts, N., Banaschewski, T., Jones, E. J.
- H., Mason, L., Bölte, S., Meyer-Lindenberg, A., Persico, A. M., Durston, S., Baron-Cohen, S., Spooren, W.,
 Loth, E., Freitag, C. M., Charman, T., Dumas, G., Bourgeron, T., Beckmann, C. F., Buitelaar, J. K. & Murphy,
- D. G. M. Interindividual differences in cortical thickness and their genomic underpinnings in autism
 spectrum disorder. American Journal of Psychiatry 179, 242-254 (2022).
- 645 https://doi.org/10.1176/appi.ajp.2021.20050630
- 646 35. Erisman, B. E., Bolser, D. G., Ilich, A., Frasier, K. E., Glaspie, C. N., Moreno, P. T., Dell'Apa, A., de Mutsert,
- 647 K., Yassin, M. S., Nepal, S., Tang, T. & Sacco, A. E. A meta-analytical review of the effects of environmental
- 648 and ecological drivers on the abundance of red snapper (Lutjanus campechanus) in the U.S. Gulf of
- 649 Mexico. Reviews in Fish Biology and Fisheries 30, 437-462 (2020). https://doi.org/10.1007/s11160-020-650 09608-w
- 36. Doney, S. C., Fabry, V. J., Feely, R. A. & Kleypas, J. A. Ocean acidification: the other CO₂ problem. Annual
 Review of Marine Science 1, 169-192 (2009). https://doi.org/10.1146/annurev.marine.010908.163834
- 653 37. Schoepf, V., Grottoli, A., Warner, M., Cai, W. -J., Melman, T., Hoadley, K., Pettay, D., Hu, X., Li, Q., Xu,
- H., Wang, Y., Matsui, Y. & Baumann, J. Coral energy reserves and calcification in a high-CO₂ world at two
- 655 temperatures. PloS one 8, e75049 (2013). https://doi.org/10.1371/journal.pone.0075049
- 656 38. Gattuso, J. P., Magnan, A., Billé, R., Cheung, W. W. L., Howes, E. L., Joos, F. & Turley, C. Contrasting
 657 futures for ocean and society from different anthropogenic CO₂ emissions scenarios. Science 349(6243),
 658 aac4722 (2015). https://doi.org/10.1126/science.aac4722
- 659 39. Munday, P.L., Cheal, A. J., Dixson, D. L., Rummer, J. L. & Fabricius, K. E. Behavioural impairment in reef
- 660 fishes caused by ocean acidification at CO₂ seeps. Nature Climate Change 4(6), 487-492 (2014).
- 661 https://doi.org/10.1038/nclimate2195
- 66240. Claiborne, J. B., Edwards, S. L. & Morrison-Shetlar, A. I. Acid-base regulation in fishes: cellular and663molecularmechanisms.JournalofExperimentalZoology293(3),302-319

- 664 (2002). https://doi.org/10.1002/jez.10125
- 665 41. Brauner, C.J. & Val, A. L. Fish Physiology: Homeostasis and Toxicology of Non-Essential Metals 666 (Academic Press, 2019).
- 42. Clark, T. D., Raby, G. D., Roche, D. G., Binning, S. A., Speers-Roesch, B., Jutfelt, F. & Sundin, J. Ocean
 acidification does not impair the behaviour of coral reef fishes. Nature 577(7790), 370–375 (2020).
 https://doi.org/10.6084/m9.figshare.7871522
- 43. Munday, P. L., Dixson, D. L., Welch, M. J., Chivers, D. P., Domenici, P., Grosell, M., Heuer, R. M., Jones,
- 671 G. P., McCormick, M. I., Meekan, M., Nilsson, G. E., Ravasi, T. & Watson, S. A. Methods matter in repeating
- 672ocean acidification studies. Nature 586(7830), E20–E24 (2020). https://doi.org/10.1038/s41586-020-6732803-x
- 44. Williamson, P., Pörtner, H. O., Widdicombe, S. & Gattuso, J. P. Ideas and perspectives: When ocean
- acidification experiments are not the same, repeatability is not tested. Biogeosciences 18(5), 1787-1792
 (2021). https://doi.org/10.5194/bg-18-1787-2021
- 45. Rummer, J. L., Couturier, C. S., Stecyk, J. A. W., Gardiner, N. M., Kinch, J. P., Nilsson, G. E. & Munday,
- P. L. Life on the edge: thermal optima for aerobic scope of equatorial reef fishes are close to current day
- 679 temperatures. Global Change Biology 20, 1055–1066 (2014). https://doi.org/10.1111/gcb.12455
- 46. Vargas, C. A., Cuevas, L. A., Broitman, B. R., San Martín, V. A, Lagos, N. A, Gaitán-Espitia, J. D. & Dupont,
 S. Upper environmental pCO₂ drives sensitivity to ocean acidification in marine invertebrates. Nature
- 682 Climate Change 12, 200–207 (2022). https://doi.org/10.1038/s41558-021-01269-2
- 47. Vargas, C. A., Lagos, N. A., Lardies M. A., Duarte C., Manríquez P. H., Aguilera V. A., Broitman, B.,
 Widdicombe S. & Dupont S. Species-specific responses to ocean acidification should account for local
 adaptation and adaptive plasticity. Nature, Ecology and Evolution 1(4), 0084 (2017).
 https://doi.org/10.1038/s41559-017-0084
- 48. Thomsen, J., Stapp, L. S., Haynert, K., Schade, H., Danelli, M., Lannig, G., Wegner, K. M. & Melzner, F.
 Naturally acidified habitat selects for ocean acidification-tolerant mussels. Science Advances 3(4),
 e1602411 (2017). https://doi.org/10.1126/sciadv.1602411
- 690 49. Burton, T., Ratikainen, I. I. & Einum, S. Environmental change and the rate of phenotypic plasticity.
 691 Global Change Biology 28(18), 5337-5345 (2022). https://doi.org/10.1111/gcb.16291
- 692 50. DeWitt, T. J., Sih, A. & Wilson, D. S. Costs and limits of phenotypic plasticity. Trends in Ecology and 693 Evolution 13(2), 77-81 (1998). https://doi.org/10.1016/S0169-5347(97)01274-3
- 694 51. Pörtner, H. O., Bock, C. & Mark, F. C. Oxygen-and capacity-limited thermal tolerance: bridging ecology
 695 and physiology. Journal of Experimental Biology 220(15), 2685-2696 (2017).
 696 https://doi.org/10.1242/jeb.134585
- 52. Sperling, E. A., Frieder, C. A. & Levin, L. A. Biodiversity response to natural gradients of multiple
 stressors on continental margins. Proceedings of the Royal Society B: Biological Sciences 283(1829),
 20160637 (2016). https://doi.org/10.1098/rspb.2016.0637
- 53. Nagelkerken, I. & Connell, S. D. Ocean acidification drives global reshuffling of ecological communities.
 Global Change Biology 28, 7038-7048 (2022). https://doi.org/10.1111/gcb.16410
- 54. Connell, S. D., Doubleday, Z. A., Foster, N. R., Hamlyn, S. B., Harley, C. D. G., Helmuth, B., Kelaher, B.
 P., Nagelkerken, I., Rodgers, K. L., Sarà, G. & Russell, B. D. The duality of ocean acidification as a resource
- 704 and a stressor. Ecology 99(5), 1005-1010 (2018). https://doi.org/10.1002/ecy.2209
- 55. Timmers, M. A., Jury, C. P., Vicente, J., Bahr, K. D., Webb, M. K. & Toonen, R. J. Biodiversity of coral
 reef cryptobiota shuffles but does not decline under the combined stressors of ocean warming and
 acidification. Proceedings of the National Academy of Sciences 118(39), e2103275118 (2021).
 https://doi.org/10.1073/ pnas.2103275118
- 56. Bindoff, N. L., Cheung, W. W. L., Kairo, J. G., Arístegui, J., Guinder, V. A., Hallberg, R., Hilmi, N., Jiao,
- 710 N., Karim, M. S., Levin, L., O'Donoghue, S., Purca Cuicapusa, S. R., Rinkevich, B., Suga, T., Tagliabue, A. &
- 711 Williamson, P. Changing ocean, marine ecosystems, and dependent communities. In: IPCC Special Report

- on the Ocean and Cryosphere in a Changing Climate [Pörtner, H. -O., Roberts, D. C., Masson-Delmotte,
- 713 V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., Alegría, A., Nicolai, M., Okem, A., Petzold, J., Rama,
- B. & Weyer, N. M. (eds.)]. (Cambridge University Press, Cambridge, UK and New York, NY, USA, 2019).
 https://doi.org/10.1017/9781009157964.007
- 716 57. Tanvet, C., Camp, E., Sutton, J., Houlbreque, F., Thouzeau, G. & Rodolfo-Metalpa, R. Corals adapted to
- 717 extreme and fluctuating seawater pH increase calcification rates and have unique symbiont communities.
- 718 Ecology and Evolution 13, e10099 (2023). https://doi.org/10.1002/ece3.10099
- 58. Wang, W., Xu, N., Zhang, L., Andersen, K. H. & Klaminder, J. Anthropogenic forcing of fish boldness
 and its impacts on ecosystem structure. Global Change Biology 27(6), 1239-1249 (2021).
 https://doi.org/10.1111/gcb.15473
- 722 59. Page, M. J., McKenzie, J. E., Bossuyt, P. M., Boutron, I., Hoffmann, T. C., Mulrow, C. D., Shamseer, L.,
- 723 Tetylaff, J. M., Akl, E. A., Brennan, S. E., Chou, R., Glanville, J., Grimshaw, J. M., Hrobjarsson, A., Lalu, M.
- 724 M., Li, T., Loder, E. W., Mayo-Wilson, E., McDonald, S., McGuinness, L. A., Stewart, L. A., Thomas, J., Tricco,
- A. C., Welch, V. A., Whiting, P. & Moher, D. The PRISMA 2020 statement: an updated guideline for
 reporting systematic reviews. International Journal of Surgery 88, 105906 (2021).
 https://doi.org/10.1016/j.ijsu.2021.105906
- 728 60. Enzor, L. A., Zippay, M. L. & Place, S. P. High latitude fish in a high CO₂ world: Synergistic effects of
- elevated temperature and carbon dioxide on the metabolic rates of Antarctic notothenioids. Comparative
- 730 Biochemistry and Physiology, Part A 164, 154-161 (2013). https://doi.org/10.1016/j.cbpa.2012.07.016
- 731 61. Nowicki, J. P., Miller, G. M. & Munday, P. L. Interactive effects of elevated temperature and CO₂ on
- foraging behavior of juvenile coral reef fish. Journal of Experimental Marine Biology and Ecology 412, 4651 (2012). https://doi.org/10.1016/j.jembe.2011.10.020
- 734 62. Glandon, H. L., Kilbourne, K. H., Schijf, J. & Miller, T. J. Counteractive effects of increased temperature
- and pCO₂ on the thickness and chemistry of the carapace of juvenile blue crab, Callinectes sapidus, from
- the Patuxent River, Chesapeake Bay. Journal of Experimental Marine Biology and Ecology 498, 39-45
- 737 (2018). https://doi.org/10.1016/j.jembe.2017.11.005
- 738 63. Stubler, A. D., Furman, B. T. & Peterson, B. J. Sponge erosion under acidification and warming
- scenarios: differential impacts on living and dead coral. Global Change Biology 21, 4006-4020 (2015).
 https://doi.org/10.1111/geb.13002
- 64. Leo, E., Graeve, M., Storch, D., Pörtner, H. -O. & Mark, F. C. Impact of ocean acidification and warming
 on mitochondrial enzymes and membrane lipids in two Gadoid species. Polar Biology 43, 1109-1120
 (2020). https://doi.org/10.1007/s00300-019-02600-6
- 744 65. Viechtbauer, R. Meta-Analysis Package for R: Package "metafor" version 2.4-0 (2019)
- 66. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical
 Computing (https://www.R-project.org/) (2022).
- 747 67. Duval, S. & Tweedie, R. Trim and fill: a simple funnel-plot-based method of testing and adjusting for
 748 publication bias in meta-analysis. Biometrics 56(2), 455-463 (2000). https://doi.org/10.1111/j.0006749 341X.2000.00455.x
- **750** 68. Shi, L. & Lin, L. The trim-and-fill method for publication bias: practical guidelines and recommendations
- 751
 based
 on
 a
 large
 database
 of
 meta-analyses.
 Medicine
 98(23),
 e15987
 (2019).

 752
 https://doi.org/10.1097/MD.00000000015987

 </
- 753 69. Alter, K., Jacquemont, J., Joachim, C., Lattuca, M., Barrantes, M., Marras, S., Manriquez, P., Gonzalez,
- C., Fernandez, D., Peck, M., Cattano, C., Milazzo, M., Mark, F. & Domenici, P. Hidden impacts of climate
 change on biological responses of marine life. Zenodo, 10223034 (2023)
- 755 change on biological responses of marine life. Zenodo, 1022303
- 756

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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.

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780 **COMPETING INTERESTS STATEMENT**

- 781 The authors declare no competing interests.
- 782 783

784 FIGURE



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/ https://thenounproject.com/icon/molluskand 793 5552214, respectively.

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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

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Number of metrics per biological response category

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Figure 3: Effect of metric's increase on fitness and number of metrics per biological response category.
 Magenta, blue and gray fillings indicate metrics for which an increase leads to a negative, positive, or
 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
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Figure 4: Directional effects of climate drivers on biological responses of marine animals. Directional effect 811 812 (InRR) 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

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822 Figure 5: Directional effects of climate drivers by intensity level. (a) Directional effects (InRR) 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/ https://thenounproject.com/icon/molluskand 831 5552214, respectively.

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835 Figure 6: Deviation effects of climate drivers on biological responses of marine animals. Deviation 836 (abs(InRR)) 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 https://thenounproject.com/icon/fish-1464319/ 841 project website: and

842 https://thenounproject.com/icon/mollusk-5552214, respectively.



a. Directional and deviational effects of climate drivers by intensity level

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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 website: https://thenounproject.com/icon/fish-1464319/ at on the noun project and 856 https://thenounproject.com/icon/mollusk-5552214, respectively.