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# Upper environmental *p*CO<sub>2</sub> drives sensitivity to ocean acidification in marine invertebrates

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Minimizing the impact of ocean acidification requires an understanding of species responses and environmental variability of population habitats. Whereas the literature is growing rapidly, emerging results suggest unresolved species- or population-specific responses. Here we present a meta-analysis synthesizing experimental studies examining the effects of  $pCO_2$  on biological traits in marine invertebrates. At the sampling locations of experimental animals, we determined environmental  $pCO_2$  conditions by integrating data from global databases and  $pCO_2$  measurements from buoys. Experimental  $pCO_2$ scenarios were compared with upper  $pCO_2$  using an index considering the upper environmental  $pCO_2$ . For most taxa, a statistically significant negative linear relationship was observed between this index and mean biological responses, indicating that the impact of a given experimental  $pCO_2$  scenario depends on the deviation from the upper  $pCO_2$  level experienced by local populations. Our results highlight the importance of local biological adaptation and the need to consider present  $pCO_2$  natural variability while interpreting experimental results.

Since the beginning of the industrial era, the ocean has absorbed more than 500 billion tons of CO<sub>2</sub> from the atmosphere and around 31% of anthropogenic CO<sub>2</sub> emissions since the 1970s<sup>1</sup>. As a major consequence, seawater has become more acidic and experienced changes in carbonate chemistry, which is known as ocean acidification (OA)<sup>2</sup>. Currently, the ocean exhibits the fastest acidification rate in at least the past 55 million years<sup>3</sup>. There is no doubt that OA will profoundly impact marine life and ecosystem functioning, leading to major concerns for human food security and well being<sup>4-6</sup>. The threat of OA has therefore reached both the public and political spheres, and the 2030 Agenda for Sustainable Development from the Intergovernmental Oceanographic Commission of UNESCO incorporated target 14.3, which is focused on "minimizing and addressing the impacts of ocean acidification"<sup>7</sup>.

Biological effects of OA are not uniform across the globe<sup>8</sup>; therefore, understanding why populations differ in their responses to low pH or high pCO<sub>2</sub> levels is critical for the development of adaptation strategies at different scales, including for economically relevant sectors such as fisheries and aquaculture<sup>5,9,10</sup>. Different approaches have been used by the scientific community to understand the biological impacts of OA, including the paleo-reconstruction of ancient pH levels<sup>11</sup>, field experiments<sup>12</sup> and the use of natural analogues for future predicted OA13, that is, volcanic vents14,15, low pH oxygen minimum zones16 and naturally corrosive coastal environments (for example, freshwater-influenced areas and estuaries<sup>17-19</sup>). Laboratory experiments also have been extensively used over the past two decades<sup>20,21</sup>, with most of the experiments having exposed marine organisms over brief periods (from hours/days to weeks) to different  $pH/pCO_2$  experimental conditions. These studies have considered best-practice guides that recommend experimental

scenarios based on current (for example, ~415 ppm) and future atmospheric CO<sub>2</sub> levels<sup>22</sup>. However, translating atmospheric CO<sub>2</sub> levels to seawater pCO<sub>2</sub> in coastal ecosystems is not an easy task, and many ecologically and economically important species live close to coasts (for example, bivalves, gastropods, corals, sea urchins, crabs, fish and so on), where the dynamics of seawater pH and  $pCO_2$  can be modulated by at least three main processes: (1) local metabolism (photosynthesis/respiration ratio), (2) discharge of low-alkalinity freshwater (either by river runoff or ice melting)<sup>23</sup> and (3) coastal upwelling (that is, water masses rising to the surface as a result of wind action along the coast)<sup>24,25</sup>. The dynamic interplay between these processes defines seascapes of natural variability in pH and  $pCO_2^{25,26}$  and upper environmental  $pCO_2$  levels (i.e. the highest pCO<sub>2</sub> level recorded in a geographic area) (Fig. 1). In coastal environments, both oxygen and pH conditions can decline as a result of local metabolism or net ecosystem respiration<sup>27,28</sup>, being more intense in tidal pools, subtidal and intertidal habitats<sup>29,30</sup>. In areas dominated by marine calcifiers (for example, corals), the seawater chemistry can be modified through biological processes related to biomineralization and organic carbon production<sup>31,32</sup>. Similarly, temporal and spatial variation in  $pH/pCO_2$  in coastal regions can be influenced by upwelling dynamics<sup>24</sup> and/or the interaction of processes such as freshwater runoff<sup>25,26</sup> and the day/night metabolism of submerged kelp-forests<sup>33,34</sup> (Fig. 1). These processes constrain changes in  $pH/pCO_2$  to predictable ones over the diurnal and diel cycles, which are superimposed on the seasonal variability scale<sup>34,35</sup> (Fig. 1). Therefore, recreating natural variation in  $pCO_2$  and pH in lab experiments is logistically challenging, and as a consequence, many experimental studies have scarcely considered these natural processes when defining future  $pCO_2$  scenarios. Even when

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**Fig. 1 | Examples of pCO\_2 natural variability in the coastal ocean driven by different local and long-term processes. a**, Local metabolism in intertidal, subtidal and kelp forest environments are characterized by a 'daily cycle' based on the photosynthesis-to-respiration ratio, almost doubling the O<sub>2</sub> consumption and  $pCO_2$  production nightly. **b, c**, **F** reshwater runoff creates episodic events (hours/days) of low alkalinity/low salinity and high  $pCO_2$  conditions (due to terrestrial organic matter remineralization) (psu = practical salinity unit) (**b**), and upwelling of high- $pCO_2$  waters occurs on a seasonal basis during periods of days/weeks in temperate regions (**c**). **d**, In contrast, oceanic environments are characterized by more stable temporal  $pCO_2$  variability, and long-term changes (>10 years) are presently driven by OA. Examples were based on records from buoys deployed in the coastal areas of the United States, Chile and the open ocean (for example, Stratus Mooring, Pacific Marine Environmental Laboratory-National Oceanic and Atmospheric Administration). The different colours of the lines were used to differentiate among variables with blue representing salinity, green representing oxygen and red representing  $pCO_2$ . Credit: diagram by Felipe Gamonal.

using constant  $pCO_2$  treatments, some studies with coastal species inhabiting estuaries or coastal upwelling areas have assumed an ocean-atmosphere equilibrium similar to what is observed in oceanic waters<sup>36</sup>. Whereas the equilibrium approach is probably accurate for organisms inhabiting open-ocean environments, it does not address the dynamic nature of some coastal environments, which are characterized by a mosaic of carbon chemistry features such as changing alkalinity, pH and  $pCO_2$  conditions<sup>37–39</sup>.

To project the sensitivity of marine organisms to changing ocean conditions, we need to improve our understanding of the variability in pH and  $pCO_2$  conditions experienced by natural populations living in coastal habitats<sup>40,41</sup>. In a geographic context, natural variability may impose divergent selection gradients, such that populations of the same species can experience contrasting selective pressures for physiological traits, behavioural or life-history responses that provide fitness advantages under local conditions<sup>42</sup>. Moreover, natural variability can also influence geographic differences in plastic responses of invertebrate organisms to future OA, particularly for populations that experience sudden changes in  $pCO_2$  levels, for instance, planktonic organisms distributed across contrasting physiochemical conditions<sup>43</sup>. It is now clear that differences in local dynamics of pH/pCO<sub>2</sub> underlie these geographic patterns of divergent selection and plasticity, promoting local adaptation and phenotypic diversity in nature<sup>18</sup>. Therefore, natural ranges of pCO<sub>2</sub> conditions should be considered in experimental designs to discriminate between the present range of exposure and future scenarios. This approach can also be used to re-evaluate existing literature and revisit the tested scenarios, considering pCO<sub>2</sub> conditions currently experienced by marine organisms.

Following this idea, an earlier study<sup>18</sup> focusing on the eastern South Pacific coast of Chile proposed an index (that is,  $\Delta pCO_2$  exposure index) calculating how an experimental scenario deviated from the natural variability experienced by a set of marine species. This index was shown to be a good predictor of marine invertebrates' sensitivity to pH/pCO<sub>2</sub> because it clearly shows that marine organisms exposed to large changes in pCO<sub>2</sub> from the mean environmental conditions found in their geographic area are the ones that show the largest negative effect upon experimental high pCO<sub>2</sub>-driven OA

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scenarios. The aim of this Article is to expand and test this concept by re-evaluating studies at a global scale and address the apparent contradictions that exist in the current literature regarding the sensitivities of coastal marine organisms to OA.

We present a meta-analysis synthesizing results of >80 studies, selected from a total of 380 publications, examining the effects of pH/pCO<sub>2</sub> on different biological traits (for example, ingestion, respiration, calcification, growth and so on) for a comprehensive group of coastal invertebrates (that is, gastropods, bivalves, crustaceans, corals and sea urchins). Using the geographic location where experimental animals were sampled, we explored the regional variability of environmental  $pCO_2$  conditions by integrating information from the global surface pCO<sub>2</sub> database at Lamont-Doherty Earth Observatory (LDEO) and from deployed sensors. With this information, we characterized environmental conditions experienced by the marine species considered in our study, summarizing the global  $pCO_2$  pattern for surface waters (upper 10 m to 15 m depth; Supplementary Dataset 1). These data are based on research cruises, buoys/sensors and local time series, which match the vertical distribution of the species considered in our analyses above 20 m depth (with the exception of the clam Astarte borealis; Supplementary Fig. 1). Therefore, our dataset allows a relatively conservative characterization of  $pCO_2$  environmental conditions experienced by the different populations where experimental animals were sampled.

#### Surface *p*CO<sub>2</sub> distribution along coastal systems

Using the same  $pCO_2$  database, we analysed nine coastal regions, including the areas where animals were collected for the 86 independent OA experimental laboratory studies considered (Supplementary Dataset 2) and highly biologically relevant ecoregions<sup>44</sup>.The analysis of the pCO<sub>2</sub> database clearly reflected major differences in  $pCO_2$  for regions along coastal systems worldwide (Fig. 2). In almost half of the studied regions, the average surface  $pCO_2$  in coastal areas tends to be less than 100 µatm higher than the actual atmospheric level (that is, ~415 ppm as of August 2021; https://www.co2levels.org/). However, in some coastal regions, high  $pCO_2$  levels (>800 µatm) can be observed, especially those associated with mid-latitude eastern-boundary upwelling regions (for example, in California and Oregon along the West Coast of the United States and Vancouver in British Columbia, Canada; Fig. 2a); river-influenced areas along the Gulf of Mexico, the US East Coast (Fig. 2b,c) and the European coast (Fig. 2e) or the upwelling centres in Chile along western South America (Fig. 2f) and marginal sea areas (Fig. 2j).

Our analysis showed high pCO<sub>2</sub> variability in coastal upwelling areas, river-influenced coastal areas and marginal sea areas (Fig. 2). Episodic events of high  $pCO_2$  values (>1,000  $\mu$ atm) are typically associated with the upwelling regime during spring along the Peru-Chile current system<sup>45</sup> and river discharges during winter months in central-southern Chile<sup>18,25</sup>. Similarly, the highest pCO<sub>2</sub> levels in the US West Coast region are also associated with upwelling during spring/summer periods<sup>24</sup> and winter months in some freshwater-influenced areas such as the Strait of Georgia and Puget Sound<sup>46,47</sup>. Extreme  $pCO_2$  values were also associated with the US East Coast, especially near Long Island Sound<sup>48</sup>; freshwaterinfluenced marginal seas such as the Baltic and North seas<sup>49,50</sup>; and occasionally in the Arctic Ocean<sup>51,52</sup>. On the contrary, lower  $pCO_2$ values and ranges were observed for those sites located in the Mediterranean Sea, Antarctic and northern and southern Western Pacific, although some regions are represented by only a few individual studies, especially in polar oceans, which have been studied mostly during summer or late-autumn periods when  $pCO_2$  levels in such regions are well below atmospheric saturation<sup>53</sup> (Fig. 2i). Our pCO<sub>2</sub> dataset characterizes well the local conditions in these regions. For instance, the spatial-temporal variability in  $pCO_2$  in coastal areas of the northwestern Mediterranean Sea has been extensively

reported to be very low (<70 µatm  $pCO_2$ )<sup>54</sup>, and the southwestern Pacific—especially the sub-Antarctic waters—are one of the largest net oceanic sinks of atmospheric CO<sub>2</sub>, where the upper surface layer is CO<sub>2</sub>-sub-saturated for a substantial part of the year<sup>55</sup>. The data used for our analysis of global  $pCO_2$  did not have the resolution to resolve the patchiness and spatial–temporal natural variability in most of these geographic areas. However, by comparing the  $pCO_2$  values reported in the LDEO database with  $pCO_2$  data recorded at an hourly frequency by oceanographic buoys within a range of 1.5 km up to ~40 km in some specific locations (Supplementary Fig. 2 and Supplementary Table 1), we observed that general patterns of variability within regions are well captured by data points from the LDEO dataset for purposes of geographic comparisons at the global scale.

## *p*CO<sub>2</sub> sensitivity and habitat-specific environmental influence

Our meta-analysis considered individuals collected from populations inhabiting different geographic areas and habitats. We excluded studies where organisms were collected in habitats typically characterized by extremely high and randomly local variability (for example, CO<sub>2</sub> seeps, tidal flats and pools), driven by different oceanographic processes and net ecosystem metabolism<sup>56,57</sup> and short episodic events, which cannot be captured by the spatial and temporal resolution of global databases. In summary, we included studies (N=86) if (1) they included the geographic location where animals were sampled, (2) the time of experimental exposition was longer than a week, (3) they considered the collection of animals from areas represented in global  $pCO_2$  databases and/or through data from moored pH/pCO<sub>2</sub> sensors, (4) they used sessile and low-vagility organisms, (5) organisms living in habitats where the seawater chemistry is mostly influenced by oceanic water and (6) they provide experimental pH and  $pCO_2$  levels (Methods).

Around 16% of the studies were from coral reefs, 55% from rocky shore environments, 3.5% from fjord ecosystems, 15% from embayments and estuaries and 8% from coastal aquaculture areas. Almost half of the studies (48%) considered early life stages (eggs and larvae) while the other half studied juveniles and adults (52%). A substantial fraction of the selected studies (>40%) considered experimental high  $pCO_2$  levels based on the trajectories for atmospheric CO<sub>2</sub> (Intergovernmental Panel on Climate Change-based), assuming equilibrium for oceanic waters, even when the studied species were coastal or neritic. Few of the selected studies recorded local natural pH or pCO<sub>2</sub> variability by using autonomous sensors or monitoring based on regular water sampling (4.4%). Most of the studies defined the experimental pCO<sub>2</sub> levels based on environmental information from the literature for the corresponding study area. Finally, a relevant fraction of the selected studies (14%) did not justify the selection of the corresponding experimental  $pCO_2$  levels (Supplementary Dataset 2).

A linear regression between the log response ratio (ln RR), the ratio of the mean effect in the acidification treatment to the mean effect in a control group, and the  $\Delta p CO_2$  exposure index (that is, the difference between the experimental high  $pCO_2$  level and the upper environmental  $pCO_2$  at the sampling site<sup>18</sup>; Fig. 3) revealed a negative trend in the response to high  $pCO_2$  across different biological traits. The overall trend was negative and statistically significant for most taxonomic groups and for all species pooled together (*p*-values <0.05; Table 1a). The bootstrapped estimates for the  $\Delta pCO_2$  exposure index showed that slopes were significantly different from zero for all groups except crustaceans and clams, with mussels showing the steepest response (Supplementary Fig. 3a). Moreover, pooling all taxa together in the bootstrapped estimation also indicated a significantly negative slope in the relationships between the ln RR across traits and the  $\Delta pCO_2$  exposure index (Table 1a). These results indicate that the  $\Delta p CO_2$  exposure index is a simple but ecologically

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relevant predictor of biological response to high pCO<sub>2</sub>, not only at the regional level<sup>18</sup> but also at the global level (Fig. 3). To some extent, the steepness of the slope of this relationship reflects the  $pCO_2$  sensitivity of the studied taxa on the different biological traits reported; a steeper slope reflects a more sensitive taxon. Thus, crustaceans appear to be the least sensitive (no significant relationship), followed by sea urchins (slope of -0.0001), gastropods and corals (slope of -0.0003) and bivalves (oysters, scallops and mussels, slope of  $\geq$  -0.0005; Table 1a). No clear correlation was detected between the steepness of the slope and the degree of natural variability experienced by these taxa (Supplementary Fig. 4), which suggests that the  $pCO_2$  sensitivity may be the result of habitat-specific environmental influences on the taxa more than their broad geographic distribution. To this end, the low sensitivity in crustaceans' populations from the selected studies can be explained by the large  $pCO_2$  variability, from around 200  $\mu$ atm pCO<sub>2</sub> up to 1,200  $\mu$ atm pCO<sub>2</sub> in these geographic regions (Supplementary Fig. 4), which can lead to local adaptation and selection of genotypes more resilient to high  $pCO_2$ conditions. Previous studies investigating the effects of elevated pCO<sub>2</sub> on intertidal crustaceans have concluded that both adults and larvae were relatively resilient58-60. Nevertheless, upon similar conditions of high  $pCO_2$  variability in the geographic area of the selected studies (Supplementary Fig. 4), mussels, ovsters and scallops exhibited the steepest negative slopes, especially for early larval stages (for example, mussels), which could have been overrepresented in our database for groups such as gastropods but not for mussels or scallops (Fig. 3). Most of these taxa have a feeding trochophore larval stage that is very sensitive to changes in the carbonate chemistry of the seawater, especially during early development from fertilization to the D-larva via the trochophore stage<sup>61</sup>. Moreover, most of these larvae are lecitotrophic and therefore depend on nutrients in the egg to provide energy for embryogenesis, and the rate of shell accretion is not rapid enough to exceed the limits of calcium carbonate precipitation by purely physicochemical means<sup>62</sup>. The range of  $pCO_2$ variability in the geographic location of sea urchin populations considered in our study was narrower (200 µatm up to 800 µatm) than those for bivalve species, and sea urchins showed only a moderate negative slope. Previous studies have suggested the high tolerance and plasticity of local populations of sea urchins already experiencing greater local variation in seawater  $pCO_2^{63-65}$ , low pH/high  $pCO_2$ conditions in naturally occurring CO2 vents66 and even the potential to adapt to concurrent warming and OA67. Sea urchins may exhibit physiological compensatory responses upon increasing pCO<sub>2</sub> conditions68, buffering capacity of intracellular fluid66,69,70 and transgenerational effects inducing within-generation plasticity<sup>34</sup>.

Because sensitivity can be different depending on the biological traits considered, a more detailed analysis showed a significantly negative slope in the relationships between the ln RR for specific traits and the  $\Delta pCO_2$  exposure index (Supplementary Fig. 5). The bootstrapped estimates for the  $\Delta p CO_2$  exposure index showed that slopes were significantly different from zero only for those traits directly relevant for fitness such as growth and reproduction (slope of -0.0002) but especially survival (slope of -0.0007; Table 1b and Supplementary Fig. 3b). This negative relationship showing a lower negative impact of high pCO<sub>2</sub> (ln RR) in fitness-related traits in populations inhabiting high-pCO<sub>2</sub> coastal areas reinforces the idea that local adaptation to high-pCO<sub>2</sub> environments allows organisms to develop compensatory mechanisms to maintain fitness<sup>71</sup>. It also agrees with the recent evidence that multi-generational exposure to OA can lead to local adaptation processes in marine metazoans<sup>71-74</sup>. In this sense, the  $\Delta p CO_2$  exposure index provides a conceptual framework and a useful tool for future meta-analyses and synthesis.

This approach is not limited to OA research but can be used to assess the effects of other stressors such as salinity or temperature in the framework of ocean freshening and warming, respectively. For instance, many experiments aiming to test the impact



Fig. 3 | Mean response of different species grouped on eight marine taxa in relation to the  $\Delta pCO_2$  exposure index. a-h, (a) clams, (b) oysters, (c) gastropods, (d) sea urchins, (e) crustaceans, (f) corals, (g) scallops, and (h) mussels. The ratio of the mean effect in the acidification treatment to the mean effect in a control group (ln RR) and  $\Delta pCO_2$  (µatm) is represented as the difference between the experimental high  $pCO_2$  levels used in the corresponding experiments minus the extreme  $pCO_2$  level recorded at each coastal area. Filled grey squares correspond to those studies focused on eggs and larval stages, whereas open symbols represent both juvenile and adults of marine invertebrates. The black line is the linear regression fit with dark blue dashed lines representing the 95% confidence interval.

of ocean warming have been conducted using an increase of <4 °C above average temperature, which sometimes falls within the range of natural variability. This has generated apparent contradictory responses as moderate warming can be tolerated by the life-history

#### **Table 1** | Statistical descriptors of the relationships between ln RR and our $\Delta pCO_2$ index of exposure ( $\mu atm$ )

(a) Marine taxa								
In RR	$\Delta p CO_2$ exposure index (µatm)							
	N		Lower bound	Upper bound	All data	F-value	p-value	
Clams	16	slope	-0.0005	0.0001	-0.0002			
		$R^2$	0.0005	0.5803	0.1301	2.0947	0.1698	
Corals	24	slope	-0.0005	0.0000	-0.0003			
		$R^2$	0.0068	0.6955	0.3652	12.6571	0.0018	
Crustaceans	28	slope	-0.0001	0.0001	0.0000			
		$R^2$	0.0001	0.2857	0.0071	0.1863	0.6696	
Gastropods	47	slope	-0.0004	-0.0001	-0.0003			
		$R^2$	0.0623	0.5806	0.2795	17.4594	<0.001	
Mussels	44	slope	-0.0016	-0.0002	-0.0008			
		$R^2$	0.0531	0.5491	0.2401	13.2701	<0.001	
Oysters	24	slope	-0.0006	-0.0003	-0.0005			
		$R^2$	0.3948	0.8417	0.6285	37.2262	<0.001	
Scallops	21	slope	-0.0014	-0.0002	-0.0007			
		$R^2$	0.1935	0.8435	0.4891	18.1862	<0.001	
Sea urchins	41	slope	-0.0002	0.0000	-0.0001			
		$R^2$	0.0045	0.6032	0.2034	9.9585	0.003	
All species	245	slope	-0.1491	-0.0323	-0.0002			
		R <sup>2</sup>	0.0223	0.1615	0.0863	21.0720	<0.001	

#### (b) Most-studied biological traits

In RR				$\Delta p CO_2$	exposure index (µat	m)	
	N		Lower bound	Upper bound	All data	F-value	<i>p</i> -value
Abnormality	6	slope	-0.0017	0.0013	0.0004		
		R <sup>2</sup>	0.0011	0.9591	0.1183	0.5369	0.5044
Calcification	40	slope	-0.0004	0.0001	-0.0001		
		R <sup>2</sup>	0.0000	0.1796	0.0132	0.5100	0.4795
Feeding	23	slope	-0.0002	0.0001	0.0000		
		R <sup>2</sup>	0.0000	0.1599	0.0033	0.0701	0.7937
Growth	95	slope	-0.0003	-0.0001	-0.0002		
		R <sup>2</sup>	0.0419	0.2704	0.1404	15.1880	0.0002
Reproduction	14	slope	-0.0003	-0.0001	-0.0002		
		R <sup>2</sup>	0.3077	0.8808	0.6912	26.8637	0.0002
Respiration	31	slope	-0.0004	0.0002	-0.0001		
		R <sup>2</sup>	0.0000	0.1646	0.0060	0.1740	0.6797
Survival	32	slope	-0.0011	-0.0003	-0.0007		
		R <sup>2</sup>	0.2564	0.6959	0.4334	22.9469	<0.001

The descriptors were estimated separately for both the different marine taxa (**a**) and for the most-studied (more than five studies) biological traits (**b**). The columns labelled as "Lower bound" and "Upper bound" correspond to the bootstrap estimates of the upper and lower bounds of the slope and  $R^2$  values. Significant bootstrapped slope estimates are in boldface. The exact slope and  $R^2$  estimate in the "All data" column, together with the *F*- and *p*-values correspond to the sample statistics of the bivariate plots presented in Fig. 3 and Supplementary Fig. 5, respectively. Note that all *p*-values in the exact test are significant, highlighting in bold the importance of the bootstrap approach to prevent a type I error. N is the number of pairwise comparisons.

stages of many marine organisms and can lead to beneficial effects on fitness-related traits (for example, faster growth and larger size<sup>75</sup>). The  $\Delta pCO_2$  exposure index also allows for comparisons across studies already conducted with different experimental treatments and different present patterns of natural variability at the site of animal collection. It is also evident from our analysis that the index is suitable for comparison of biological responses resulting from experiments conducted with different populations from coastal regions with high variability such as upwelling areas, coastal embayments and estuaries (that is, rather than making comparisons by using directly experimental  $pCO_2$  or pH)<sup>76,77</sup>.

Several factors limit the implementation of such a strategy. For instance, we were not able to consider the whole spectrum of studies published in the literature examining the impact of OA in marine organisms, mostly due to a lack of detailed information about the geographic location where animals were collected. This limitation highlights the importance of properly reporting the origin of organisms used in experimental studies. The second limitation came from

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the lack of information on the natural pH/pCO<sub>2</sub> conditions experienced by the tested species in these localities and in their habitats. This limitation calls for carbonate chemistry monitoring at the relevant spatial-temporal scale ('weather' or synoptic) in parallel with biological experiments. Other experimental and conceptual limitations (for example, relevant duration of exposure driving biological response) also limit our ability to fully solve the question of what makes an organism sensitive to OA. Nevertheless, our results demonstrate that a substantial fraction (>50%) of the selected studies may have underestimated the local impacts of future OA by exposing organisms to  $pCO_2$  conditions that they currently experience in their geographic areas. Our findings further suggest that even for the same species, the responses of local marine populations may be variable at local scales<sup>18</sup>, which emphasizes the risk of extrapolating results from a few model species or from one population to another. As local carbon chemistry conditions vary both in space and time, we also recommend considering a range of pCO<sub>2</sub> values as a control in OA experiments (for example, mean, mode and extreme values), rather than a single value<sup>63</sup>.

#### **Online content**

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/ s41558-021-01269-2.

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#### **NATURE CLIMATE CHANGE**

#### Methods

**Data selection.** We conducted a detailed search of the literature for studies that reported the effects of  $pCO_2$  on marine invertebrates published from 2009 to 2019. For this purpose, we used the *Data Compilation on the Biological Response to Ocean Acidification: Environmental and Experimental Context of Data Sets and Related Literature* in PANGAEA (https://doi.org/10.1594/PANGAEA.149999), Web of Science and Scopus, together with the literature cited in such studies, resulting in ~380 published studies.

A first round of selection from our dataset was restricted to studies reporting the geographic location where organisms were collected (latitude/longitude) and the  $pCO_2$  values for the respective laboratory manipulations. From the selected studies (that is, 150 studies), a second round of selection was conducted by considering five key points: (1) we kept only studies considering exposure times greater than one week, (2) we excluded studies from extreme environments such as CO<sub>2</sub> seeps, tidal flats and tidal pools and (3) those that were not represented in global pCO<sub>2</sub> databases and/or through data from moored pH sensors due to the impossibility of being able to environmentally characterize the habitats from which these organisms were collected. We also selected (4) studies that were focused on only sessile (for example, oysters, mussels and corals) and gregarious or low-vagility benthic organisms (for example, clams, crustaceans, scallops and sea urchins and/or their larvae, juveniles and adults), and (5) we considered only studies reporting both pH and pCO<sub>2</sub> in experimental treatments (that is, some studies report only pH with any mention about pH scale considered, which prevents its inclusion for comparative purposes). On the basis of these criteria, our initial dataset was culled from 380 to 86 independent studies.

A wide range of biological traits were considered, including fertilization, settlement, clearance, ingestion, excretion, respiration, heart rate, somatic growth, shell size/weight, calcium content, calcification, condition index, predation and survival, among others (Supplementary Dataset 2). For those studies manipulating more than one factor (for example, factorial manipulation of both temperature and  $pCO_2$ ), we used only the response to experimental treatments that manipulated carbonate chemistry and kept other parameters under present conditions. In those studies testing different biological traits, all traits were considered only if different animals were used in each trait's estimation (for example, mortality, survival, growth and so on). In the case of experiments reporting temporal series of pCO<sub>2</sub> (for example, days or weeks), in each treatment we have averaged the pCO<sub>2</sub> along the temporal series and adequately reported it in Supplementary Dataset 2. The mean depth at the site of animal collection was recorded when available (~40% of the total studies); otherwise the mean habitat depth of each invertebrate species was estimated based on literature searches reporting its vertical distribution. On the basis of this information, we checked that our analysis could be focused on species distributed on the ocean's upper 20 m surface layer.

The geographic coordinates of the sampling sites were extracted from each article (Supplementary Dataset 2). A maximum of 0.4° latitude and longitude radius (average 111 km per degree of latitude and average 111 km per degree of longitude, decreasing close to 0 km at the poles) were used to extract the corresponding surface  $pCO_2$  data from the Global Ocean Surface Water Partial Pressure of CO2 Database: Measurements Performed During 1957-2019 (LDEO database)78 using the Ocean Data View 2017 software (Fig. 2). From the resulting pCO<sub>2</sub> dataset, we chose only sites with at least two contrasting sampling periods (at least two different seasons or years) to represent a general overview of the natural conditions to which the organisms are naturally exposed at each study site. Surface pCO2 data did not necessarily correspond with the time period when experiments were carried out. The final dataset includes only measurements using equilibrator CO<sub>2</sub> analyser systems-quality controlled by the system performance, CO2 calibrations and internal consistency of the data (LDEO database)-and pH and alkalinity measurements for some sites in the temperate South American region. Datasets for the eastern South Pacific Ocean (that is, from 23.5° S to 45.7° S latitude; Fig. 2f) were extracted using a compilation of monitoring programmes, including time series studies (that is, some longer than one year) and specific seasonal research cruises, all collected above 10-15 m depth. Additionally, we conducted a comparative analysis between the pCO<sub>2</sub> variability reported by the LDEO database and high-frequency data from autonomous pCO<sub>2</sub> sensors placed within a mean radius of 50 km from the LDEO database. The objective of this complementary analysis was to evaluate the capacity of the global LDEO database in capturing the average variability and upper magnitude levels between more or less variable coastal areas in terms of surface pCO<sub>2</sub>. The complete dataset is shown in Supplementary Dataset 1.

**Data analysis.** To evaluate the mean effect of high  $pCO_2$  conditions on different biological traits among taxa, we calculated the ln-transformed response ratio<sup>76</sup> as

$$\ln RR = \ln \left( \bar{X}_{\rm E} \right) - \ln \left( \bar{X}_{\rm C} \right)$$

where  $\bar{X}_{\rm E}$  and  $\bar{X}_{\rm C}$  are the mean responses in the experimental and control treatments, respectively. A positive ln RR indicates a positive effect, and a negative value indicates a negative effect.

We also estimated the  $\Delta pCO_2$  exposure index proposed in Vargas et al.<sup>18</sup> calculated as the difference between the experimental high  $pCO_2$  level used in the experiment and the upper  $pCO_2$  level at the geographic area or region where animals were collected. The upper  $pCO_2$  level basically refers to the highest  $pCO_2$  recorded either by water sampling field monitoring and/or data from a deployed buoy.

Linear regression and sensitivity analysis. To examine organismal responses, represented by the ln RR, to a high-pCO<sub>2</sub> treatment across the selected studies (that is, the dependent and independent variables, respectively), we first calculated the slope of the linear relationship between ln RR and the  $\Delta p CO_2$  exposure index<sup>18</sup>. The analysis was carried out pooling all studies together and then for each taxonomic group separately. Then, we ran a similar analysis by pooling all taxonomic groups' most-studied biological traits (that is, traits with less than five studies were not considered in this analysis). We implemented a Monte Carlo procedure to bootstrap the calculation of the linear slope using 10.000 uniform random samples of the ln RR and the  $\Delta p \text{CO}_2$  exposure index for each taxonomic group and biological trait. We then examined the distribution of frequency of the resulting slopes and used the 95% confidence interval to test the hypothesis that the simulated slopes were significantly different from zero and reported their upper and lower bounds together with their central estimate<sup>79,80</sup>. These results are summarized in Table 1 and Supplementary Fig. 3. All calculations were carried out using MATLAB 2014a.

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

#### Data Availability

Data used in this paper is available online as Supplementary Dataset 1 and 2.

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#### Author contributions

All authors provided input into data availability and preliminary discussions. C.A.V., B.R.B. and L.A.C. carried out data analysis, and C.A.V. designed the main structure of the study. C.A.V. led the drafting of the text with contributions from S.D., B.R.B., L.A.C., J.D.G.-E., N.A.L. and V.A.S.M.

#### Competing interests

The authors declare no competing interests.

#### Additional information

(1)

**Supplementary information** The online version contains supplementary material available at https://doi.org/10.1038/s41558-021-01269-2.

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# Behavioural & social sciences study design

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Study description	Not applicable
Research sample	Not applicable
Sampling strategy	Not applicable
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Study description	The study comprises a meta-analysis of partial pressure of carbon dioxide in coastal areas worldwide (pCO2), in order to characterize the mean and upper pCO2 conditions in theese coastal areas, and then to explore tis relationship with the biological/physiological responses reported in different studies with a wide range of marine invertebrates, including scallops, mussels, corals, crustaceans, sea urchins, and clams. We then, propose an index exploring the potential for local adaptation of different populations of marine organisms in coastal ecosystems worlwide to experimental pCO2 conditions, which also give us insight about the potential for underestimation of ocean acidification impacts by the scientific community.
Research sample	We analyze information from 86 independent studies reporting the effects of high pCO2 levels on marine invertebrates published from 2009 to 2019.
Sampling strategy	We used the Data compilation on the biological response to ocean acidification: environmental and experimental context of data sets and related literature in PANGAEA (https://doi.org/10.1594/PANGAEA.149999), ISI Web of Science <sup>®</sup> , and Scopus <sup>®</sup> , together with the literature cited in such studies, resulting in ca. 380 published studies.
Data collection	A first round of selection from our dataset was restricted to studies reporting the geographic location where organisms were collected (latitude/longitude) and the pCO2 values for the respective laboratory manipulations. From the selected studies (i.e. 150 studies), a second round of selection was conducted by considering five key points; (1) we kept only studies considering exposure times greater than one week, (2) we excluded studies from extreme environments, such as CO2 seeps, tidal flats, and tidal pools, and (3) those that were not represented in global pCO2 data-bases and/or through data from moored pH sensors, due to the

	impossibility of being able to environmentally characterize the habitat from where these organisms were collected, and we also selected (4) studies that were focused on only sessile (e.g. oysters, mussels, corals) and gregarious or low vagility benthic organisms (e.g. clams, crustaceans, scallops, and sea urchins and/or their larvae, juvenile and adults), and finally (5) we only considered studies reporting both pH and pCO2 in experimental treatments (i.e. some studies only report pH, with any mention about pH scale considered, which prevents its inclusion for comparative purposes). Based on these criteria, our initial dataset was culled from 380 to 86 independent studies.				
Timing and spatial scale	We focused on studies conducted between 2009 and 2019, and the spatial scale cover different coastal regions worldwide, including coastal regions from the US West Coast, US East Coast, North Atlantic, and Baltic-North Sea, Arctic, Mediterranean Sea, Temperate South America, North Western Pacific, South Western Pacific, and Southern Ocean region				
Data exclusions	As previously mentioned, we excluded studies from extreme environments, such as CO2 seeps, tidal flats, and tidal pools, and those that were not represented in global pCO2 data-bases and/or through data from moored pH sensors, due to the impossibility of being able to environmentally characterize the habitat from where these organisms were collected.				
Reproducibility	Not applicable since it was based on meta-analysis, bot our own experiments.				
Randomization	literature searching was random based on the criterium initially established, such as to studies reporting the geographic location where organisms were collected (latitude/longitude) and the pCO2 values for the respective laboratory manipulations.				
Blinding	Not applicable				
Did the study involve fiel	d work? 🗌 Yes 🛛 🔀 No				

# Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

#### Materials & experimental systems Methods Involved in the study n/a n/a Involved in the study Antibodies $\boxtimes$ $\boxtimes$ ChIP-seq $\boxtimes$ $\boxtimes$ Eukaryotic cell lines Flow cytometry $\boxtimes$ $\boxtimes$ MRI-based neuroimaging Palaeontology and archaeology $\boxtimes$ Animals and other organisms $\boxtimes$ Human research participants 1 1 $\times$ Clinical data $\boxtimes$ Dual use research of concern