Species-specific responses to ocean acidification should account for local adaptation and adaptive plasticity

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Global stressors, such as ocean acidification, constitute a rapidly emerging and significant problem for marine organisms, ecosystem functioning and services. The coastal ecosystems of the Humboldt Current System (HCS) off Chile harbour a broad physical–chemical latitudinal and temporal gradient with considerable patchiness in local oceanographic conditions. This heterogeneity may, in turn, modulate the specific tolerances of organisms to climate stress in species with populations distributed along this environmental gradient. Negative response ratios are observed in species models (mussels, gastropods and planktonic copepods) exposed to changes in the partial pressure of CO2 (pCO2) far from the average and extreme pCO2 levels experienced in their native habitats. This variability in response between populations reveals the potential role of local adaptation and/or adaptive phenotypic plasticity in increasing resilience of species to environmental change. The growing use of standard ocean acidification scenarios and treatment levels in experimental protocols brings with it a danger that inter-population differences are confounded by the varying environmental conditions naturally experienced by different populations. Here, we propose the use of a simple index taking into account the natural pCO2 variability, for a better interpretation of the potential consequences of ocean acidification on species inhabiting variable coastal ecosystems. Using scenarios that take into account the natural variability will allow understanding of the limits to plasticity across organismal traits, populations and species.

During the past two centuries, human activities exerted a growing influence over the global climate system, mostly through greenhouse gas emissions and chiefly CO2 derived from burning fossil fuels1,2. This increasing global footprint of human activities on the biosphere has led some to use the term 'the Anthropocene', to denote the present period of anthropogenically induced global environmental change3. The ongoing oceanic absorption of atmospheric CO2 has helped to restrict present global warming by reducing the total amount of manmade CO2 in the atmosphere. However, this massive oceanic uptake of CO2 (28% of anthropogenic CO2 emissions since the 1970s) has altered carbonate chemistry cycles in the global ocean, disturbing its delicate geochemical balance4. This disruption of carbonate chemistry processes, known collectively as ocean acidification, has been of great scientific interest and of growing public concern5. Ocean acidification has been one of the most studied scientific topics in marine science worldwide for the past 15 years6, a period during which this topic has reached both the public and political spheres. Nowadays, it is well known that conditions of low pH/high partial pressure of CO_2 (*p*CO_2) can impact marine organisms, from molecular, physiological, developmental and behavioural processes, all the way to species interactions at the ecosystem level7,8. Scientists have now conducted many different ocean acidification experiments on a variety of marine species, usually exposing these organisms over short- or mid-term periods to experimental conditions based on scenarios modelled for oceanic waters9, typically simulating present (for example, ~400 μ atm) and near-future ocean pCO_2 levels (for example, 650, 750 and/or 1,000 μ atm)10. Through this experimental approach, a variety of different biological responses have been studied, including photosynthesis, growth, ingestion, calcification, reproduction, behaviour, gene expression and biological interactions, among others11.

The application of standard exposure scenarios was proposed to facilitate comparison between studies10 and was based on those changes expected to occur in the surface open ocean. However, most marine species studied largely inhabit highly variable coastal environments, such as coral reefs, intertidal, sandy or rocky shores, upwelling zones, estuaries or fjords, salt marshes and so on, where pH/pCO_2 levels vary far more dramatically over different temporal and spatial scales than in open ocean environments12. Such variability results from a number of natural and anthropogenic coastal processes such as river discharges, upwelling, ice melting, eutrophication, pollution and so on13–15. Indeed, many nearshore areas experience intense pH/pCO_2 fluctuations, with levels of variability often being significantly higher than would be expected if driven solely by a process of equilibration with the atmosphere16,17. This diversity of causative drivers and the high degree of variability in coastal environments, when compared with open ocean systems, limits the direct extrapolation of ocean acidification concepts and scenarios between these different environments18. In addition, this environmental variability can drive associated local adaptation, which can also play a key role in setting sensitivity of a species to changes in pH/pCO_2. For example, the precise physiological19,20 and evolutionary processes21 involved can be different depending on whether experimental scenarios are within or outside of the natural range of variability experienced by that organism.

To be able to project how future ocean acidification will affect marine organisms, populations and ecosystems, it is therefore necessary to monitor present day pH/pCO_2 conditions16,22,23 and design relevant ocean acidification experimental scenarios accordingly. Surprisingly, many scientists continue to expose coastal species to ocean acidification scenarios derived for the open ocean24. In doing so, the baseline or control conditions chosen can be unrepresentative of the organism’s normal environment experienced in the field, with generally lower, more stable levels of pCO_2 than the organism is used to. Assessments of the effects of pH/pCO_2 using such unrealistic scenarios do not represent realistic future projections and often treatments aimed at simulating future conditions actually represent an organism’s present condition. Consequently, many previous experiments are more likely to have given us insights about the generic role of pH/pCO_2 levels as a natural environmental driver, than the likely impacts of elevated levels of CO_2 17. This has significant implications for meta-analyses and experimental designs, which should take into account the deviation of CO_2 conditions from a natural range of variability rather than a single assumed control pH/pCO_2 level.

Here, we conducted a meta-analysis of different studies focused on determining the reaction norm, that is, the range of phenotypes expressed by a given population as a function of environmental variation25, under high pCO_2 conditions, for different local populations of marine organisms (mussels, gastropods and planktonic copepods) inhabiting contrasting coastal environments along the Humboldt Current System (HCS) off Chile. These experimental results were contrasted with local pCO_2 data available for the different environments from where experimental organisms were collected. Using these insights, we propose the use of a simple index taking into account natural pCO2 variability, to shed light on the interpretation of experiments focused on understanding the potential consequences of ocean acidification on species inhabiting coastal ecosystems.

Results and discussion

pCO2 environmental variability. Figure 1 shows the temporal series and frequency analysis of surface (upper 10 m depth) pCO2 (μ atm) for different and contrasting coastal environments along the Chilean coast. Contrasting spatial patterns arise when comparing the pCO2 frequency distribution among sites. Episodic events of extremely high pCO2 levels are observed in upwelling areas off central to northern Chile (30–40° S), with values up to ~1,800 μ atm. Despite the low sampling frequency, river plume areas display persistently high pCO2 conditions (> 450 μ atm), where the resident marine biota are exposed chronically to acidic waters, mostly resulting from the export of organic and inorganic carbon from the watershed to the ocean[26]. Seasonal differences are observed along the latitudinal range, with unimodal distributions in the northern region, whereas in higher latitudes, different processes drive bi-modal frequency distributions. Among these processes are the strong seasonal effects, due to differences in phytoplankton productivity (that is, winter versus spring/summer) and therefore pCO2 uptake (for example, estuarine and tidal inlets; Fig. 1). In general, the vertical structure of pCO2 in the upper 10 m depth is characterized by relatively similar values, especially for upwelling areas. However, stratification owing to freshwater runoff in estuarine waters, river plumes and river-influenced fjords drives differences in pCO2 levels between surface (1–5 m depth) and subsurface (5–10 m depth) waters, resulting in bi-modal frequency distributions (Fig. 1). In southern Patagonia, tidal inlets and river-influenced fjord regions can also experience frequent periods where pCO2 levels are higher than atmospheric levels (> 400 μ atm). We used an autocorrelation analysis (Supplementary Fig. 1) to compare the two time series in our data set, which had the longest period of daily records (see Fig. 1), one from the northern upwelling area and the other from a tidal inlet. This analysis showed that pCO2 levels fluctuated over shorter temporal scales in the upwelling region in contrast to the tidal inlet, where pCO2 levels were more stable. These data illustrated that the use of average atmospheric pCO2 level is not appropriate when establishing the baseline conditions for ocean acidification experiments on near-surface-dwelling (< 10 m depth) marine organisms in either of these different coastal environments (Fig. 1). To include this natural variability in an experimental design, several treatments should be included, covering present and future natural variability[19]. Moreover, the variability on different timescales can also play a key role in modulating the species response and should therefore be included.

Adaptive responses. Evaluating experimentally how marine organisms with multi-year generation times will respond to changes in physical–chemical conditions over long timescales can be extremely difficult. Comparative studies using species with geographic ranges spanning large environmental gradients in pH/pCO2 may help us to understand how long-term adaptation to different environments can modulate individual sensitivity to additional stressors[27,28]. However, there are few studies that have assessed how responses to changing pH/pCO2 conditions vary among individuals (that is, within the same species) from geographically distant populations[29–31]. The heterogeneous coastal ecosystem across the long latitudinal range off Chile (more than 35° and 6,000 km of coast) provides suitable conditions and a natural laboratory in which we can evaluate intraspecific variability in ocean acidification responses using individuals from different geographic areas and experiencing contrasting oceanographic regimes. This unique setting, in turn, has the potential to provide us with considerable insights into the responses that species may have under different ocean acidification scenarios along the Chilean coast.

An interesting result emerging from the comparison of conspecifics from habitats with different pCO2 levels (for example, coastal versus estuarine areas and/or river-influenced areas) is the difference in the mean effects of experimentally elevated pCO2 conditions.
For instance, Acartia tonsa individuals from low pH/high pCO2 estuarine waters are more tolerant to the same level of high pCO2 than individuals from more oceanic populations (Table 1). A similar pattern can be observed when the intraspecific variability in the response to elevated pCO2 is evaluated in veliger larvae, gastropods and mussels collected from contrasting habitats (Table 1).

The meta-analysis performed to evaluate the mean effects of elevated pCO2 conditions on different physiological traits of the studied taxa indicated that individuals from areas naturally exposed to both high mean pCO2 levels and high pCO2 variability show null and/or lower mean negative effect on specific physiological traits, both for plankton (for example, copepod and veliger ingestion or veliger survival) and juvenile/adult molluscs (for example, mussel ingestion, calcification and growth, Fig. 2). Meanwhile, organisms from areas characterized by low variability and lower mean pCO2 conditions show a significant negative effect when exposed to elevated pCO2 on different traits, such as ingestion, survival, respiration, calcification and growth (Fig. 2). The negative effect of high pCO2 levels was most pronounced for copepod ingestion, larval survival, gastropod respiration and mussel ingestion (Fig. 2). In consequence, we hypothesized that pH/pCO2 constitutes an important and selective agent for physiological traits suiting local conditions of high environmental variability.

We devised an index aimed to estimate how far an organism has been exposed to conditions departing from its environmental range, represented as 'ΔpCO2 exposure' and based on the difference between the 'experimental high' pCO2 level used in micro/mesocosm conditions and the mode of pCO2 observations at each location. The relationship between the mean effect of high pCO2 levels and the Δ pCO2 exposition indicated that marine organisms exposed to large changes in pCO2 relative to the most frequent conditions found in their natural environment (that is, chronic exposure) showed the largest negative mean effect (Fig. 3a). This negative trend can be observed even within the same taxa, and suggests that increased tolerance to chronic high pCO2 conditions might lead to an adaptive response. Such analysis can provide insight into how individuals at different points along an environmental gradient differ in their tolerance to high pCO2 and/or low pH levels.

Extreme events play a disproportionately large role in shaping the physiology, ecology and evolution of organisms32,33. Therefore, we also estimated a Δ pCO2 exposition—as the difference between the 'experimental high' pCO2 level used in micro/mesocosm conditions and the extreme or highest pCO2 level recorded at each location on an annual basis—and then correlated this value with the experimental mean effect (Fig. 3b). Extreme high pCO2 events were not necessarily observed in areas with the highest mode in the pCO2 frequency analysis (Supplementary Fig. 2), therefore the significant negative correlation suggests that organisms such as juvenile and adult mussels from local populations exposed to extremely high pCO2 levels (> 1,100 μ atm)—even higher than exposed at the laboratory in the high pCO2 treatment (i.e. negative Δ pCO2)—experienced the lower mean effect. In consequence, environmental exposure to extremely high pCO2 levels may have significant implications in the selection of genotypes more resilient to high pCO2 conditions and potential future ocean acidification conditions34.

The analysis of our results highlights that before experimentally evaluating pH/pCO2 effects for coastal species it is necessary to firmly establish the natural pH conditions (average, variability) experienced at the location from which the organisms are sampled. This is critical to determine the most appropriate control and future ocean acidification scenarios, instead of exposing the organisms to a range of conditions that they may already be familiar with in nature35. Phenotypic responses are important for population persistence in changing environments36 and our understanding of the limits of plasticity must therefore be an important research goal when assessing the environmental challenges that the Anthropocene poses on marine organisms. The synthesis of published experimental information for the coastal sector of the HCS showed that populations of marine organisms from this highly heterogeneous environment harbour significant resilience, suggesting they have the potential to adapt to new niches and cope with the unprecedented selective processes posed by ocean acidification. However, because evolution is a multivariate process, to project future evolutionary pathways will require a deeper understanding of more phenotypic traits and their correlations with each other at the organism level37.

Conclusions

To better understand the potential impacts of ocean acidification on marine ecosystems, future studies should use realistic scenarios that consider the habitat-specific natural variability in seawater chemistry, particularly the patchiness in oceanographic conditions of coastal ecosystems. Therein, the lack of environmental data regarding pH/pCO2 variability and geographic distributions of species are critical research gaps for studies dealing with the projection of organismal responses to ocean acidification. A large set of published experiments conducted with coastal marine species exposed to ocean acidification scenarios in the open ocean (that is, using pCO2 levels predicted by the Intergovernmental Panel on Climate Change emission scenarios10) might have significantly underestimated the impact of ocean acidification on different physiological traits. This shortcoming is particularly relevant for species that may have inhabited low pH/high pCO2 conditions throughout their evolution and bears major implications for the emphasis on neutral responses of benthic organisms when confronted with experimental ocean acidification conditions. Instead, a large body of research has probably explored the environmentally induced variation in selected phenotypic traits under natural pH variability and not their responses under the extreme scenarios posed by future and progressive ocean acidification. The simulation of scenarios that better represent both present and future pH/pCO2 conditions will require a step change in how the ocean acidification experiments are designed, to improve understanding of how plasticity changes across organismal traits, populations and species, and how the obtained results can be interpreted, communicated and utilized elsewhere. Thus, we suggest that reporting the Δ pCO2 on the relevant spatial–temporal scale from natural conditions in any experiment using coastal species should become an accepted practice and would help those seeking to determine projected ocean acidification impacts at individual, population and ecosystem levels.

Methods

Study region. The HCS extends along the west coast of South America, from the Patagonian region in southern Chile (ca. ~42° S) up to Ecuador and the Galapagos Islands near the Equator (~5° N), and is one of the most productive marine ecosystems in the world38. This system, and particularly the coastal region off Chile, is characterized by large spatial–temporal heterogeneity in pCO2 conditions39,40, and is an area in which the effects of low pH/high pCO2 conditions can already be seen (Fig. 1). Moreover, one of the most striking biogeographic features of the Chilean coast is its large latitudinal extent, covering almost 6,000 km and containing extremely diverse marine habitats. These habitats range from the almost straight coastline in central and northern Chile (from 18° 20′ to 41° 45′ S) to a highly fragmented coast with a large number of islands, tidal inlets, channels and fjords in the Patagonia region (down to ca. 56° S), which includes many calving glaciers and massive rivers draining the largest ice field outside the polar regions. Almost all of the different natural processes that contribute to temporal variability in coastal zone carbonate chemistry can be found at some point in this region, including variable photosynthesis/respiration ratio, wind-driven coastal upwelling, riverine discharges and ice melting39.

Data compilation on pCO2 variability in coastal environments. During the past five years, several observation programmes focussing on ocean acidification have been carried out along the Chilean coast. Most observational data come from regular monitoring programmes (on a biweekly, weekly and/or monthly basis)26,41, buoys deployed in specific regions (this study) and/or specific seasonal research cruises41. To characterize natural variability along the Chilean coast, we have compiled and plotted all the temporal time series data available for different coastal habitats along with a frequency analysis of regional pCO2 data collected over at least one year at different time intervals (daily, weekly, biweekly, monthly and so on; Supplementary Table 1). The data set created captures a wide environmental spectrum averaged for the upper 10 m of the water column and includes coastal upwelling areas, river plumes, river-influenced upwelling areas, estuarine ecosystems, river-influenced fjords and tidal inlets (Fig. 1). All geographic sites selected for these pCO2 observation programmes correspond to areas far from the direct effects of human activities that could lead to high pCO2 levels resulting from respiration of anthropogenic organic matter (Supplementary Table 1).

Autocorrelation analyses were carried on raw data using the longest continuous records of pCO2 observations available from contrasting environmental settings, using the xcorr function with MATLAB R2013A. Significant differences ($P < 0.01$) between autocorrelation functions were observed at lag-1 using a Bonferroni correction for multiple comparisons. Data analysis of biological response experiments. In the present meta-analysis, we have compiled all the published information available with the aim of both characterizing the reaction norm and evaluating the effect of high pCO2 levels (that is, from 910 to 1,500 μ atm) on several physiological traits, such as ingestion, respiration, larval survival, calcification and growth in marine organisms along the HCS off Chile (Table 1). All this information came from studies that used individuals from populations inhabiting different geographic regions along the Chilean coast, each with contrasting environmental pCO2 levels and encompassing different habitat such as coastal ocean, estuaries, river-plume areas and tidal inlets (Table 1). Furthermore, all these studies were conducted between 2009 and 2012 using the same semi-automatic system designed for long-term seawater carbonate chemistry manipulation42. Low pCO2 conditions for all these experiments were nearly atmospheric pCO2 conditions at that time period (that is, 347–398 μ atm). They include several taxa, such as the small planktonic copepod A. tonsa43, newly hatched planktonic larvae and juveniles of the benthic gastropod Concholepas concholepas29,30,44, adult individuals of the intertidal mussel Perumytilus purpuratus30 and juveniles of the intertidal/subtidal mussel Mytilus chilensis31.

To evaluate the mean effect of high pCO2 conditions on different physiological traits among taxa, we estimated the ln-transformed response ratio 11 as

$$\mathrm{LnRR} = \ln(\bar{X}E) - \ln(\bar{X}C)$$

where $\bar{X}E$ and $\bar{X}C$ are the mean responses in the experimental and control treatments. A positive ln-transformed response ratio indicates a positive effect and a negative value indicates a negative effect.

Data availability. Data on the experimental response of target marine organisms under laboratory conditions can be obtained from the Ocean Acidification International Coordination Center (OA-ICC) data compilation site45 through Pangaea (http://www.pangaea.de/) and is open access to everyone. Any data used in this paper can be obtained by contacting the corresponding author.

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Author contributions

All authors provided input into data availability and preliminary discussions.
C.A.V. led the drafting of the text with main contributions in the same order from S.D., B.R.B., S.W., N.A.L., M.A.L., C.D., P.H.M. and V.M.A. C.A.V. carried out data analysis and the main structure of the study.

Figures and tables

Table 1 | Intraspecific variability in the physiological responses of different taxa collected in environments with naturally contrasting pCO2 levels on laboratory exposition to low pH/high pCO2 levels.

Group	Taxon	Life stage	Environment	Mean ± s.d. environmental p_{CO_2} level (μatm)	Control level p_{CO_2} (μatm)	Experimental level p_{CO_2} (μatm)	Response	Mean effect (%)	*n*	Reference
Gastropod	*C. concholepas*	J	Coastal ocean	555.6 ± 157.5	380	1,500	Respiration	+213†	30	29
Gastropod	*C. concholepas*	J	Estuarine	623.42 ± 233.68	380	1,500	Respiration	+147†	30	29
Gastropod	*C. concholepas*	VL	Coastal ocean	555.6 ± 157.5	376	980–1100	Ingestion	−47*	180	30
Gastropod	*C. concholepas*	VL	Estuarine	623.42 ± 233.68	376	980–1,100	Ingestion	−33*	180	30
Gastropod	*C. concholepas*	VL	River-plume area	811.0 ± 185.7	376	980–1,100	Ingestion	−17	180	30
Gastropod	*C. concholepas*	VL	Estuarine	623.42 ± 233.68	365–398	979–1,077	Larval survival	−60*	120	44
Gastropod	*C. concholepas*	VL	River-plume area	811.0 ± 185.7	365–398	979–1,077	Larval survival	−17	120	44
Mussel	*P. purpuratus*	A	Estuarine	623.42 ± 233.68	347–377	910–960	Ingestion	−60*	30	30
Mussel	*P. purpuratus*	A	River-plume area	811.0 ± 185.7	347–377	910–960	Ingestion	−13	30	30
Mussel	*M. chilensis*	J	Tidal inlet	500.8 ± 140.2	388	979	Calcification	−37*	30	31
							Growth	−35*		
Mussel	*M. chilensis*	J	Freshwater-influenced tidal inlet	608.9 ± 319.3	388	979	Calcification	−4	30	31
							Growth	−13		
Copepod	*A. tonsa*	A	Coastal ocean	405.9 ± 95.4	398–405	1,255	Ingestion	−72*	36	43
Copepod	*A. tonsa*	A	Estuarine	623.42 ± 233.68	398–405	1,255	Ingestion	+5	36	43

Different life stages were considered in these studies (A, adults; J, juveniles; VL, veliger larvae). *Negative mean effects higher than 30% in high p_{CO_2} treatments in comparison with control treatments. †Positive mean effects on high p_{CO_2} conditions. *n*, sample size; s.d., standard deviation.

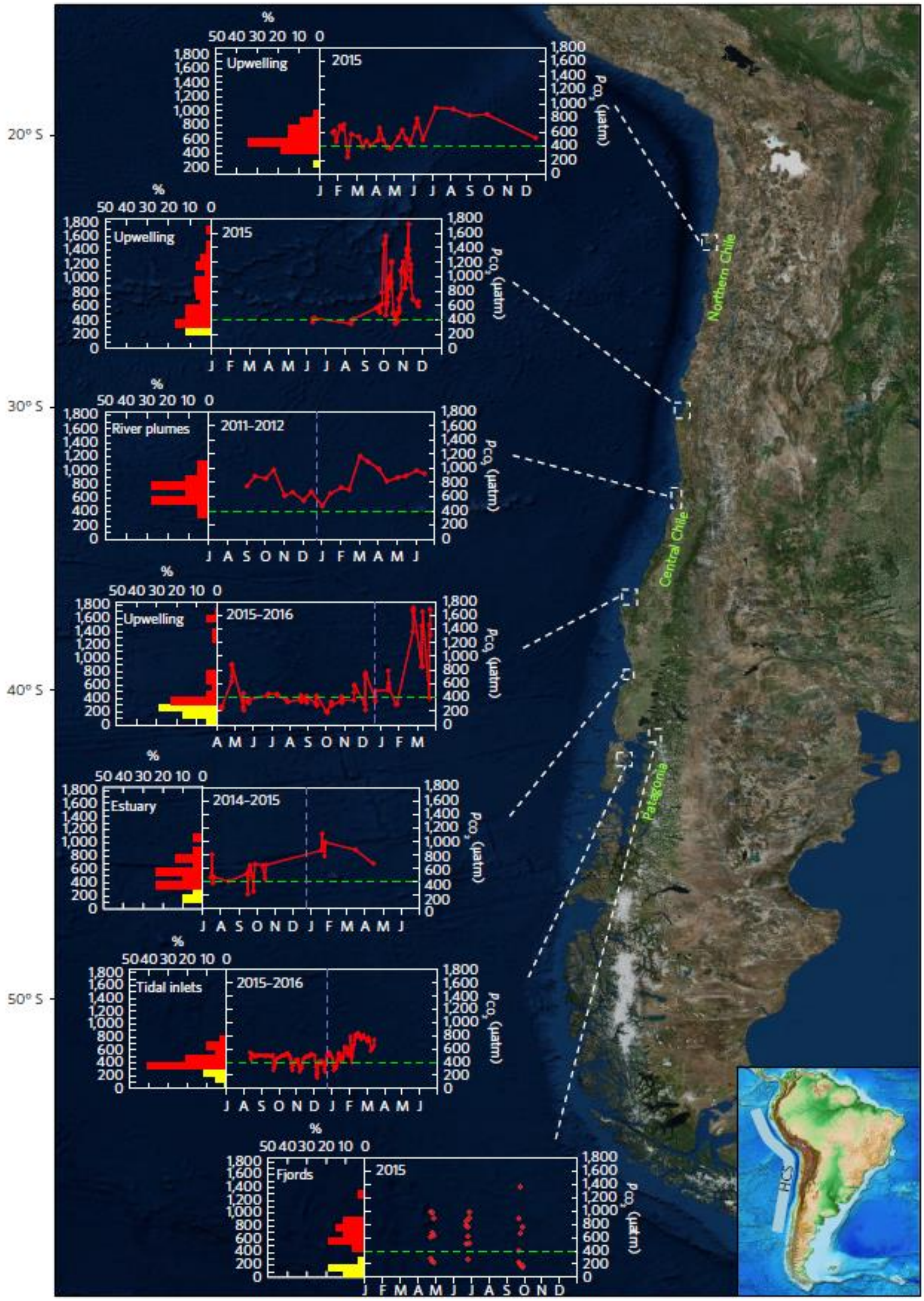

Figure 1 | Temporal series (line plots) and frequency analysis (bars plots) of surface (upper 10 m depth) pCO2 (µatm) for different coastal environments along the Chilean coast. Analysis was based on research cruises, field-monitoring programmes and buoys deployed in different coastal stations (see Supplementary Material 1). The green dashed line in the temporal series represents the pCO2 level of 400 µ atm, the baseline level used as a control in most ocean acidification experiments. Dashed blue vertical lines represent the end of the respective year. Yellow bars in the frequency analysis correspond to frequency ranges < 400 μ atm. Red bars highlight those pCO2 frequency ranges higher than 400 μ atm. Letters along the x axis represent months from January to December. Base map from Trackline Geophysical Data, National Centers for Environmental Information, NOAA (https://maps.ngdc.noaa.gov/viewers/geophysics/).

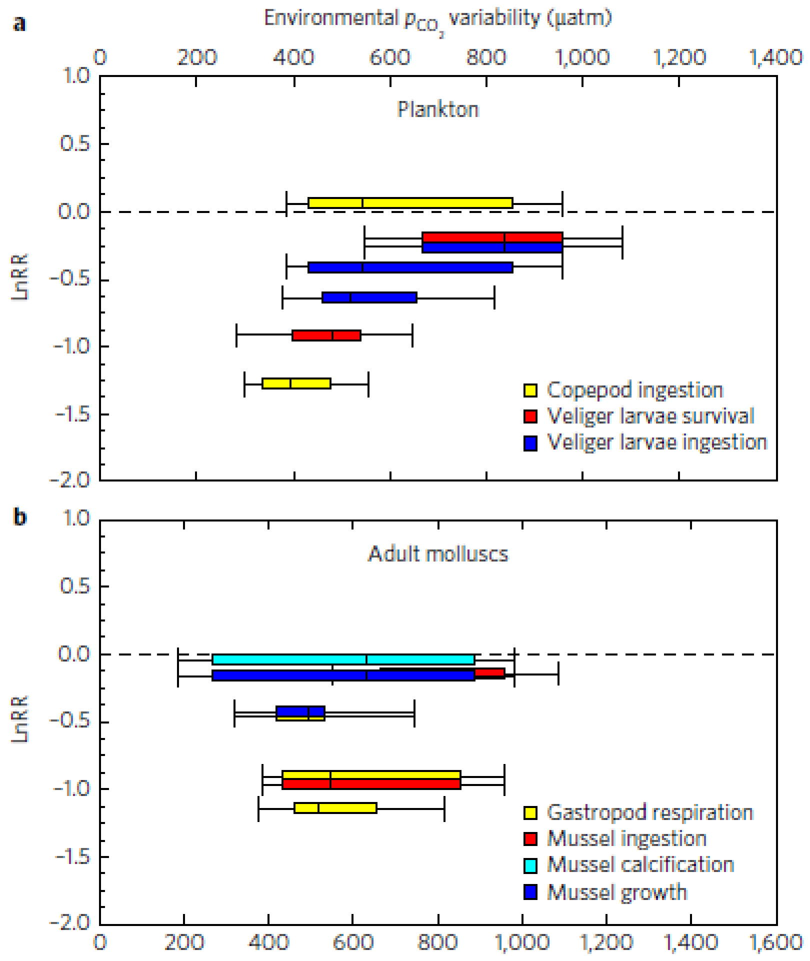

Figure 2 | The mean effect of near-future (2100) CO2-driven ocean acidification on different physiological traits in marine organisms. a,b, Box and whisker plots showing the median and range of environmental pCO2 variability where experimental organisms from different geographic areas were collected versus the ln-transformed response ratio (LnRR) in high pCO2 level scenarios (910–1,500 μ atm). The relationship was analysed separately both for planktonic organisms (a) and marine molluscs (b).

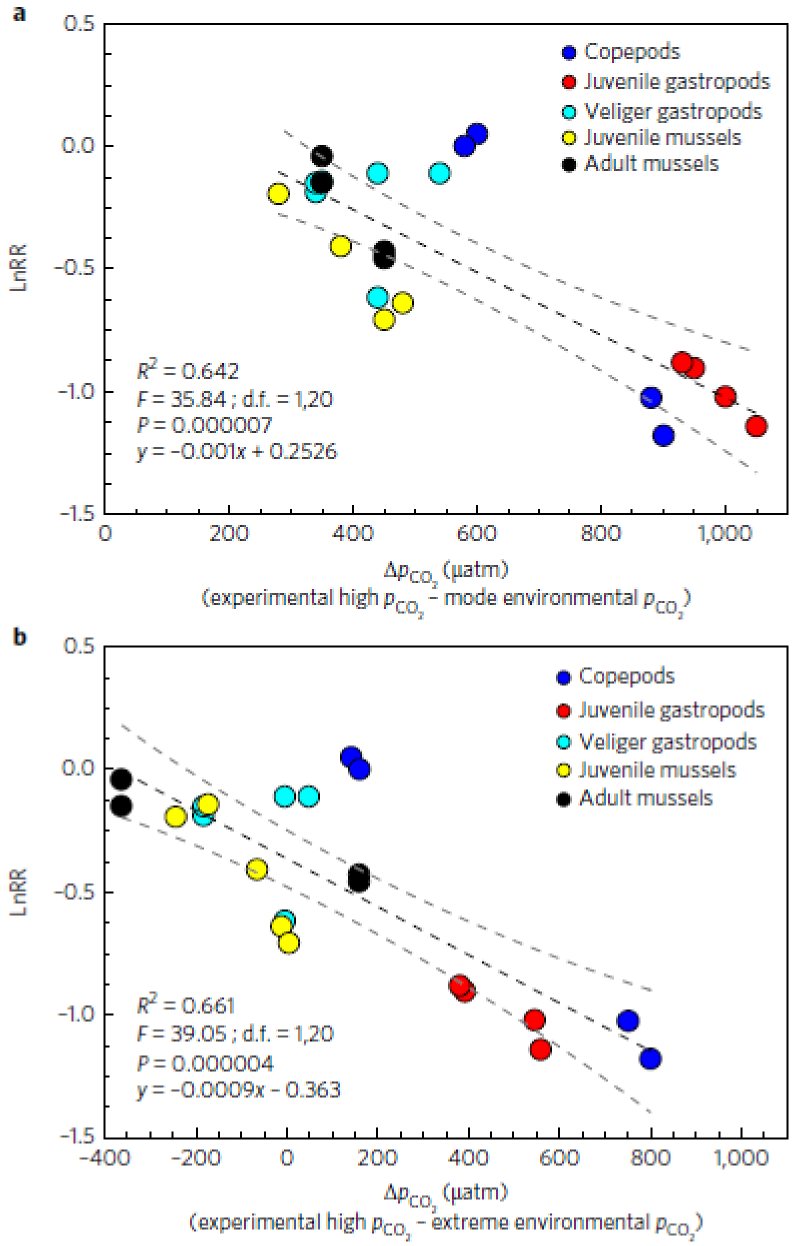

Figure 3 | Mean response of different marine taxa in relation to a Δ pCO2 level exposition. a,b, Δ pCO2 (μ atm) is represented as the difference between the experimental high pCO2 level used in the corresponding mesocosms experiments less the mode in the frequency analysis of environmental pCO2 (a) and/or the extreme pCO2 level recorded at each local habitat (b). Black and grey lines represent the regression line and the 95% confidence interval, respectively. Inset shows the coefficient of determination (R2), F value, degrees of freedom (d.f.), P value of the linear regression model and the estimated regression model.

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