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Vulnerability of marine biodiversity to ocean acidification: A meta-analysis

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ABSTRACT

The ocean captures a large part of the anthropogenic carbon dioxide emitted to the atmosphere. As a result of the increase in CO_2 partial pressure the ocean pH is lowered as compared to pre-industrial times and a further decline is expected. Ocean acidification has been proposed to pose a major threat for marine organisms, particularly shell-forming and calcifying organisms. Here we show, on the basis of meta-analysis of available experimental assessments, differences in organism responses to elevated $p\mathrm{CO}_2$ and propose that marine biota may be more resistant to ocean acidification than expected. Calcification is most sensitive to ocean acidification while it is questionable if marine functional diversity is impacted significantly along the ranges of acidification predicted for the 21st century. Active biological processes and small-scale temporal and spatial variability in ocean pH may render marine biota far more resistant to ocean acidification than hitherto believed.

1. Introduction

The ocean has captured between 28 and 34% of the anthropogenic carbon dioxide emitted to the atmosphere between 1980 and 1994 (Millero, 2007; Sabine et al., 2004). The ensuing increase in ocean CO_2 concentration (Millero, 2007; Sabine et al., 2004) has lead to a reduction of about 0.1 pH units in ocean surface waters compared to pre-industrial times (Caldeira and Wickett, 2003) and a further decline by 0.3–0.5 pH units is expected by 2100 (Caldeira and Wickett, 2005). Ocean acidification has been proposed to pose a major threat for marine organisms, particularly shell-forming and calcifying organisms (Kleypas et al., 1999; Riebesell et al., 2000).

Warnings that ocean acidification is a major threat to marine biodiversity (Kleypas et al., 1999; Orr et al., 2005; Raven, 2005; Sponberg, 2007; Zondervan et al., 2001) are largely based on the analysis of predicted changes in ocean chemical fields (Caldeira and Wickett, 2005; IPCC, 2007; Raven, 2005), with limited experimental support (Doney et al., 2009). These inferences have prompted substantial investments in research funds to support major increases in research efforts, which are providing evidence that the responses of organisms to ocean acidification may be more complex than previously thought (Fabry, 2008; Iglesias-Rodriguez et al., 2008). There is a need to test the generality and magnitude of the predicted negative impact of ocean acidification on marine biota. Here we evaluate the vulnerability of marine biota to ocean acidification through a meta-analysis of available experimental assessments of the impacts of acidification on a range of functions across marine organisms.

2. Methods

We examined reports of the response of marine organisms to experimental acidification. Our search included published articles, retrieved using the Web of Science 7 (Table 1). From these, we extracted the response of the investigated organism and/or process to the experimental treatment (manipulated $p\mathrm{CO}_2$ or pH) and the corresponding values of the control treatment. We discarded results obtained using HCl-acidified seawater and included results of CO_2-enriched seawater, in case both methods were used. If several treatments were presented, the time-series with the longest exposure time was selected. Only studies which presented a realistic control for present day or pre-industrial levels of $p\mathrm{CO}_2$, with these control treatments averaging 349 ± 8.2 ppmv CO_2 (range 206–446 ppmv $p\mathrm{CO}_2$) were included in the database. Only data from treatments with increasing $p\mathrm{CO}_2$ were included. Studies that lowered the $p\mathrm{CO}_2$ or increased pH to study organism responses were discarded as they do not address the problem at hand. The data in the database were classified according to the response variable evaluated (growth, mortality, metabolism, fertility and calcification).

The database contained a total of 372 experimentally evaluated responses of 44 species and three types of communities (sand, phytoplankton and coral) to ocean acidification that met the requirements (Supplementary information Table S1 1). This

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Table 1
Search strings and number of returned articles as found on the Web of Science 7 (Thomson Reuters). Keywords within one search are connected with the connector AND. Last rows represent the number of returned articles when all searches are combined (with the connector OR) and the total number of articles within the resulting database reporting extractable experimental results (with control values).

Search no.	Keyword	Keyword	Keyword	No. returned
1	Ocean	Acidification		234
2	Marine	Acidification		525
3	(Ocean or marine)	Acidification		621
4	Carbon dioxide	Seawater	Growth	368
5	Carbon dioxide	Seawater	Mortality	41
6	Effects	Carbon dioxide	Marine	1061
Combined				1949
Articles with experimental results				59

coverage was larger than those in earlier reports, for example 37 responses of 36 different species included in Doney et al. (2009).

To allow comparisons among experiments examining different traits, we normalized data by calculating "effect size", *s*, defined as the dimensionless ratio of the treatment over the control response value (Gurevitch and Hedges, 1993). Consequently, if *s* was 1 there was no effect of acidification on the studied variable; for $s < 1$, the studied variable responded negatively to the acidification treatment, while $s > 1$ indicates an increase in the studied variable with increasing acidification.

3. Results

Published reports included significance of responses relative to controls in only 154 out of 330 studies. Of these 154 reports, 47 concluded no significant response ($p > 0.05$), while 107 data points were reported as significantly different from the controls, 49 of these with $p \leq 0.05$, 22 responses with $p \leq 0.01$ and 36 responses with $p \leq 0.001$. Thus, only a minority of studies demonstrate significant responses to acidification.

When all biological responses were pooled the extracted data in the database showed no general consistent effect of ocean acidification, as the general effect size across species and processes did not differ significantly from the null value of 1 indicative of no effect (mean $s \pm SE = 1.01 \pm 0.099$; $p = 0.18$, Table 2). However, this result is an average of the effect of ocean acidification on a wide range of processes with intrinsic positive (plant growth) or negative responses (calcification) and indeed there were important and significant differences in the responses of acidification among the processes studied (one-way ANOVA, $F_{4,349} = 15.94$; $p < 0.0001$) and across taxonomic groups ($F_{16,336} = 9.82$; $p < 0.0001$, Table 2).

Table 2
Effect size, *s*, for processes and taxonomic groups. Mean ± SE of the effect size, *s* (i.e. the ratio of treatment to values of the response variable), for (A) all treatments, ranging from 477 to 60,0000 ppmv pCO_2 and (B) the dataset limited to experiments with treatment values between 477 and 2000 ppmv pCO_2. Values between brackets are the number of experimental values used for the calculations.

Effect level	Family	(A) All treatments	(B) Limited scenario
		Effect size ± SE (*N*)	Effect size ± SE (*N*)
Calcification	Bivalves	0.57 ± 0.069 (29)	0.61 ± 0.067 (27)
	Coccolithophores	0.84 ± 0.074 (2)	0.84 ± 0.074 (2)
	Coral community	0.91 ± 0.013 (3)	0.91 ± 0.013 (3)
	Corals	0.70 ± 0.072 (26)	0.71 ± 0.074 (25)
	Sand community	0.49 ± 0.135 (2)	0.49 ± 0.135 (2)
Total Calcification		0.65 ± 0.045 (62)	0.67 ± 0.045 (59)
Fertility	Copepods	0.60 ± 0.102 (9)	0.67 (1)
	Sea urchin embryos	0.66 ± 0.064 (24)	0.91 ± 0.031 (11)
Total Fertility		0.64 ± 0.054 (33)	0.89 ± 0.035 (12)
Growth	Algae	1.31 ± 0.121 (9)	1.48 ± 0.143 (5)
	Bivalves	0.63 ± 0.152 (9)	1.11 ± 0.331 (2)
	Coccolithophores	1.05 ± 0.151 (15)	1.05 ± 0.113 (20)
	Corals	0.79 (1)	–
	Cyanobacteria	1.17 ± 0.237 (5)	1.17 ± 0.106 (5)
	Harmful algae	1.23 ± 0.082 (2)	1.23 ± 0.082 (2)
	Nematodes	0.82 ± 0.087 (10)	1.08 ± 0.103 (2)
	Phytoplankton	1.08 ± 0.072 (15)	1.06 ± 0.076 (14)
	Sea urchin embryos	0.77 ± 0.042 (13)	0.84 ± 0.030 (8)
	Seagrass	5.29 ± 3.105 (11)	1.47 ± 0.147 (6)
	Gastropods	0.68 ± 0.156 (2)	0.68 ± 0.156 (2)
	Sea urchins	0.38 ± 0.232 (4)	0.38 ± 0.232 (4)
Total growth		1.43 ± 0.372 (96)	1.06 ± 0.055 (65)
Metabolism	Algae	1.47 ± 0.176 (15)	1.39 ± 0.179 (13)
	Bivalves	0.50 ± 0.150 (2)	–
	Coccolithophores	1.17 ± 0.164 (12)	1.17 ± 0.164 (12)
	Coral community	0.96 ± 0.090 (5)	0.96 ± 0.090 (5)
	Corals	1.18 ± 0.100 (6)	1.18 ± 0.100 (6)
	Cyanobacteria	1.21 ± 0.100 (12)	1.21 ± 0.100 (12)
	Fishes	0.92 (1)	–
	Harmful algae	1.16 ± 0.089 (7)	1.16 ± 0.089 (7)
	Nematodes	0.92 ± 0.089 (10)	1.13 ± 0.082 (2)
	Phytoplankton	1.15 ± 0.132 (17)	1.19 ± 0.351 (5)
	Seagrass	1.51 ± 0.130 (22)	1.36 ± 0.131 (10)
Total metabolism		1.20 ± 0.052 (101)	1.23 ± 0.055 (75)
Survival	Bivalves	1.25 ± 0.076 (8)	1.32 ± 0.201 (2)
	Copepods	0.81 ± 0.037 (9)	1.00 (1)
	Fishes	0.52 ± 0.059 (45)	–
	Gastropods	0.93 ± 0.033 (2)	0.93 ± 0.033 (2)
	Nematodes	0.77 ± 0.086 (12)	0.95 ± 0.020 (2)
	Sea urchins	0.88 ± 0.055 (4)	0.88 ± 0.055 (4)
Total survival		0.69 ± 0.045 (80)	0.99 ± 0.060 (11)
Overall average *s*		1.01 ± 0.099 (372)	1.00 ± 0.031 (222)