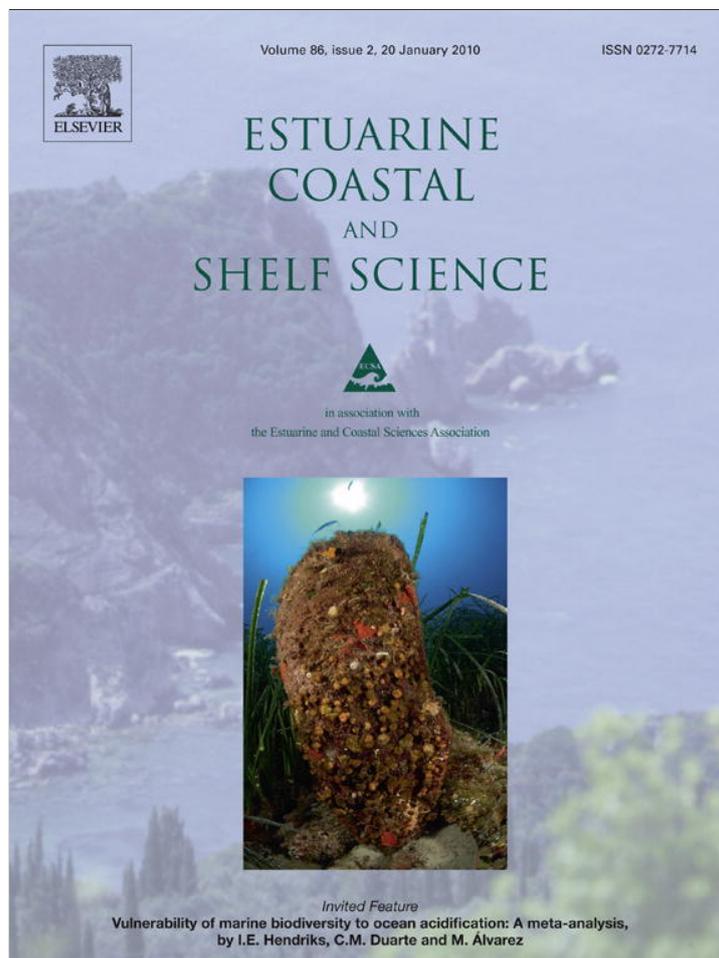


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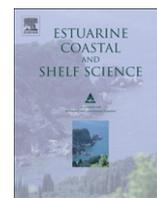
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# Vulnerability of marine biodiversity to ocean acidification: A meta-analysis

I.E. Hendriks\*, C.M. Duarte, M. Álvarez

Department of Global Change Research, IMEDEA (CSIC-UIB), Instituto Mediterráneo de Estudios Avanzados, C/Miquel Marqués 21, 07190 Esporles (Mallorca), Spain

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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<sub>2</sub> 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 pCO<sub>2</sub> 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.

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## 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<sub>2</sub> concentration (Millero, 2007; Sabine et al., 2004) has led 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 pCO<sub>2</sub> or pH) and the corresponding values of the control treatment. We discarded results obtained using HCl-acidified seawater and included results of CO<sub>2</sub>-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 pCO<sub>2</sub>, with these control treatments averaging 349 ± 8.2 ppmv CO<sub>2</sub> (range 206–446 ppmv pCO<sub>2</sub>) were included in the database. Only data from treatments with increasing pCO<sub>2</sub> were included. Studies that lowered the pCO<sub>2</sub> 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

\* Corresponding author.

E-mail addresses: [iris.hendriks@uib.es](mailto:iris.hendriks@uib.es) (I.E. Hendriks), [carlosduarte@ifisc.uib-csic.es](mailto:carlosduarte@ifisc.uib-csic.es) (C.M. Duarte), [marta.alvarez@uib.es](mailto:marta.alvarez@uib.es) (M. Álvarez).

**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* ≤ 0.05, 22 responses with *p* ≤ 0.01 and 36 responses with *p* ≤ 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* ± SE = 1.01 ± 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*<sub>4,349</sub> = 15.94; *p* < 0.0001) and across taxonomic groups (*F*<sub>16,336</sub> = 9.82; *p* < 0.0001, Table 2).

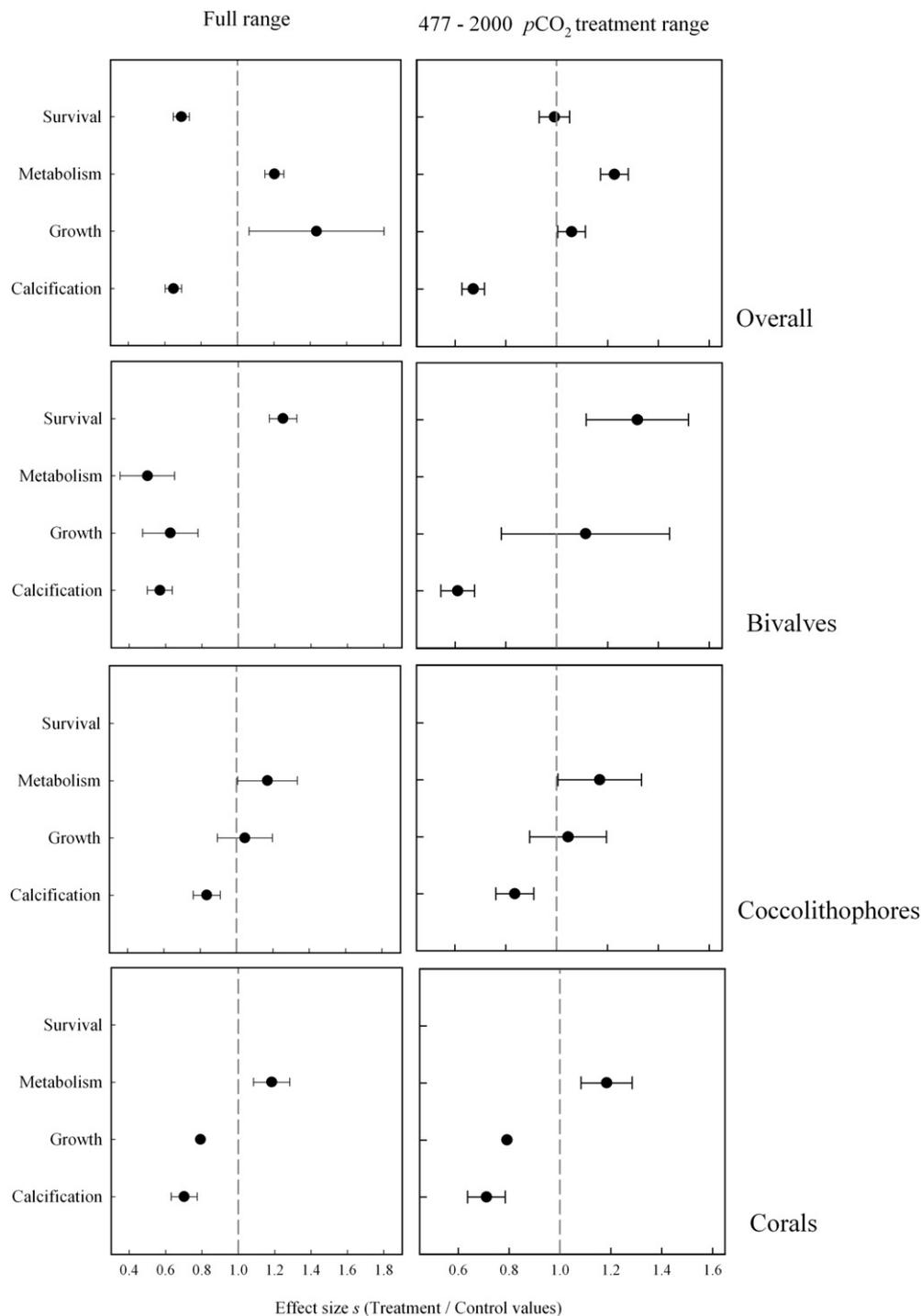
**Table 2**

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 60,000 ppmv pCO<sub>2</sub> and (B) the dataset limited to experiments with treatment values between 477 and 2000 ppmv pCO<sub>2</sub>. 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 <i>s</i>		1.01 ± 0.099 (372)	1.00 ± 0.031 (222)	

Acidification led to both negative and positive effects. Experimental acidification increased metabolic rates by an average of  $20 \pm 5.2\%$ . Autotrophs showed increases in metabolic rates while heterotrophs showed decreases. Corals showed increases in metabolic rates, due to enhanced photosynthetic rates of autotrophic symbionts, while for the coral community as a whole the metabolic rate decreased (Table 2A). Organism growth augmented by, on average,  $34 \pm 37.2\%$ . Sea urchins, nematodes, bivalves and

gastropods demonstrated reduced growth with acidification, up to 62% for sea urchins, but in contrast photosynthetic organisms showed higher growth rates, as much as five-fold or higher for seagrasses (Table 2A). Survival rates of the tested organisms showed an overall decrease by, on average,  $31 \pm 4.5\%$ . Only bivalves had a higher survival rate with acidification (Table 2A). Reproduction rates also declined with increasing  $p\text{CO}_2$  by, on average, 34% for copepods to 40% for sea urchins, the only organisms tested for this



**Fig. 1.** Response of biological processes (as effects size  $s$ ) among key functional groups to experimental  $p\text{CO}_2$  manipulation (A) over the full range of  $p\text{CO}_2$  and response of biological processes (as effects size  $s$ ) for key functional groups to experimental  $p\text{CO}_2$  manipulation over the range 477–2000 ppmv  $p\text{CO}_2$  (B). Dotted line represents  $s = 1$ , or no effect of the treatment compared to control values.

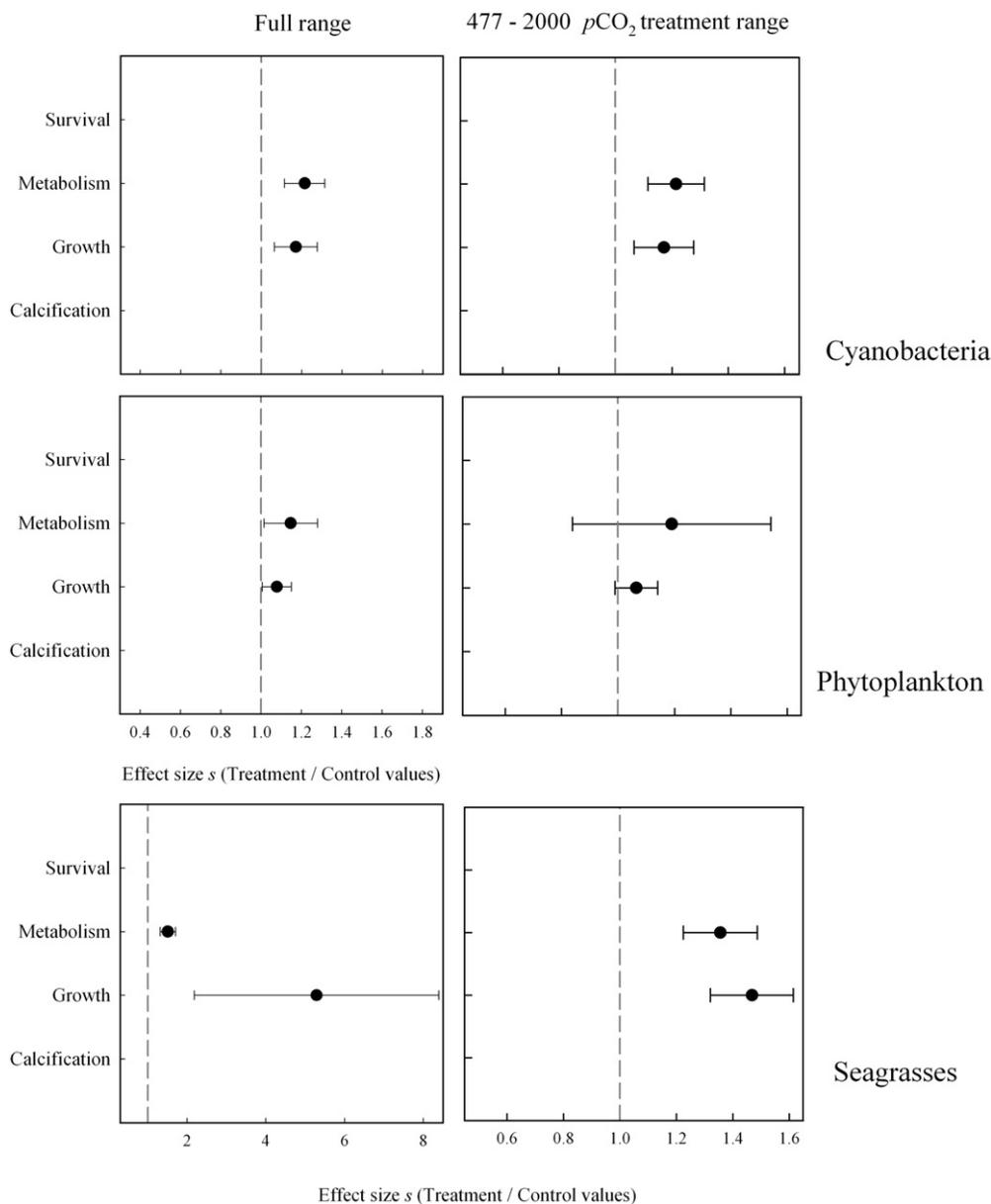


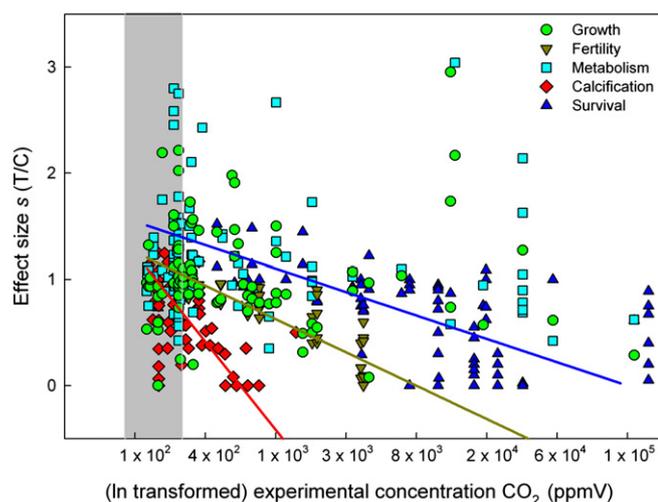
Fig. 1. (continued).

trait (Table 2A). All calcifying groups tested showed a tendency to reduce calcification rates with increasing  $p\text{CO}_2$ , with this decline ranging between 9% and 51% across functional groups (Table 2A).

Extrapolating the impacts of forecasted ocean acidification from these results is not straightforward since the experimental designs included extreme acidification rates. The experimental  $p\text{CO}_2$  spans up to  $5.9 \times 10^5$  ppmv  $p\text{CO}_2$  whereas, while the maximum  $p\text{CO}_2$  expected in the 21st century is  $\sim 790$  ppmv (IPCC, 2007). We thus reanalyzed the data for studies on experimental responses to treatments up to 2000 ppmv  $p\text{CO}_2$ , a value used in previous evaluations of acidification impacts and to be reached approximately around the year 2300 (Caldeira and Wickett, 2003). When the effect size was calculated only for experiments testing responses across a  $p\text{CO}_2$  range of 477–2000 ppmv the overall response including all biological processes and functional groups was not significantly different from 1 ( $s = 1.00 \pm 0.031$ ,  $t$ -test,  $p = 0.34$ , Table 2B). Calcification was reduced by on average  $33 \pm 4.5\%$  and fertility by  $11 \pm 3.5\%$  across groups; survival and growth showed no significant ( $H_0: s = 1$ ,  $t$ -test,  $p > 0.05$ ) overall response, and metabolism

increased by, on average,  $23 \pm 5.5\%$  (Table 2B). The reduction of calcification rates by 9% to 51% with increasing  $p\text{CO}_2$  is similar within the range of 477–2000 ppmv as in response to the full experimental range of  $p\text{CO}_2$ , while corals showed a reduction of 29% in their calcification rates. Reproductive rates within this range declined only by 9% compared to control values for sea urchins, only one study looking at copepods fell within the limited experimental range (Table 2B). The growth of gastropods and sea urchins was reduced under elevated  $p\text{CO}_2$  values by 62% for the latter, while other organisms, including heterotrophs like bivalves and nematodes, showed enhanced growth (Table 2B). Fig. 1 summarizes the responses (as effect size) of biological processes for key functional groups to ocean acidification over the full range of  $p\text{CO}_2$  tested (Fig. 1A) and effect size calculated over experimental ranges of 477–2000 ppmv  $p\text{CO}_2$  (Fig. 1B).

Response size depended on the range of experimental acidification (Fig. 2). There was a weak, but significant, decrease in effect size with increasing experimental acidification (Table 3; Fig. 2) for all processes combined over the full range of experimental  $p\text{CO}_2$ .



**Fig. 2.** The relationship between the effect size,  $s$  (i.e. the ratio of treatment to control values of the response variable), of biological responses, assessed by different processes, to experimental  $p\text{CO}_2$  manipulation and the corresponding experimental  $p\text{CO}_2$  over the full range (log transformed) of experimental treatments. The shaded area represents the limits of future  $p\text{CO}_2$  values expected under the different IPCC scenarios (IPCC, 2007).

The analysis of experimental responses across the entire range of experimental  $p\text{CO}_2$  pointed at a threshold  $p\text{CO}_2$  before consistent reductions (here taken as 25% reduction in response compared to the control;  $s = 0.75$ ) in fertility were observed of 2016 ppmv  $p\text{CO}_2$ . In contrast, consistent reductions (i.e.  $s = 0.75$ ) in calcification might be expected within the ranges of  $p\text{CO}_2$  predicted for the 21st century, at 731 ppmv  $p\text{CO}_2$ . These thresholds were identified on the basis of experiments done over the entire range of experimental  $p\text{CO}_2$  treatments, which included a range of  $p\text{CO}_2$  values extending beyond those expected to occur. Across the more realistic experimental range of 477–2000 ppmv  $p\text{CO}_2$  there was no significant overall relationship between effect size and increasing  $p\text{CO}_2$  ( $p = 0.47$ ).

The relationship between the response and the extent of experimental acidification (limited to 2000 ppmv  $p\text{CO}_2$ ) differed greatly across processes (Fig. 3). There was no significant relationship between the magnitude of acidification effects on growth and metabolism and  $p\text{CO}_2$  across the experimental range ( $p > 0.50$ ), but

**Table 3**

Type II (orthogonal) regression for effect sizes of response variables under (A) the full range (log transformed) of increasing  $p\text{CO}_2$  treatments as  $y = (e^a)x + \text{intercept}$  with  $F$ -values and probability ( $p$ ) for slope  $a$ ; and (B) limited to 477–2000 ppmv experimental treatments as  $y = ax + \text{intercept}$  with  $F$ -values and probability ( $p$ ) for slope  $a$ . Non-significant regression slopes ( $p > 0.01$ ) are not represented in the figures as lines.

	Intercept	Slope ( $a$ )	$F$ -value	$p$
<b>A</b>				
Calcification	6.226	−0.830	15.00	<0.001
Fertility	3.141	−0.314	67.59	<0.0001
Growth	−17.142	2.460	1.82	0.18
Metabolism	3.566	−0.316	0.91	0.34
Survival	2.864	−0.220	29.34	<0.0001
All	−7.383	1.058	12.81	<0.001 <sup>a</sup>
<b>B</b>				
Calcification	1.553	−0.00106	12.60	<0.001
Fertility	1.171	−0.00024	17.18	0.002
Growth	0.068	0.001082	1.13	0.29
Metabolism	2.523	−0.0016	0.02	0.88
Survival	0.640	0.000337	1.07	0.33
All	2.077	−0.00123	0.55	0.46

<sup>a</sup> Although significant, this regression slope is not represented as a line in the graph.

fertility and calcification rates declined significantly with increasing  $p\text{CO}_2$ . The corresponding effect sizes  $s$  were consistently lower than 0.75 (a 25% reduction) at  $p\text{CO}_2 > 1753$  for fertility and 759 ppmv  $p\text{CO}_2$  for acidification, just inside the bounds of  $\text{CO}_2$  forecasts for the 21st century (IPCC, 2007). Survival rates were not consistently different from the null value of 1 across the  $p\text{CO}_2$  range investigated.

Calcification rates are most sensitive to ocean acidification with reductions of, on average, 25% expected during the 21st century. However, the response of different functional groups to experimentally enhanced  $p\text{CO}_2$  differed greatly (GLM,  $\chi^2 = 19.46$ ,  $p < 0.001$ ). Between bivalves and corals, the only functional groups with sufficient data available (Table 3, Fig. 4), only bivalves showed a significant decrease in calcification rates with increasing experimental  $p\text{CO}_2$  ( $\chi^2 = 12.51$ ,  $p < 0.001$ ). However, only one species, *Mytilus edulis*, was examined in this group, while the group denominated “corals” is more heterogeneous (nine species).

#### 4. Discussion

The meta-analysis of our database, which includes 372 published experimental evaluations with control values assembled from literature (Supplementary information Table S1), confirmed that acidification effects differed considerably across taxonomic groups and functions, but that the magnitude of the changes were, overall, modest for acidification levels within ranges expected during this century. Acidification does not occur in isolation, but in concert with other challenges such as warming, eutrophication, and increased UV radiation. There are, however, few studies examining the interactive effect of acidification and other direct or indirect results of global change, which may aggravate the effect of ocean acidification on marine organisms.

This analysis suggests that marine biota do not respond uniformly to ocean acidification. Some experiments report significant impacts for vulnerable taxa at  $p\text{CO}_2$  values expected within the 21st century, but there was no consistent evidence that suggests biological rates, apart from calcification for one functional group, the bivalves, might be significantly suppressed across the range of  $p\text{CO}_2$  anticipated for the 21st century. Some organisms, particularly autotrophs, even showed enhanced growth under elevated  $p\text{CO}_2$ .

The data do suggest that calcification rate, the most sensitive process responding directly to ocean acidification (Gattuso et al., 1998; Gazeau et al., 2007; Leclercq et al., 2000; Riebesell et al., 2000), will decline by, on average, 25% at elevated  $p\text{CO}_2$  values of 731–759 ppmv. These values will be reached within the 21st century (IPCC, 2007). However, the 25% decline in biological calcification rates at elevated  $p\text{CO}_2$  values of approximately 750 ppmv is likely to be an upper limit, considering that all experiments involve the abrupt exposure of organisms to elevated  $p\text{CO}_2$  values, while the gradual increase in  $p\text{CO}_2$  that is occurring in nature may allow adaptive and selective processes to operate (Widdicombe et al., 2008). These gradual changes take place on the scale of decades, permitting adaptation of organisms even including genetic selection. Short-term experimental results are likely to overestimate the impacts of acidification rates on marine organisms. The ambition and sophistication of experimental approaches need be expanded, to assess complex communities, rather than single species, and to assess responses to enhanced  $\text{CO}_2$  over long terms. Such long-term experiments to observe community responses to long-term exposure to enhanced  $\text{CO}_2$  have been successfully conducted for terrestrial systems. Experiments comparable to those conducted on land (e.g. Hättenschwiler et al., 2003), should be planned and conducted. The only such experiment so far available is the Biosphere 2 experiment, where responses of coral-reef

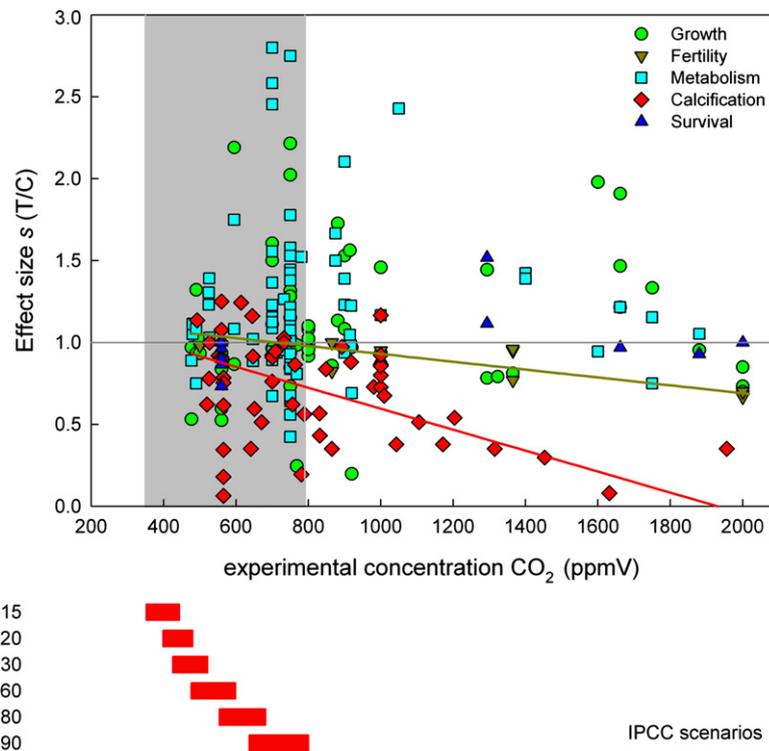


Fig. 3. The relationship between the effect size,  $s$ , of biological responses, assessed by different processes, to experimental  $p\text{CO}_2$  manipulation over the range 477–2000 ppmv  $p\text{CO}_2$ . The shaded area and lower part of the graph shows the future  $p\text{CO}_2$  values expected under the different IPCC scenarios (IPCC, 2007).

communities included in the “ocean” biome of the Biosphere 2 facility were assessed (Atkinson et al., 1999).

Also important, most experiments assessed organisms in isolation, rather than whole communities, whereas the responses within the community may buffer the impacts. For instance, sea-grass photosynthetic rates may increase by 50% with increased  $\text{CO}_2$ , which may deplete the  $\text{CO}_2$  pool, maintaining an elevated pH that may protect associated calcifying organisms from the impacts of ocean acidification.

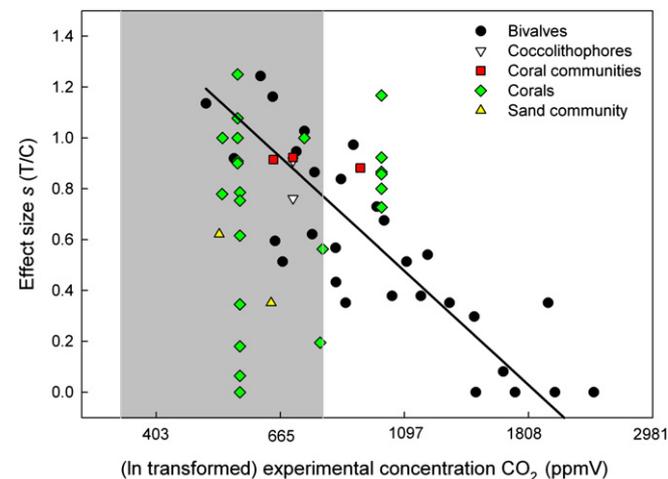


Fig. 4. The relationship between the effect size,  $s$  (i.e. the ratio of treatment to control values of the response variable), of calcification rates, to experimental  $p\text{CO}_2$  over the full range (log transformed) of experimental treatments. The shaded area represents the limits of future  $p\text{CO}_2$  values expected under the different IPCC scenarios (IPCC, 2007). The solid line shows the fitted type II regression of effect size vs increasing experimental treatment of  $p\text{CO}_2$  for bivalves.

Marine biota is unlikely to respond uniformly to the magnitude of ocean acidification expected during the 21st century. For instance there was no consistent effect of experimental acidification on calcification of corals, considered one of the most vulnerable groups to ocean acidification. The effects of ocean acidification on biological processes may therefore not be biologically significant, even for calcification rates, the process most sensitive to ocean acidification. This conclusion is in contrast with previous claims of ocean acidification as a major threat to marine biodiversity (Kleypas et al., 1999; Riebesell et al., 2000). This difference may be explained by a suite of at least three features that have not as yet been considered in models predicting the impacts of future ocean pH: existing gradients in concentrations, boundary layer effects and intracellular regulation of concentrations.

#### 4.1. Fluctuations in concentrations

Marine biota experience broad fluctuations in  $p\text{CO}_2$  along diel to seasonal time scales (Wootton et al., 2008), in contrast to the smooth increase in  $p\text{CO}_2$  with time depicted by models. For instance, seasonal changes in  $p\text{CO}_2$  are in the range 236–517  $\mu\text{atm}$  in the waters of the northern East China Sea (Shim et al., 2007), and metabolically-active coastal ecosystems experience broad diel changes in pH, such as the diel changes of  $>0.5$  pH units reported for seagrass ecosystems (Invers et al., 1997), a broader range than that expected to result from ocean acidification expected during the 21st century. These fluctuations do offer opportunities for adaptation to the organisms involved.

#### 4.2. Boundary layer effects

Models focus on bulk water chemistry and fall sort of addressing conditions actually experienced by organisms. The surface of

organisms is separated from the bulk water phase by a diffusive boundary layer (DBL), across which mass transfer is effected by molecular diffusion, an extremely inefficient transport mechanism (Liu and Dreybrodt, 1997). DBLs around benthic organisms are typically in the order of <math>0.1\text{--}1\text{ mm}</math> in thickness, with steep gradients of concentrations of metabolic gases. Respiration leads to enhanced  $p\text{CO}_2$  and reduced pH within the boundary layer, whereas photosynthetic activity depletes  $p\text{CO}_2$  and raises pH (Kuhl et al., 1995) so that the pH actually experienced by organisms may differ greatly from that in the bulk water phase (Sand-Jensen et al., 1985). Hence, the actual pH effective within the boundary layer of organisms by the end of the century does not necessarily correspond to that predicted to occur in the bulk water phase, as pH within the boundary layer is strongly affected by the metabolism of organisms themselves.

#### 4.3. Intracellular regulation

Calcification is an active process where biota can regulate intracellular calcium concentrations. Marine organisms, like calcifying coccolithophores (Brownlee and Taylor, 2004), actively expel  $\text{Ca}^{2+}$  through the ATPase pump to maintain low intracellular calcium concentrations (Corstjens et al., 2001; Yates and Robbins, 1999). As one  $\text{Ca}^{2+}$  is pumped out of the cell in exchange for  $2\text{H}^+$  pumped into the cell, the resulting pH and  $\text{Ca}^{2+}$  concentrations increase the  $\text{CaCO}_3$  saturation state near extracellular membranes and appear to enhance calcification (Pomar and Hallock, 2008). The speed and energetics of the ion pumps determine ion concentrations and calcification rates (Pomar and Hallock, 2008), and active carbon uptake rather than passive diffusion alone supplies  $\text{CO}_2$  for fixation. A variety of phytoplankton taxa possess carbon concentrating mechanisms (Tortell, 2000), relaxing the dependence of calcification rates on water chemistry. Furthermore there are huge differences between the optimum pH for maximum growth of phytoplankton species (Hinga, 2002). Adult bivalves are able to successfully construct their valves in acid ( $\text{pH} \ll 7$ ) estuarine and river waters, even though growth is faster under more alkaline conditions (Ringwood and Keppler, 2002). There is evidence that calcification could even increase in acidified seawater, contradicting the traditional belief that calcification is a critical process impacted by ocean acidification (Findlay et al., 2009). Hence, biological processes can provide homeostasis against changes in pH in bulk waters of the range predicted during the 21st century.

Models that aim at predicting the impacts of increased  $p\text{CO}_2$  in ocean waters to marine organisms must extend beyond predictions of the pH in bulk waters to consider boundary layer effects and active biological processes, such as those discussed above.

#### 5. Conclusion

In summary, our analysis shows that marine biota is more resistant to ocean acidification than suggested by pessimistic predictions identifying ocean acidification as a major threat to marine biodiversity (Kleypas et al., 1999; Orr et al., 2005; Raven, 2005; Sponberg, 2007; Zondervan et al., 2001), which may not be the widespread problem conjured into the 21st century. Ocean acidification will enhance growth of marine autotrophs and reduce fertility and metabolic rates, but effects are likely to be minor along the range of  $p\text{CO}_2$  predicted for the 21st century, and feedbacks between positive responses of autotrophs and pH may further buffer the impacts. Particularly sensitive processes like calcification may be affected, while bivalves seem to be most vulnerable to changes in ambient pH. Modellers and chemical oceanographers need to improve their predictions on the impacts of ocean acidification by incorporating natural variability in  $p\text{CO}_2$  in marine

waters, the small-scale physical processes that detach the organismal chemosphere from the bulk water properties and the potential for homeostasis resulting from active processes at the cellular level. The predictions need also consider how the gradual changes conducive to the changes in pH expected during the 21st century may depart from the impacts extrapolated from experiments involving the sudden exposure of organisms to reduced pH. Ocean acidification needs to be carefully monitored and its effects better understood, while especially synergistic effects and complex interactions between acidification and other stressors need to be studied, as these synergies may amplify the otherwise limited impacts of ocean acidification. Science and society should not forget other major threats to marine biodiversity like overfishing, habitat destruction, increased nutrient inputs and associated oxygen depletion and warming (Dobson et al., 2006; Jackson et al., 2001; Kennish, 2002; Thomas et al., 2004; Valiela, 2006). The attention that ocean acidification as a sole threat to marine biodiversity has drawn recently might not be fully justified concerning the limited impact of experimental acidification on organism processes as shown by the meta-analysis presented here.

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#### Appendix A. Supplemental material

Supplementary information for this manuscript can be downloaded at doi:10.1016/j.ecss.2009.11.022.

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