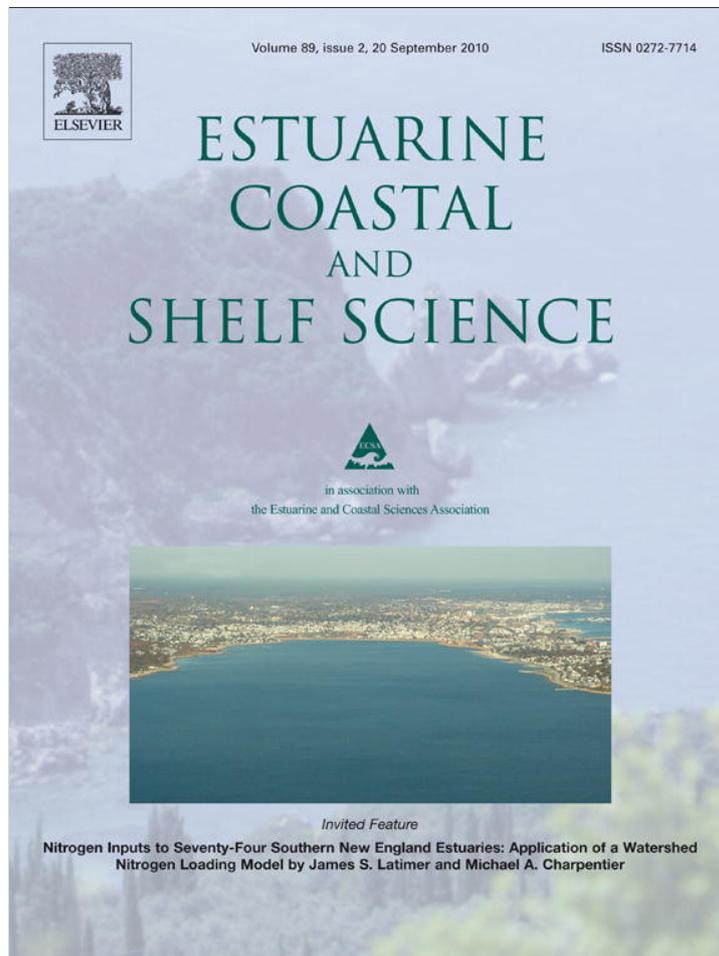


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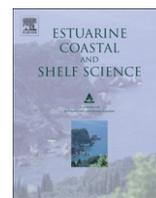
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Discussion

Ocean acidification: Separating evidence from judgment – A reply to Dupont et al.

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ABSTRACT

Recently ocean acidification as a major threat for marine species has moved from a consensus statement into a much discussed and even challenged conception. A simple meta-analysis of Hendriks et al. (2010) showed that based on results of pooled experimental evidence, marine biota may turn out to be more resistant than hitherto believed. Dupont et al. (in press) indicate the importance of evaluating the most vulnerable stages in the life cycle of organisms instead of only adult stages. Here we evaluate additional material, composed of experimental evidence of the effect of ocean acidification on marine organisms during adult, larval, and juvenile stages, and show that the observed effects are within the range predicted by Hendriks et al. (2010). Species-specific differences and a wide variance in the reaction of organisms might obscure patterns of differences between life stages. Future research should be aimed to clarify underlying mechanisms to define the effect ocean acidification will have on marine biodiversity. Conveying scientific evidence along with an open acknowledgment of uncertainties to help separate evidence from judgment should not harm the need to act to mitigate ocean acidification and should pave the road for robust progress in our understanding of how ocean acidification impacts biota of the ocean.

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1. Introduction

Ocean acidification, a consequence of anthropogenic emissions of CO₂ (Caldeira and Wickett, 2003), has emerged as a process potentially impacting marine species and ecosystems (Kleypas et al., 1999; Riebesell et al., 2000; Orr et al., 2005). Whereas the trends and forecasts for a sustained decline in ocean pH are based on solid principles and models, the assessment of the impacts on marine species and ecosystems offers many more uncertainties. A Royal Society working group concluded in 2005 that there is still much uncertainty around the impacts of ocean acidification and recommended that a major international effort be launched into this relatively new area of research (Raven, 2005). In response to this and similar concerns, the experimental evidence to assess the impacts of ocean acidification on marine species and ecosystems is growing rapidly, with an exponential yearly growth rate $r = 0.25$ ($r^2 = 0.92$; calculated from the online database of Nisumaa et al., 2010; see also their Fig. 2). However the evidence is still limited both in terms of the number and range of species and, particularly, the ecosystems examined (Hendriks et al., 2010). Indeed, Dupont et al. (in press) caution in their commentary that “because the relatively small data set available, it may be premature to use meta-

analysis to assess the real impact of ocean acidification on marine biodiversity”. This statement acknowledges that a robust assessment of what the impacts of ocean acidification will be on marine biodiversity is hindered by the paucity of data, a statement with which we concur.

Yet, despite acknowledging the insufficient empirical evidence to draw a general conclusion on the impacts of ocean acidification on marine biodiversity, a paradigm has emerged, apparently embraced by Dupont et al., and phrased by them, as “ocean acidification will be a major threat for marine species and ecosystems”. This paradigm has percolated the realm of the scientific literature to be repeated by scientific societies and conferences, scientific academies, powerful advisory bodies, such as the IPCC (Fischlin et al., 2007), and the mass media (Supplementary information Table S1). Moreover, media reports on the consequences of ocean acidification are increasing in dramatism, with those reporting catastrophic consequences and extinctions increasing rapidly over time (Supplementary information Fig. S2a and b).

Thus, there is a disconnection between the paradigm and the ensuing dramatic statements it has sprouted on one hand and the acknowledged limitations of the available experimental evidence on the other. The commentary by Dupont et al. invites a reassessment of the experimental evidence available, taking into account different life stages as well as to critically examine the robustness of the results derived from our original meta-analysis on the light of experimental evidence published after our analysis was conducted, thereby helping to assess the status of the scientific evidence of

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ocean acidification impacts on marine biota and ecosystems. We first examine the criticisms Dupont et al. issue of our original paper (Hendriks et al., 2010) and the analysis they report. We then test the robustness of our analysis against new, independent experimental evidence. On that basis, we reassess the evidence and address the basis for the various judgments that can be derived from it.

2. Evidence for bottlenecks during the life cycle of organisms

First we need to clarify some misconceptions in the analysis Dupont et al. present. They argue that their experimental conditions (0.4 reduction in pH) “closely mimic the on-going and future changes in the seawater carbonate chemistry”. However a sudden exposure to 0.4 units of reduction in pH does not closely mimic on-going ocean acidification, since a 0.4 unit reduction at the end of this century would mean an approximate rate of 0.0044 pH units year⁻¹. Since there are still many uncertainties in the predictions, with forecasts ranging between a decrease of 0.14 and 0.35 units in the 21st century, adding to the present decrease of 0.1 units from pre-industrial times (Meehl et al., 2007), the conditions seem unlikely to “closely mimic future changes”, as these are still uncertain. Dupont et al. indicate that “effect size was used in a descriptive way and no statistics were used”. Hence, no statistical significance is assigned, yet they argue that their results show “greater impact after 6 months ($s = 0.73 \pm 0.08$, $n = 6$) than in the shorter term (<2 weeks, $s = 0.89 \pm 0.03$, $n = 54$)”. However, we estimated that the effect sizes after 6 months and <2 weeks are not significantly different from one another (unpaired *t*-test; $t_{d.f. = 58} = 1.702$, $p = 0.094$) so their analysis does not provide evidence for greater effects with increased exposure.

Dupont et al. claim that Hendriks et al. (2010) ignored possible bottlenecks due to a higher susceptibility to ocean acidification during some parts of an organisms' life cycle in their analysis, which were “hidden using a global data analysis that mixes different life-cycle stages”. This statement must result from incomplete examination of Hendriks et al., as we reported differences between echinoderm adults and embryos and analyzed effects on reproduction rates and survival where data were available (Table 2 in Hendriks et al., 2010). Dupont et al. point out that “Discrepancies between meta-analyses are documented in the literature even when similar methodologies are used” but this does not apply to our analyses, for the results presented by Dupont et al. are in clear agreement with those we derived. Comparison of the average effect size of the response of echinoderm larvae ($s = 0.88 \pm 0.023$ SE, $n = 19$) derived in Hendriks et al. and the effect size calculated for larvae in Dupont et al. ($s = 0.88 \pm 0.03$ SE, $n = 42$) shows that there is a perfect agreement in *s* between the two studies (unpaired *t*-test, $t_{d.f. = 59} = 0.00$, $p = 1.00$, see also Fig. 2). There is however, a tendency for the results of Dupont, based on a larger database on experimental evidence for echinoderms than that available when our original dataset was compiled, to show smaller negative effects for echinoderms than stated in Hendriks et al. (2010). In the new data, 4 out of 6 comparable effect sizes are more positive than reported by Hendriks et al. (Fig. 3). These include the positive response of adult echinoderms in the analysis by Dupont et al. to ocean acidification ($s = 1.40 \pm 0.36$ SE, $n = 10$ compared to $s = 0.63 \pm 0.144$ SE, $n = 8$ reported by Hendriks et al.), which they do not address in their discussion.

Dupont et al. claim to test the hypothesis that “a bottleneck in one process or one life-cycle stage can drive the whole species response”. However, examining this hypothesis requires demonstration that the effects on larval survival represent a bottleneck at the population level, which would require an examination of the resulting effects on population dynamics. It is questionable if results from short-term experiments can be extrapolated to

population-level trends, which need to be assessed across multiple generations of the organisms. This would require extrapolation from days to many years, the time scales involved in the population turnover of the benthic organisms of concern.

For instance, most benthic invertebrates, certainly corals, echinoderms and bivalves, are mass spawners, releasing massive amounts of propagules to counterbalance high pelagic mortality rates (Thorson, 1950), to ensure that a few (<1%) settle and survive to the reproductive age (Morgan, 1995). However, most of the sources of this large mortality of propagules are removed from the experimental designs used in ocean acidification thus far used, as they typically do not contain predators, nor competitors for space, nor allow for advective losses of the eggs, embryos or larvae. Hence, a statistically significant decline in propagule survival does not necessarily involve a subsequent decline in population size. Furthermore, Dupont et al. provide evidence, but do not discuss, for positive effects on adult echinoderms, which could, for instance lead to the production of more and/or more robust propagules. Indeed, whereas the experimental evidence may show increased larval mortality, extrapolating this to population-level bottlenecks in the field involves speculation and, thus, uncertainties that need be tested at the adequate level of complexity.

3. How general are the results from the meta-analysis?

The analysis by Dupont et al. is focused on echinoderms therefore the consistency in results for larvae does not validate the results derived for other taxa. Therefore we sampled the literature published after our original dataset was compiled to examine the robustness of our results against new, independent experimental evidence. We did so by searching the contents of Biogeosciences and Biogeosciences Discussions (2009–2010), arguably the journal reporting most of the experimental evidence on ocean acidification during the fall of 2009 and early 2010 due to two special issues on the topic. We found a total of 16 articles (Supplementary information Table S3) reporting a total of 144 datapoints of organism responses to ocean acidification (including a control measurement). The new data presented here (Table 1 and Figs. 1–3) show that the results by Hendriks et al. (2010) are a reasonable predictor for the experimental results published in BG and BGD during the last year and half. Linear regression of the two datasets gives a slope of 1.14 indicating that the new data are indicative of similar or even smaller impacts of ocean acidification ($r^2 = 0.11$). Separating life stages does not lead to a discernible difference of the effect of ocean acidification on the (pooled between species) organisms (Fig. 3). Moreover, a recent experimental analysis of a broad range of calcifiers (Ries et al., 2009), using a very different approach (examination of calcification rates as a function of saturation constant), also concluded that “our results suggest that the impact of elevated atmospheric pCO_2 on marine calcification is more varied than previously thought”.

We agree, however, that neither the agreement between the results in Hendriks et al. and those of Dupont et al. nor experimental results recently published and the analysis by Ries et al. (2009), are indicative that a consensus has been achieved, as we concur with the statement by Dupont et al. that “the assumption that a meta-analysis represents the final and accurate viewpoint in an area of research is not always warranted”. Hendriks et al. identified important limitations of the existing experimental evidence that limit our understanding of the impacts of ocean acidification, including the prevalence of single species tested over short time scales, and called for and expansion of “the ambition and sophistication of experimental approaches ... to assess complex communities, rather than single species, to assess responses to enhanced CO_2 over long terms, and ... (to study) synergistic effects and complex

Table 1
Effect size *s* (T/C) for 141 datapoints out of in total 16 studies published in BG or BGD in 2009 and 2010. Average values plus SE, number of datapoints between brackets.

Effect level	Family	Life stage	<i>s</i>	<i>n</i>
Calcification	Coral		0.73 ± 0.186	(5)
	Thecosome pteropod		0.72	(1)
Total calcification			0.73 ± 0.152	(6)
Development	Bivalve	Larvae	0.86 ± 0.093	(2)
Fertility	Bivalve	Gametes	1.02 ± 0.015	(49)
	Cephalopod	Embryos	1.98 ± 0.308	(2)
Total fertility			1.05 ± 0.031	(51)
Growth	Amphipod	Adult	0.83 ± 0.066	(2)
		Juvenile	0.90 ± 0.043	(2)
	Benthic foraminifera		1.10 ± 0.076	(6)
	Bivalve	Larvae	0.91 ± 0.031	(2)
		D-veliger	0.91 ± 0.040	(2)
	Cephalopod	Juveniles	0.99 ± 0.080	(2)
	Crustacea	Larvae	0.89 ± 0.081	(4)
	Planktonic foraminifera		0.84 ± 0.126	(3)
Total growth			0.95 ± 0.166	(23)
Metabolism	Coccolithophore + bacteria		4.28	(1)
	Natural plankton		7.00	(1)
Total metabolism			5.64 ± 1.362	(2)
Metal accumulation	Cephalopod	Embryos	1.24 ± 0.296	(6)
Nutrient flux	Ophiuroid		0.91 ± 0.220	(14)
Primary production	Coral		2.05 ± 0.732	(6)
	Phytoplankton		1.43 ± 0.103	(18)
	Plankton (whole community)		1.13 ± 0.219	(4)
Total primary production			1.52 ± 0.172	(28)
Respiration	Coral		1.39 ± 0.282	(4)
Survival	Amphipod	Adult	1.23 ± 0.260	(2)
		Juvenile	1.11 ± 0.084	(2)
	Bivalve	Larvae	0.99	(1)
Total survival			1.14 ± 0.097	(5)
Overall average <i>s</i>			1.18 ± 0.068	(141)

interactions between acidification and other stressors” (Hendriks et al., 2010), among other recommendations.

4. Separating evidence from judgment

Extrapolating beyond the evidence derived from the experimental assessments conducted thus far involves many uncertainties. For instance, calcification is the process most sensitive to ocean acidification, with an average decline by about 25% over the range of pCO₂ likely observed along the 21st century, as indicated by the analysis presented by Hendriks et al. (2010), corroborated by new evidence (Table 1). To infer, based on this evidence, what the significance of this reduction is for the biology of calcifying organisms involves a value judgment that needs to be clearly separated from the evidence at hand. Reduced calcification has been often claimed to compromise the species affected, however, there is, to the best of our knowledge, no evidence to show that a 25% reduction in calcification rates maybe conducive to population decline or loss of fitness by either affecting recruitment or mortality. That the 25% reduction in calcification rate, on average, was statistically significant across experiments (Hendriks et al., 2010), does not necessarily imply that it was biologically significant. Indeed a 25% reduction in calcification rates between 2010 and 2100 implies a rate of decline of only about 0.28% year⁻¹, too low to compromise organisms on a year-to-year basis. Regrettably, unambiguous evidence for population-level impacts is nil and the question that must be resolved before continuing to assert that ocean acidification is a threat to calcifying organisms is what is the threshold for reduced calcification before populations decline. We submit that this maybe entirely unknown, pointing to a pressing research need to evaluate the biological significance of ocean acidification. Indeed, consideration

of the impact of ocean acidification should consider that ocean acidification does not operate on isolated species, but on species embedded in ecosystems, and does not occur in isolation of other perturbations that have already occurred, such as increased

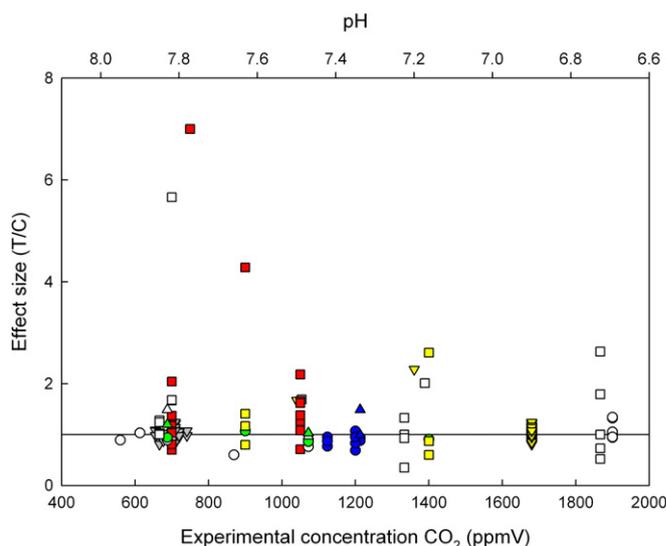


Fig. 1. The relation between effect size *s* and increasing pCO₂ or decreasing pH as experimentally evaluated in BG and BGD papers in 2009/2010 (<May 2010). Squares represent processes linked to metabolism, circles growth, downward facing triangles fertility, diamonds calcification and upward facing triangles survival. Colors represent the life stage evaluated, white for adults, green for juveniles, blue for larvae, yellow for embryos, and grey for gametes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

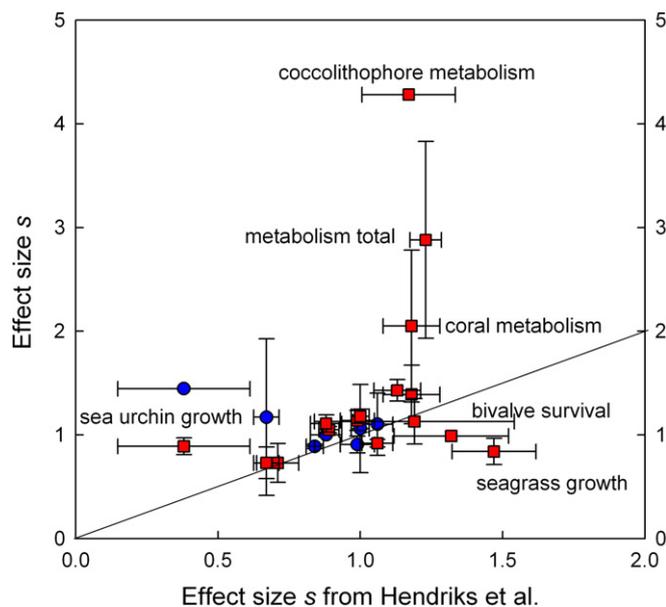


Fig. 2. Effect size (mean \pm SE) of experimental evaluations reported by Dupont et al. in press (blue circles) and the BG(D) database vs. effect sizes calculated by Hendriks et al. (2010) for various processes (calcification, growth, fertility, survival) over a treatment range of 400–2000 ppmV pCO₂. The solid line represents a 1:1 relationship. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

warming and UV, proliferating hypoxia, overfishing and eutrophication, all of which are already – not in a distant future – affecting marine species and ecosystems at the population and ecosystem level. Hence, when all these factors are allowed to operate the 0.3% reduction in calcification rate per year implicit in the 25% reduction by 2100 might not be a significant source of population decline.

Lack of knowledge does not dissipate concern, as the precautionary principle must prevail in situations where uncertainties preclude evaluation of impacts on species and ecosystems, as agreed by the Convention of Biological Diversity (principle 15, Report A/CONF.151/26 (Vol I)), that states that “Where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation” (Nations, 1992). Hence, concern that ocean acidification may negatively impact some species should suffice to prompt action to reduce CO₂ emissions, without a need to overstate the case beyond the boundaries of scientific knowledge.

The paradigm that “ocean acidification will be a major threat for marine species and ecosystems” enunciated by Dupont et al., and implicit in many publications and reports, is a value judgment that lies beyond available scientific evidence. The extent of the threat remains to be robustly quantified and will certainly not be equally severe for all marine species and ecosystems, since some will not suffer or even benefit from increased ocean CO₂ (Iglesias-Rodriguez et al., 2008; Ries et al., 2009; Hendriks et al., 2010). Evidence that there are species-specific differences in the response to ocean acidification is increasing also for vulnerable life stages like larvae (Kurihara, 2008) and even within one single species studies find contrasting results, such as in the case of coccolithophores (Ridgwell et al., 2009).

The current paradigm depicting ocean acidification as a major threat encroached in the scientific literature without a solid basis might bias the literature towards supporting views and may lead authors and readers to fail to clearly separate evidence from judgment. For instance, Dupont et al. concluded that “Gametes and early development appear to be far more impacted by ocean acidification than adult stages ... compromising species survival in near-future conditions”. However, the effect of acidification to the extent expected on year 2100 on calcification by juveniles and larvae was not statistically significant (Fig. 2 in Dupont et al.). Another recent example (Gazeau et al., 2010) showed that there was no significant effect of a 0.25–0.34

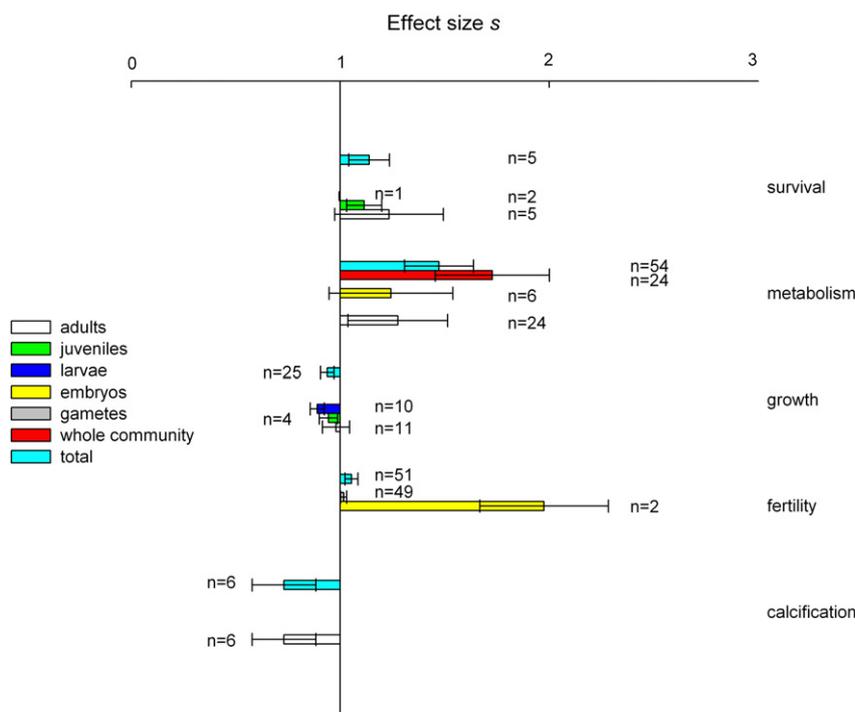


Fig. 3. Effect size (mean \pm SE) of different biological processes (survival, metabolism, growth, fertility and calcification) assessed for different life-cycle stages (adults, juveniles, larvae, embryos, gametes) exposed to ocean acidification.

pH unit decrease on hatching and mortality rates of planktonic blue mussel larvae prior to settlement and that significant effects (24% lower hatching rates) appeared only when pH was reduced by 0.5 units, with size decreasing significantly by 6% to 12% with declining pH. Yet, in the discussion version of the manuscript, Gazeau et al. (2010) conclude that “decreases of hatching rates and shell growth suggest a negative impact of ocean acidification on the future survival of bivalve populations potentially leading to significant ecological and economical losses”. Similarly, Arnold et al. (2009) conclude that “despite there being no observed effect on survival, carapace length, or zoeal progression, ocean acidification related (indirect) disruption of calcification and carapace mass might still adversely affect the competitive fitness and recruitment success of larval lobsters with serious consequences for population dynamics and marine ecosystem function”. While all of these papers do contain important, useful results worth publishing, reviewers and editors should ensure that conclusions are supported by the results presented.

As discussed by Maynard et al. (2008) and Hoegh-Guldberg (2009) in a interchange of opinions about the evidence and uncertainties surrounding the paradigm of coral reef loss as a consequence of climate change, including ocean acidification, there is a danger in simplifying and exaggerating effects in order to get the attention of the public or impel policy makers into action. As Maynard et al. (2008) warn “predictions made today will not be forgotten quickly and if incorrect, might constrain the capacity of the scientific community to influence future policy”. Moreover, climate change research is penetrated by political and economic interests, and is under close scrutiny and attack by skeptics (Hanson, 2010). As recent evidence shows (Schiermeier, 2009a,b, 2010; Hanson, 2010; Jasanoff, 2010; Kintish, 2010; Sarewitz, 2010), the entire scientific evidence maybe discredited in the eyes of the public (Gleick et al., 2010) from a few overstatements, with extremely negative impacts for the action that the evidence on hand demands. That ocean acidification is occurring is supported by both overwhelming empirical evidence and basic chemical principles (Raven, 2005), and its impacts on biota remain, beyond doubt, an issue of concern for its likely negative effects on vulnerable species and ecosystems. Hence, the risk of such biological impacts must suffice, in accord with the Convention for Biological Diversity, to act to mitigate this problem despite present scientific uncertainties. Conveying the scientific evidence along with an open acknowledgement of uncertainties clearly helping separate evidence from judgment should not harm the need to act to mitigate ocean acidification and should pave the road for robust progress in our understanding of how ocean acidification impacts ocean ecosystems.

Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ecss.2010.06.007.

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