

Short communication

What meta-analysis can tell us about vulnerability of marine biodiversity to ocean acidification?

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ABSTRACT

Ocean acidification has been proposed as a major threat for marine biodiversity. Hendriks et al. [Hendriks, I.E., Duarte, C.M., Alvarez, M., 2010. Vulnerability of marine biodiversity to ocean acidification: a meta-analysis. *Estuarine, Coastal and Shelf Science*, doi:10.1016/j.ecss.2009.11.022.] proposed an alternative view and suggested, based on a meta-analysis, that marine biota may be far more resistant to ocean acidification than hitherto believed. However, such a meta-analytical approach can mask more subtle features, for example differing sensitivities during the life-cycle of an organism. Using a similar metric on an echinoderm database, we show that key bottlenecks present in the life-cycle (e.g. larvae being more vulnerable than adults) and responsible for driving the whole species response may be hidden in a global meta-analysis. Our data illustrate that any ecological meta-analysis should be hypothesis driven, taking into account the complexity of biological systems, including all life-cycle stages and key biological processes. Available data allow us to conclude that near-future ocean acidification can/will have dramatic negative impact on some marine species, including echinoderms, with likely consequences at the ecosystem level.

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1. Introduction

As a consequence of increasing atmospheric CO₂, the world's oceans are warming and slowly becoming more acidic (ocean acidification, OA) and profound changes in marine ecosystems are expected. In a recent article aiming at a quantitative review of the literature, Hendriks et al. (2010) conclude: "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." This conclusion, contrasting with the current paradigm that ocean acidification will be a major threat for marine species and ecosystems (e.g. Doney et al., 2009), was based on a simple meta-analysis of 42 articles (372 experimentally evaluated responses of 44 species). This database includes a range of processes (calcification, fertility, growth, metabolism and survival) and taxa (from unicellular algae to fishes). When all the data were pooled, no effect of ocean acidification was observed (effect size, $s = 1.01 \pm 0.099$, see Methods). This response was modulated by the studied process, the taxonomical position and experimental CO₂ concentration

(Hendriks et al., 2010). However, a species response to ocean acidification (or any other stressor) should be assessed at different levels from individual to ecosystem. (1) At the individual level, the whole life-cycle of the organism should be investigated, including various fitness related biological processes (e.g. fecundity, fertility and survival) and all life-cycle stages (e.g. gonads, embryos, larvae, juveniles and adults). This is particularly true for mero-benthic or mero-planktonic species. For example, many benthic marine invertebrates develop by means of a free-living dispersive planktonic larval stage (Fig. 1). These larvae are morphologically and ecologically distinct from the adult until they reach the juvenile stage at metamorphosis. As a consequence, each life stage could differ in form and function with various degrees of autonomy and thus have differing sensitivities to environmental stressors. The species success when facing a stress such as ocean acidification should then be expressed as the survival over the whole reproductive cycle. (2) At the population level, intra-population variability should be taken into account (e.g. through multi-generation perturbation experiments and selection of resistant genotypes). (3) At the species level, different populations of a same species may present different sensitivities to the same stressors as a consequence of differential environmental and selection histories. (4) At the ecosystem level, direct and indirect ecological interactions may have consequences for species survival. For example, an increase of

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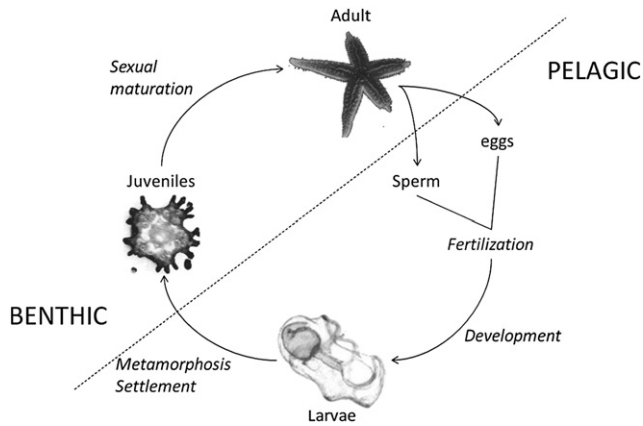


Fig. 1. Classic life-cycle of a benthic species. The adult is living in a benthic environment and reproduces by releasing eggs and sperm in the water where fertilization occurs. Embryos and larvae develop in the pelagic environment for a given period (usually several weeks) and then metamorphose and settle on the benthic environment. Juveniles grow till reaching sexual maturity.

developmental time may have a significant cost due to increased larval predation. A bottleneck or a dead-end in one of these processes or one (or more) life-cycle stage can drive the whole species response (Dupont et al., 2010a).

2. Methods

To test this hypothesis and show limitations associated with using a small data set, we employed the same simplistic methodology as that used by Hendriks et al. (2010): calculation of an “effect size”, *s*, defined as the dimensionless ratio of the treatment over the control response value (Gurevitch and Hedges, 1993). A *s* = 1 corresponds to no effect, *s* < 1 a negative effect and *s* > 1 a positive effect of OA on the tested process. Because of the small size of the database and the simplistic aspect of this metric not taking into account the variance measured in original papers, effect size was used in a descriptive way and no statistics were involved. To limit the effect of confounding factors such as taxonomical position and experimental CO₂ conditions, we focused on echinoderms, a group of marine calcifiers predicted to be very sensitive to ocean acidification (Dupont et al., 2010a) together with a decrease up to 0.4 pH units (predicted for the end of the century, 2100, Caldeira and Wickett, 2003) using experimental conditions that closely mimic the on-going and future changes in the seawater carbonate chemistry (see Dupont et al., 2010a for more information). The database contained a total of 100 experimentally evaluated responses extracted from 23 articles (Kurihara and Shirayama, 2004a; Kurihara et al., 2004; Shirayama and Thornton, 2005 also used by Hendriks et al., 2010; Kurihara and Shirayama, 2004b; Carr et al., 2006; Miles et al., 2007; Dashfield et al., 2008; Dupont et al., 2008, 2010b; Havenhand et al., 2008; Wood et al., 2008, 2009, 2010; Byrne et al., 2009a,b, 2010; Clark et al., 2009; Gooding et al., 2009; O’Donnell et al., 2009, 2010; Morita et al., 2010; Ries et al., 2009; Reuter et al., 2010 not included in Hendriks et al., 2010). This includes 4 echinoderm classes (brittlestars (2 species), seastars (2 species), sea urchins (13 species) and sea cucumbers (1 species)), all life-cycle stages (gametes, embryos, larvae, juveniles and adults) and a range of processes (fertility, growth, metabolism, homeostasis, feeding, survival and calcification).

3. Results

Under the realistic scenario of a decrease of up to 0.4 units of pH, the biological response to ocean acidification measured

as the effect size on the pooled database showed no effect (*s* = 0.99 ± 0.05, *n* = 99) and one could conclude, based on this global meta-analysis, that echinoderms are robust to ocean acidification. However, this is modulated by several experimental parameters such as time of exposure (e.g. greater impact after 6 months (*s* = 0.73 ± 0.08, *n* = 6) than in the shorter term (<2 weeks, *s* = 0.89 ± 0.02, *n* = 66)), species (*s* ranged between 0.43 and 2.78) and biological processes (Fig. 2). The response is also modulated by life-cycle stages, an important parameter that can drive the whole species response. Thus, adults appear to be resistant to ocean acidification (*s* = 1.30 ± 0.19, *n* = 23) while juveniles (*s* = 0.90 ± 0.19, *n* = 11), embryos/larvae (*s* = 0.93 ± 0.05, *n* = 47) and gametes (*s* = 0.88 ± 0.04, *n* = 18) are negatively impacted.

4. Discussion

Meta-analyses aim to provide a more objective and informative alternative to narrative reviews. However, the assumption that a meta-analysis represents the final and accurate viewpoint in an area of research is not always warranted. Discrepancies between meta-analyses are documented in the literature (LeLorier et al., 1997), even when similar methodologies are used. Techniques for meta-analysis were developed in the medical, physical, and behavioral sciences and introduced into ecology in the early 1990s. To fit ecological questions, this set of statistical methods for quantitative research synthesis need to be adjusted to account for the structure of biological and ecological data and address specific ecological issues and problems. This is complicated when different taxonomical positions and different processes are involved (e.g. Hendriks et al., 2010).

To facilitate comparison with Hendriks et al. (2010), we used the same simple meta-analysis metric, size effect (*s*). Taking into account important biological parameters driving the whole species response (ignored by Hendriks et al., 2010), we show that life-cycle bottlenecks can be identified while they are hidden using a global data analysis that mixes different life-cycle stages in a single analysis. Gametes and early development appear to be far more impacted by ocean acidification than adult stages. For example, echinoderms may appear to be resistant to ocean acidification as adults (e.g. Wood et al., 2008) and juveniles (e.g. Gooding et al., 2009) but be extremely sensitive as larvae (e.g. Dupont et al., 2008) a feature that would compromise species survival in near-future conditions.

A good example is the 100% mortality observed in the brittlestar *Ophiothrix fragilis* larvae when exposed to ocean acidification

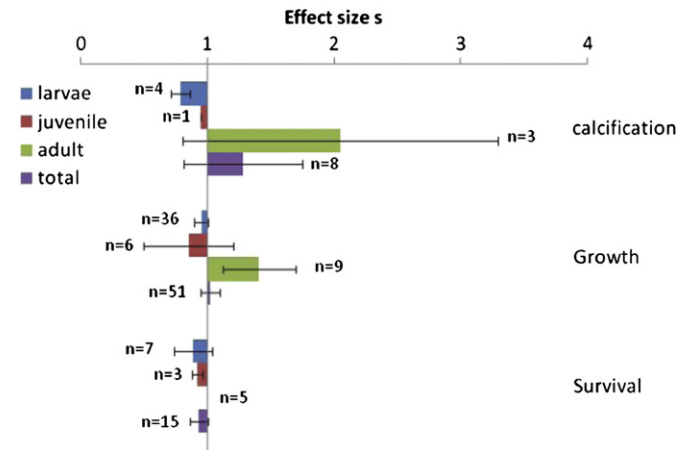


Fig. 2. Effect size (mean ± standard error of mean) of different biological processes (calcification, growth and survival) assessed for different life-cycle stages (larvae, juvenile and adults) exposed to ocean acidification.

(Dupont et al. 2008; one of the many papers not included in Hendriks et al. 2010). As a consequence, even if other life-stages and biological processes are resistant to ocean acidification, we can predict that this species could be eradicated by 2050. *Ophiothrix fragilis* is widely distributed in the eastern Atlantic and is a keystone species in many coastal communities. Eradication of this species is likely to have major consequences for many important benthic and pelagic ecosystems of the Atlantic.

Another aspect that may not be reflected in such a meta-analysis is the critical species-specific effect of OA observed for all life-stages, even when focusing on one taxonomic group (Dupont et al., 2010a). This too can be partly related to life-history strategies. Animals have evolved a variety of life-history strategies that enable them to reproduce successfully across a wide range of habitats. These reproductive strategies range from a complete lack of parental care to internal and external brooding of eggs, embryos, larval and juvenile phases (Pechenik, 1999). Two main strategies are currently recognized: (1) planktotrophy (60–90% of all benthic marine animals), where a single parent invests energy in producing millions of small eggs that will develop into planktotrophic larvae feeding on exogenous sources of energy; and (2) lecithotrophy (10%), where females produce comparatively small numbers (usually thousands) of large yolky eggs and lecithotrophic larvae that derive their nutrition from energy stored in the egg itself (Pechenik, 1999). Other rare “deviant” forms of reproduction are also documented including brooding of eggs, embryos and juveniles (Gillespie and McClintock, 2007).

Most of the work on the impact of OA on larval stages has been carried out on planktotrophic species and mostly shows a negative impact on growth rate. In striking contrast with all planktotrophic larvae tested so far ($s = 0.90 \pm 0.02$, $n = 35$), a recent paper demonstrates that lecithotrophic larvae appear to benefit from OA ($s = 1.28$, Dupont et al., 2010b). This highlights the importance of taking varying life-history strategies into account when assessing the impacts of ocean acidification. It is then tempting to speculate that planktotrophic and lecithotrophic larvae may have differing relative tolerances to environmental stressors, such as OA, and that lecithotrophy may be an advantage in unpredictable and extreme environment.

On the other hand, it is also important to remember that extinction does not require the instantaneous death of all individuals in a species. A density decreases of as little as 1% per generation may reduce many animal populations to unsustainable numbers in little more than a century. Small scale sub-lethal impacts of ocean acidification on some biological processes and some life-cycle stages can then influence the fitness and resilience of marine populations. This illustrates that any ecological meta-analysis should be hypothesis driven, taking into account the complexity of biological systems (Fig. 1).

For example, a sub-lethal impact on larval growth rate may have dramatic consequences for population maintenance. Without considering the direct impact of ocean acidification on mortality (the only one assessed in single-species experiments), indirect impact on mortality may occur in natural conditions. The cost of planktonic life can be severe because of mortality due mainly to predation and other risks such as starvation, offshore transport and exposure to intolerable environmental conditions. In sea urchins, daily mortality rate (DMR) has been estimated in the field and ranges between 0.085 and 0.164 per day due mainly to predation (Lamare and Barker, 1999). Thus, on the basis of a 30 day developmental period, larvae will experience between 92 and 99% mortality. However, OA is well known to impact developmental rates (Dupont et al., 2010a) and a slight change in larval growth rate can translate into an important impact on survival (Fig. 3). An average s value for growth rate of 0.80, corresponding to a 20%

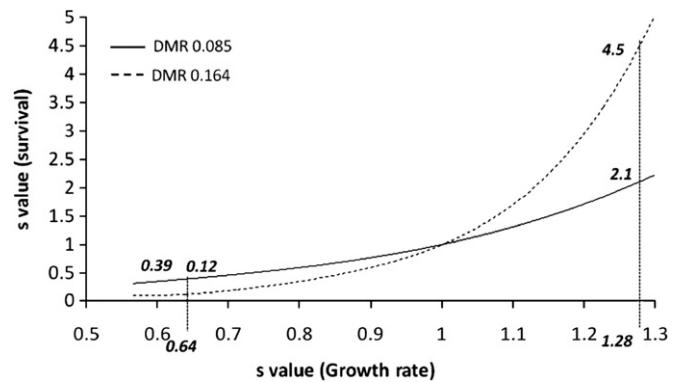


Fig. 3. Relationships between s value for larval growth and larval mortality based on two scenarios for daily mortality rates (DMR of 0.085 and 0.164, Lamare and Barker, 1999). Literature review for echinoderms revealed that the s value for echinoderm larval growth ranged between 0.64 and 1.28 with consequences for mortality ranging between a $s = 0.12$ –0.39 decrease to a $s = 2.1$ –4.5 increase in mortality.

delay in development, will translate into a s value for survival ranging between 0.39 ± 0.06 (MDR = 0.164) and 0.61 ± 0.05 (MDR = 0.085), or a 2.60–1.64 times increase in mortality respectively. The highest observed impact on growth corresponds to a s value on growth rate of 0.64 with a 2.60–8.32 time increase in mortality (Fig. 3). It is very likely that such important changes could compromise population sustainability. On the other hand, in the lecithotrophic larvae the growth rate was increased by a factor $s = 1.28$. This can translate into a 2.1–4.5 times increase in survival. However, it is also important to remember that a positive effect on a given process (e.g. an increased growth rate with a potential increase in larval survival) may have a negative impact at the ecosystem level. For example, the seastar *Crossaster papposus* is the dominant predator of its foodweb and influences the distribution of many other species, determining community structure. As a result, any change in species fitness could have profound impacts on its ecosystem (Himmelman and Dutil, 1991).

Because of 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 and more sophisticated methods (e.g. metrics taking into account variance) may be used for a better assessment of the literature (Gates, 2002). In this way, data and resultant conclusions from this present paper should not be used to generalize the impact of OA on species and ecosystem and are just illustrative of the limitations associated with the use of meta-analyses with a small and perhaps unrepresentative data set. The OA field is still in its infancy and it is very likely that future research will reveal the impact of OA on other important fitness related parameters and processes that were not previously studied (e.g. carry-over effects, fertility, etc. See Fig. 1). For example, long term exposure of adult sea urchins showed that gonad development was delayed, and the spawning period was shortened to almost half that of the control (Kurihara et al. unpubl. data in Kurihara, 2008). However, despite these caveats, enough data are available today (e.g. Dupont et al. 2008, 2010b) to conclude that near-future ocean acidification can/will have dramatic impacts on some marine species, including echinoderms, with likely consequences at the ecosystem level.

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