



Introduction to Special Issue: 'Towards a Broader Perspective on Ocean Acidification Research Part 2'

Introduction

Towards a broader perspective on ocean acidification research

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Browman, H. I. Towards a broader perspective on ocean acidification research. – ICES Journal of Marine Science, 74: 889–894.

Received 16 April 2017; revised 16 April 2017; accepted 18 April 2017.

Ocean acidification (OA) continues to be one of the most studied single topics in marine science. Almost 800 articles on OA appeared in 2016 alone. Forty-four of those were published in a special themed issue of the ICES Journal of Marine Science, "Towards a broader perspective on ocean acidification research." Submissions to that themed initiative continued well beyond the original deadline and were so numerous that we decided to publish this—a second OA-themed issue—which contains an additional 33 articles. In this Introduction, I briefly present the contributions that appear in this theme issue, and then offer an updated assessment of the status of OA research.

Keywords: academic scepticism, calcification, climate change, climate sensitivity, high CO₂, multiple environmental stressors, pH.

Background to this theme issue

Ocean acidification (OA) continues to be one of the most-studied single topics in marine science (Browman 2016, Figure 1). A Web of Science search for the term "OA", conducted on 5 April 2017, returned 4010 articles that have been cited over 87 000 times. Almost 800 of these articles appeared in 2016 alone, and 44 of those were published in a special themed issue of the ICES Journal of Marine Science (IJMS), "Towards a broader perspective on ocean acidification research." Submissions to that themed initiative continued well beyond the original deadline and were so numerous that we decided to publish this—a second OA-themed issue—which contains an additional 33 articles.

Here, I briefly present the contributions that appear in this theme issue, and then offer an updated assessment of the status of OA research.

The contributions in this theme issue

Reviews and perspectives

Schonberg *et al.* (2017) review the body of research on bioerosion in the context of OA, concluding that (i) bioerosion is increasing, (ii) environmental changes may not be as negative for bioeroders as for calcifying organisms, (iii) factors (e.g. OA) that facilitate bioerosion often reduce the rate of calcification and (iv) that the combination of these three points has resulted in bioerosion itself being (yet another) stressor of reef health and resilience.

They also identify knowledge gaps surrounding our understanding of the factors that drive bioerosion and how these are influenced by pH.

McElhany (2017) develops the provocative argument that experimental studies concluding an effect of OA are unintentionally misleading since they actually demonstrate sensitivity to CO₂ and not to OA (as also pointed out by Browman 2016, p. 531). He points out that documenting an effect of OA involves showing a change in population abundance or distribution (for example) that is clearly a consequence of anthropogenic changes in marine carbonate chemistry. He concludes that no such unambiguous demonstrations yet exist.

MacLeod (2017) reminds us that the host–parasite relationship is equivalent in importance to competition and predation in terms of its role in regulating individuals, populations, and communities. He provides an overview of the current (limited) understanding of how OA will affect parasitism as an ecological process, describes potential pitfalls of ignoring parasitism, and suggests how parasitology can be incorporated into OA research.

Humphreys (2017) explains why the rates of ocean warming (OW) and OA are linked at a level that is often underappreciated. He points out that, since carbonate system variables are affected differentially by climate change, there is a need to develop a mechanistic understanding of which specific variables are important to each biogeochemical process. He emphasizes that temperature buffering of the marine carbonate system must be

considered when designing experiments to determine marine species and ecosystem responses to OW and OA.

Fröder *et al.* (2017) studied first-shell formation in larvae of the Pacific oyster, *Crassostrea gigas*, and report that larvae utilized the same amount of total energy to complete first-shell formation regardless of the saturation state of aragonite. They also concluded that first-shell formation was not energy limited because sufficient endogenous reserves were available to meet metabolic demand. Further, different larval families exhibited reductions in shell size ranging from no effect to 28% in response to aragonite undersaturation, indicating that resilience to OA may exist among genotypes.

Robbins *et al.* (2017), in a study on different developmental stages of large benthic foraminifera (LBF), identified a bias in the design of OA experiments on LBFs that might result if only adults are used to investigate changes in test chemistry. Their results also confirm earlier reports indicating that there are different calcification mechanisms in foraminiferal orders that control the fractionation of stable isotopes in the tests and will, therefore, reflect decreasing seawater pH differently.

Ribas-Ribas *et al.* (2017) assessed the relative influences of carbonate chemistry and other environmental factors on plankton communities in northwestern European seas. They found that the spatial patterns in phytoplankton communities were driven more by nutrient and physical variables (euphotic zone depth, silicic acid availability, average irradiance in the mixed layer, and nitrate concentration) than by carbonate chemistry. Spatial variation in total phytoplankton and coccolithophore species composition were both more strongly associated with nutrients and physical variables than carbonate chemistry.

No effect, limited effect, and/or mixed effects of OA

Hassenrück *et al.* (2017) studied community composition and diversity of bacterial biofilms on settlement tiles deployed under naturally reduced pH conditions created by two CO₂ seeps in Papua New Guinea. pH did not have a strong impact on the composition of bacterial biofilms on mature settlement surfaces.

Mardones *et al.* (2017) exposed the toxigenic dinoflagellate, *Alexandrium catenella*, to variations in pCO₂/pH comparable to current and near-future levels observed in Southern Chilean fjords. They observed that Chilean strains of *A. catenella* are adapted to spatiotemporal fluctuations in pCO₂/pH and that this underlies their tolerance to climate change.

Bailey *et al.* (2017) investigated the effect of increased CO₂ (320, 530, 800, and 1700 µatm) on the early developmental stages of the Arctic copepod *Calanus glacialis*. Developmental rate, dry weight, and carbon and nitrogen mass were unaffected by CO₂, indicating that naupliar development in wild populations of *C. glacialis* will not be detrimentally affected in a future high CO₂ ocean.

Cooper *et al.* (2017) tested the hypothesis that organisms—in this case, the north Pacific krill, *Euphausia pacifica*—adapted to environments in which they are exposed intermittently to pH values approaching those predicted to result from OA, can tolerate prolonged exposure to high pCO₂ levels. They report that survival and moulting rates were unaffected by pCO₂ levels (380 and 1200 µatm), although growth was slower. Survival was unaffected down to pH 6.96 (6050 µatm).

Lee and Kim (2017) investigated the responses of the Manila clam, *Venerupis philippinarum* to pCO₂ (400, 700, and 900 µatm)

and found no significant differences in mortality, growth, respiration rate, or emergence from the sediment. They conclude that levels of CO₂ predicted for the near-future do not have a serious effect on the physiology and behaviour of adult Manila clams.

Page *et al.* (2017) tested the hypothesis that elevated pCO₂ differentially affects the relative concentrations of divalent cations in the exoskeleton of four closely related species of porcelain crabs distributed across intertidal zone gradients. Crabs were exposed for 24 days during the intermoult period to pH/pCO₂ levels of 8.0/418 and 7.4/1850 µatm. They found that the effect of reduced pH/elevated pCO₂ on exoskeleton mineral composition was small in mid-intertidal species relative to low-intertidal species, and interpreted this as indicating that adaptation to the variable intertidal zone in these crabs is associated with tolerance to OA, at least when it comes to maintaining their mineralized structures.

Long *et al.* (2017) determined the effects of a 1-year exposure to decreased pH (~8.1, 7.8, 7.5) on the morphology, growth, and survival of juvenile blue king crab, *Paralithodes platypus*. They found no effect of pH 7.8 on morphology or mortality and only a minor effect on growth. However, exposure to pH 7.5 increased mortality and decreased growth. The results also identified acclimation to the exposure, which was interpreted as indicating a scope for evolutionary adaptation in response to gradually changing pH levels.

Lonthair *et al.* (2017) use the red drum (*Sciaenops ocellatus*) as a model to assess the hypothesis that early life stages of estuarine fishes are tolerant of elevated pCO₂ because they are routinely exposed to variable conditions. Yolk depletion rate, standard length (SL), and scototaxis were unaffected by pCO₂. Survival was significantly decreased when exposed to high pCO₂ (1300 and 3000 µatm), although heart rate only increased at 3000 µatm. These effects were less pronounced than those reported for non-estuarine marine fishes. Their results support the hypothesis that estuarine life history and habitat usage are related to the sensitivity of fish species to OA.

Murray *et al.* (2017) report on a 135 day CO₂ exposure (500 and 2300 µatm) experiment in which Atlantic silverside (*Menidia menidia*) embryos, larvae, and juveniles were cultured. Survival was high in both treatments. However, fish from the high CO₂ treatment were 4% shorter and weighed 6% less, although they exhibited a higher condition factor than control juveniles. Interestingly, the length of juveniles from the high CO₂ treatment was distributed into more extreme size classes and the length distribution shifting to a positive kurtosis.

Effects of OA in combination with other environmental variables

Durán Romero *et al.* (2017) conducted an experiment to assess the effects of ultraviolet radiation (UVR), OA and increased nutrients on a post-bloom phytoplankton and bacterioplankton community. Bacterioplankton sensitivity to UVR changed during the (short) experiment from inhibition to enhancement, and future environmental conditions stimulated bacterial growth, most likely due to indirect effects caused by phytoplankton.

Fine *et al.* (2017) report on the responses of intertidal vermetid gastropods and a crustose calcareous alga that cements their shells, thereby solidifying the reef edges. They examined thermal tolerance, resilience to low pH, high light intensity and desiccation on these reef builders. Calcification by *Neogoniolithon bras-sica-florida* was significantly lower at pH 7.9 as compared with

ambient pH (8.1). Dissolution at pH 7.9 at night was higher than net calcification during the day, suggesting that *N. brassica-florida* may not be able to contribute to reef accretion under the levels of OW and OA projected by the end of this century.

Bahr *et al.* (2017) studied the seasonal interaction between temperature, pCO₂ and irradiance in the Hawaiian reef building coral, *Montipora capitata*, over an annual cycle. They conclude that increased temperature, and the interaction between high irradiance and high temperature, will be the main factors controlling net growth, with OA playing a less important role.

Comeau *et al.* (2017) tested the response of net photosynthesis, gross photosynthesis, dark respiration, and light-enhanced dark respiration (LEDR) in eight coral taxa and seven calcified alga taxa from the back reef of Moorea, French Polynesia to six different pCO₂ levels from 280 to 2000 µatm. Net photosynthesis was not affected by pCO₂ in seven of eight corals or any of the algae; gross photosynthesis did not respond to pCO₂ in six coral taxa and six algal taxa; dark respiration was also unaffected by pCO₂ in six coral and six algae; and LEDR did not respond to pCO₂ in any of the tested species. They conclude that pCO₂ levels up to 2000 µatm are unlikely to fertilize photosynthesis or modify respiration rates of most of the main calcifiers on the reef studied.

Bedwell-Ivers *et al.* (2017) measured zooxanthellae photosynthesis and calcification in the corals *Acropora cervicornis* and *Porites divaricata* cultured using seawater with natural metabolic dissolved inorganic carbon dynamics at pCO₂ levels of ~1000 and ~500 µatm. *A. cervicornis* microcolonies maintained both photosynthesis and calcification under elevated pCO₂ relative to controls. However, photosynthesis and calcification rates of *P. divaricata* microcolonies were reduced by ~80 and 20%, respectively. *P. divaricata* calcification response to elevated pCO₂ was linked to photophysiological dysfunction of the algal symbiont. Linear extension rates were unaffected by pCO₂ in both species. It is proposed that an area for future investigations is if/how elevated pCO₂ compromises zooxanthellae-coral interactions.

Rühl *et al.* (2017) simulated OW and OA in a 14-month mesocosm experiment and investigated their impacts on shell biomineralization and microstructure, and ontogeny, of juvenile *Nucella lapillus* (L.), a common gastropod predator. Elevated temperature and age determined shell density, length, width, thickness, elemental chemistry, shape, and shell surface damage. *N. lapillus* from OA treatments had weaker shells, possibly leaving them more vulnerable to predation and wave action. However, in some instances, higher CO₂ content and elevated temperature reversed these effects as individuals aged. It is suggested that compensatory development may occur in this species such that expected increases in juvenile mortality under OA and OW might be partially counteracted by high plasticity in shell formation.

Boch *et al.* (2017) exposed red abalone (*Haliotis rufescens*) gametes to a gradient of seawater pH (7.95–7.2) coupled with two levels of dissolved oxygen (DO) (~2 and 6 mg/l) and three levels of temperature (9, 13, and 18 °C) in an investigation of how current and predicted coastal upwelling conditions in the California Current Large Marine Ecosystem might influence fertilization success. Fertilization success declined significantly with decreasing pH. DO had a negligible effect. Temperatures associated with El Niño Southern Oscillation conditions (18 °C) had a positive effect on fertilization success, acting antagonistically to acidification at the lower pH levels.

Chatzinikolaou *et al.* (2017) investigated the combined effect of reduced pH (7.6) and increased temperature (25 °C) on

variability and fluctuations of shell structure and density over time in the intertidal gastropods *Nassarius nitidus* and *Columbella rustica*. For *N. nitidus*, there was a 38.1% reduction in density of the shell lip and a 47.7% decrease in the apex (the oldest shell region) at low pH and ambient temperature. *C. rustica* was also affected, although to a much lesser degree. When temperature was increased, the negative effects of reduced pH were exacerbated for *C. rustica*, but *N. nitidus* was unaffected by the combination of the two factors. Increased temperature at ambient pH had an inhibitory effect on the shell density of *N. nitidus*, whereas the shell density of the widest and lip regions of the *C. rustica* increased under the same conditions.

Lowder *et al.* (2017) measured growth, mineralization, transparency, and spectral reflectance (colouration) of the caridean grass shrimp *Hippolyte californiensis* in response to OA and OW. Shrimp were exposed to pH 8.0 and 7.5 at 17 °C and pH 7.5 at 19 °C for seven weeks. There were no differences in either Mg or Ca content in the exoskeleton nor in transparency or spectral reflectance. There was a small but significant increase in carapace length of shrimp exposed to decreased pH/increased temperature. This tolerance might stem from adaptation to the highly variable pH environment that these grass shrimp inhabit.

Cunha Sarmiento *et al.* (2017b) conducted a mesocosm experiment to assess the potential interactive effect of elevated CO₂ and temperature (pH 8.0, 7.7, 7.3, and 6.7 at 12 and 16 °C) on an intertidal harpacticoid copepod community from the extreme low intertidal zone. The dominant harpacticoid species were only affected at pH 6.7. However, even then, while some exhibited density reductions, others increased. Cunha Sarmiento *et al.* (2017a) report on a related laboratory experiment conducted to evaluate the impact of different climate change scenarios (reduced pH and increased temperature) on a coral reef meiofauna community. Although polychaetes, for example, were only negatively affected after 29 days, and only in the most severe scenario, Nematoda exhibited higher densities in all scenarios, demonstrating that community responses to OW and OA are taxon-specific.

Visconti *et al.* (2017) evaluated the effect of OW (+4 and +6 from current levels = 24 and 26 °C) and OA (−0.3 pH units from current levels) on larval development of the sea urchin *Arbacia lixula*. A slightly negative effect of pH was ameliorated by higher temperature. The broad thermal range (~10 °C) of development of *A. lixula* across its distribution underlies its tolerance to climate change and ensures population connectivity between Mediterranean sub-basin populations.

Swiney *et al.* (2017), working with young-of-the-year red king crab (*Paralithodes camtschaticus*) from Alaska, determined the effect of OW and OA on survival, growth, and morphology. Mortality increased with exposure to pH 7.8 and higher temperatures (+2 and +4 °C of current ambient), but an interactive effect of the stressors was not observed. A synergistic effect on mortality was observed in the pH 7.8 and ambient +4 °C treatment, which also had only 3% survival. However, an antagonistic effect on mortality was observed in the pH 7.8 and ambient +2 °C treatment. Lower pH and warmer temperatures affected intermolt duration, while only temperature affected percent increase in size, but carapace length was not affected. Decreased pH and increased temperature had no effect on morphology.

Glandon and Miller (2017) exposed juvenile blue crab, *Callinectes sapidus*, to one of four temperature/pCO₂ treatments (ambient/low, ambient/high, high/low, high/high) for two complete molts. Growth per molt (GPM), inter-molt period (IMP),

and food consumption, were quantified. GPM was not affected by either increased temperature or pCO₂. Although increased pCO₂ did not significantly influence the duration of crab IMP, crabs in warm water had significantly shorter IMP than crabs in ambient water. Increased pCO₂ did not significantly affect the amount of food crabs consumed, but crabs in warm water ate significantly more food than those in ambient water. These data suggest that the impact of OW outweighs the impact of pH in juvenile blue crab.

Waller *et al.* (2017) investigated the interactive effects of OW and OA on larval development of the American lobster, *Homarus americanus*. Larval stages I–III and stage IV postlarvae reared in the high temperature treatments (19 °C) experienced significantly lower survival, developed twice as fast, and had significantly higher oxygen consumption rates than those in ambient treatments (16 °C). Larvae from the ambient temperature/high pCO₂ (750 ppm) treatment had significantly longer carapace lengths, dry masses in stages I–III, and C:N masses in stage IV, than larvae from all other treatments. Stage IVs raised in the high pCO₂ treatment at 19 °C had significantly higher feeding rates and swimming speeds than stage IVs from the other three treatments. These results suggest that OW will have greater adverse effects than increased pCO₂ on larval survival and pCO₂ will have a complex effect on larval metabolism.

Bignami *et al.* (2017) exposed larval cobia (*Rachycentron canadum*) to higher CO₂ (1700–2100 µatm) and temperature (27 and 32 °C) and lower food availability. They report a negative effect of elevated pCO₂ on starvation resistance, but few synergistic effects of the combined stressors. Elevated pCO₂ caused a transient but significant reduction in larval SL, growth rate, and development rate, while warmer temperature was associated with an increase in SL, development rate, and swimming ability. Larval condition was unaffected by elevated pCO₂, although larvae fed a 25% ration had significantly reduced SL, growth rate, and development rate. Under complete feeding cessation, larvae in elevated-pCO₂ seawater demonstrated lower starvation resistance, indicating that acidification may increase starvation risk in a patchy marine environment. Nonetheless, these results indicate that larval cobia are resistant to combined elevated pCO₂, temperature and rationing stress.

Poulton *et al.* (2017) investigated the independent and combined impacts of elevated CO₂ (400 and 1000 µatm) and anthropogenic noise (pile driving) on the behaviour of European sea bass (*Dicentrarchus labrax*). Pile-driving noise increased ventilation rate (indicating stress) compared with ambient noise conditions, but elevated CO₂ did not alter the ventilation rate response to noise. *D. labrax* exhibited the same or faster startle response to a looming stimulus under elevated CO₂. There was no interaction effect between elevated CO₂ and pile-driving noise, suggesting OA is unlikely to influence startle or ventilatory responses of fish to anthropogenic noise.

The continuing progression of research on OA

The studies published in this issue add to the developing and rapidly expanding narrative of response complexity and inconsistency—at the species and local habitat levels—in OA research (also see, Ghedini and Connell, 2017; Kroeker *et al.*, 2017; Vargas *et al.*, 2017). Coming to grips with this complexity, and its basis, represents a significant challenge for OA research. In addition, it will take time to move beyond the issues with OA research that I raised earlier (Browman, 2016). For example, CO₂ effects (or lack

thereof) from acute experiments continue to be conflated with inferences about OA impacts (*sensu* McElhany, 2017). This is especially problematic when the effects observed in acute experiments are incorporated—without any adjustment for possible adaptation—into inferences about OA impacts in the coming decades. With respect to possibilities for adaptation, there are still very few studies on the heritability of traits that might confer tolerance (although see Welch and Munday, 2017), and even fewer on the potential for rapid evolution (e.g. via epigenesis or otherwise). For these, and various other reasons (e.g. Planque, 2016; Storch *et al.*, 2017), predictions about future impacts of OA based on extant bioeconomic models should be viewed with all due scepticism.

There continues to be a widespread imbalance in focus on individuals that are affected by experimental exposure to high pCO₂ (or any other climate change related variable, for that matter), and insufficient attention on inter-individual variability and within-experiment selection; that is, on the survivors. There is a richness of information in the latter that should not be ignored, as evidenced by important and exciting emerging lines of work on sources of fitness variation, selective breeding, assisted evolution and aquaculture (e.g. van Oppen *et al.*, 2015; 2017; Clements and Chopin, 2017; Ellis *et al.*, 2017; Chirgwin *et al.*, 2017).

The articles included in this theme issue that report on experiments with multiple variables, and many other such works published elsewhere, confirm that the additional driver(s)—be it temperature, irradiance, salinity, oxygen, nutrients...—typically has a stronger effect than CO₂ and that it is difficult to isolate the effect of the individual variables when they are presented simultaneously. Unfortunately, few studies have developed the functional response curves for each variable that would be necessary to more fully assess their individual and interactive effects.

Studies on the effect of CO₂ and other climate change-related drivers on species interactions are still sparse, although a small number of recent studies highlight the important, and sometimes counter-intuitive, outcomes of such indirect effects (see Ghedini and Connell, 2017). Much more work along these lines is needed if we are to move beyond single species studies.

Although my impression is that the situation is improving, it is worth repeating the main message of my introduction to the first IJMS theme issue on OA (Browman, 2016). Scientific or academic skepticism calls for critical scrutiny of research before it is accepted as new knowledge (Merton, 1973). I still contend that an insufficient level of organized skepticism is being applied to OA research. Nonetheless, I hope that the articles that appear in this theme issue will serve to move us *towards a broader perspective on OA research*.

Acknowledgements

The IJMS is grateful to the many authors who submitted their work for publication in this theme issue. A special thanks to IJMS editors Joanna Norkko, Shubha Sathyendranath, David Fields, and Brock Woodson, each of whom handled several of the articles submitted for publication in this theme issue.

Funding

H.I.B.'s contribution to this theme issue was supported by Projects no. 83192-01 (“Ocean acidification”), 81529 (“Fine scale interactions in the plankton”), and 83741 (“Scientific publishing and editing”) from the Institute of Marine Research, Norway.

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