Ocean acidification and climate change: advances in ecology and evolution

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Introduction

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Ocean acidification and climate change: advances in ecology and evolution

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1. Introduction

Atmospheric CO_2 concentration $[CO_2]$ has increased from a pre-industrial level of approximately 280 ppm to approximately 385 ppm, with further increases (700–1000 ppm) anticipated by the end of the twenty-first century [1]. Over the past three decades, changes in $[CO_2]$ have increased global average temperatures (approx. $0.2°C$ decade^{-1} [2]), with much of the additional energy absorbed by the world's oceans causing a $0.8°C$ rise in sea surface temperature over the past century. The rapid uptake of heat energy and CO_2 by the ocean results in a series of concomitant changes in seawater carbonate chemistry, including reductions in pH and carbonate saturation state, as well as increases in dissolved CO_2 and bicarbonate ions [3]: a phenomenon defined as ocean acidification. Time-series and survey measurements [4–6] over the past 20 years have shown that surface ocean pH has reduced by 0.1 pH unit relative to pre-industrial levels, equating to a 26% increase in ocean acidity [3]. Reductions of 0.4–0.5 pH units are projected to occur by the end of the twenty-first century [1] and, while atmospheric $[CO_2]$ has consistently fluctuated by 100–200 ppm over the past 800 000 years [7], the recent and anticipated rates of change are unprecedented [8].

Research has shown that ocean acidification and climate warming can independently affect many marine organisms in a variety of marine habitats from tropical to high-latitude ecosystems [9,10]. Our present understanding of the effects of ocean acidification, however, is reliant on empirical studies developed to ascertain species-specific responses to forcing. The majority of these studies report short-term (days, weeks or a few months, see [10]) 'shock' responses that do not incorporate the longer-term potential for species gradual acclimatization (i.e. respond via phenotypic plasticity, see [11]) or adaptation (the selection of extant genetic variation that moves the average phenotype of a population towards the fitness peak). In addition, ocean acidification is co-occurring with other drivers of environmental change (including warming, eutrophication, hypoxia, eutrophication, pollution [12]), yet the interactive effects and relative importance of multiple stressors on species physiology, life history and ecology, as well as species–environment interactions and ecosystem function remain poorly understood [13–17].

In less than a decade since the influential report on Ocean Acidification published by the Royal Society [18], our understanding of the direct and indirect effects of ocean acidification and climate change on biotic systems has remarkably improved [4,10,19–21]. Nonetheless, the rapid and often asymmetric growth of this interdisciplinary field has left important knowledge gaps that require urgent attention: (i) what are the effects of ocean acidification and climate change on species interactions?, (ii) are communities and their ability to maintain ecosystem functioning resilient to ongoing global change? (iii) Can organisms' capacity for phenotypic buffering and adaptation offset the consequences of environmental change? Here, we

explore advances in each of these areas and particularly focus on the following three themes:

(i) *Species interactions*. While biotic interactions play a fundamental role in defining change to species distribution and communities structure [22–24], the degree to which ocean acidification and climate change may alter the way in which species interact with one another is not fully understood. Studies that have explored species responses to biotic stimuli and interactions under ocean acidification conditions using laboratory experiments [25–28]) and field observations or manipulations around CO_2 vents [29–32] provide some evidence that species interactions and community dynamics can be fundamentally affected.

(ii) *Biotic mediation of ecosystem functioning.* Organism–ecosystem function relations are strongly influenced by environmental context [13,33–35]. Exposure to ocean acidification and warming is therefore likely to not only affect species behaviour [33,36–38] but will also have profound effects on the mediation of processes that underpin the important ecosystem functions, such as biogeochemical cycling of macronutrients [34,39] or decomposition rates [40] that support the rest of the food web and, ultimately, the delivery of goods and services necessary for human well-being [41].

(iii) *Capacity for phenotypic buffering and adaptation.* Organisms continuously adjust their physiological status as the physico-chemical environment around them fluctuates and changes ('*phenotypic plasticity*', [11,42]), in order to maintain optimal levels of energy production, fundamental to sustain cell repair, growth and reproductive investments [43]. However, plasticity often comes at a cost [44,45]. When such cost outweighs that of adaptation, this should be the favoured mechanism of response to an environmental change, and local adaptation should occur (e.g. [46]). In general, evolutionary aspects of ocean acidification, alone, and in combination with other stressors, have largely been overlooked (notable exceptions on the adaptive responses of marine microalgae to elevated pCO$_2$ include Collins [47,48], Lohbeck *et al.* [49,50] and Tatters *et al.* [51]). Consequently, projections of the likely consequences of environmental change, ignore species' capacity for phenotypic buffering and the propensity for adaptation.

This Theme Issue contains nine contributions that consider the effects of ocean acidification and climate warming, alone and in combination, on physiological and life-history responses, biotic interactions, community dynamics and ecosystem functioning over the medium to long term, across multiple generations, and from natural systems chronically exposed to elevated pCO$_2$. We review and present new evidence that supports the importance and challenges of incorporating long-term acclimatization and naturally adapted populations and communities. Evidence is presented from field observations, as well as laboratory and field-based empirical studies representing a range of phyla and life stages in both benthic and pelagic habitats, in order to provide a balanced and wide-ranging summary of how marine organisms may respond to the ongoing rapid climatic change.

Current understanding of the likely ecological consequences of warming and ocean acidification is predominantly based on studies that have focused on calcifying (shell-forming) organisms, which show a tendency to exhibit strong sensitivities to ocean acidification [10]. This focus, however, overlooks the direct and indirect effects of enhanced [CO$_2$] for non-calcareous taxa that is necessary to build a holistic appreciation of how the effects (negative, neutral and positive) of ocean acidification may be expressed at the biotic assemblage and ecosystem level [52,53]. In the first paper of this Issue, Connell *et al.* [54] consider the importance of future atmospheric [CO$_2$] as a resource, rather than a stressor, for a subdominant species of mat-forming algae. They show that enhanced [CO$_2$] has the potential to influence the competitive abilities of these species following an increase in resource availability that, in turn, causes shifts in species dominance and community structure that affect long-term ecosystem persistence and stability.

Such extended effects of ocean acidification are particularly challenging to incorporate in empirical investigations. In the second contribution to this issue, Russell *et al.* [55] introduce the importance of longer-term species acclimatization for distinguishing the confounding effects of exposure length from the effects of being held in an artificial environment over prolonged time periods. They show that primary producers (algal biofilm) and consumers (*Littorina littorea*) are likely to respond differently to one another under increasing [CO$_2$] and warming and that species acclimatization is fundamental if trophic shifts in response to changing species metabolic demands are to be avoided. In highlighting the potential for organisms to acclimatize to altered climate conditions, the authors emphasize the importance of such longer-term processes when predicting complex species and environmental responses to climate change. As the duration of experiments is extended, however, other long-term processes become increasingly important. In the longest empirical study to-date Godbold & Solan [56] demonstrate that the effects of warming and acidification on growth and behaviour of the ragworm *Alitta virens* change over time and, in turn, have significant consequences for ecosystem functioning (sediment nutrient generation). The authors argue that species responses to ocean acidification are intimately linked to seasonal variation in environmental conditions (e.g. temperature and photoperiod), such that the long-term effects of climatic forcing may be buffered, or exacerbated, at different times of the annual cycle. Hence, the natural variability of environmental and climatic stressors needs to be incorporated and accounted for in future studies if we are to reduce uncertainty in predicting the ecological consequences of climate change. This will have significant implications for the management and conservation of marine ecosystems.

The importance of species–environment interactions is considered in more detail by Laverock *et al.* [57], who show that ocean acidification has the potential to significantly modify the relationship between benthic macroinfauna (here, the burrowing shrimp *Upogebia deltaura*) and ammonia-oxidizing microorganisms inhabiting burrow walls. They show that under low pH conditions, ammonia oxidation associated with burrow walls significantly reduces and that ocean acidification has the potential to negate the positive impact that shrimp bioturbation otherwise has on microbial nitrogen cycling. Such changes in bioturbated sediments are likely to have significant impacts on the coupling of bentho-pelagic nitrogen cycling, a process of fundamental importance for the rest of the food web. Species behaviour and interactions (e.g. foraging, reproduction, predator avoidance) in many aquatic organisms are mediated through their olfactory senses

(e.g. [27]) that affect individual organisms' fitness, and ultimately change population dynamics and community structure. Leduc *et al.* [58] critically review the effect of acidification on olfaction-mediated behavior in marine and freshwater organisms, showing that the mechanisms of sensitivity in marine and freshwater species differ greatly. In marine species olfactory-mediated behavioural impairments are caused by the effects of elevated CO_2 on brain neurophysiology, whilst in freshwater fish the same impairments occur as a result of the degradation of chemosensory molecules as well as overall reduced olfactory sensitivity. The authors argue that ecosystem-specific response mechanisms need be considered before effective management and conservation strategies can be implemented.

Biological responses to ocean acidification have been shown to be highly species-specific and often idiosyncratic [10,21,59,60]. However, to-date no multispecies study has investigated a biological response to ocean acidification accounting for species evolutionary history and ecology. Byrne *et al.* [61] characterize the stunting effect of ocean acidification on the arm growth response of echinoplutei larvae of 15 species of sea urchin from different climatic regions (tropical, temperate, polar) and with different bathymetric distributions (intertidal and subtidal). Although they show reduced larval arm growth in all species investigated, species from different climatic regions varied in their sensitivity to ocean acidification. In polar and subtidal species arm growth is mainly affected by pCO_2, whilst in tropical species it was mainly affected by decreased carbonate saturation status. Variation in the sensitivity of larvae from different climatic regions may therefore lead to asymmetrical changes in sea urchin recruitment and subsequently alterations and shifts in species geographical ranges and changes in assemblage structure and dynamics.

Phenotypic plastic responses will play a major role in defining species resilience to ongoing environmental change [12,62]. However, to what extent phenotypic buffering can help species to compensate for the negative effect of ocean acidification, and whether adaptation is possible and should be favoured (particularly in metazoans) is still to be firmly established (cf. [46,63]). Using *in situ* transplantation experiments of non-calcifying polychaetes from the CO_2 vent of Ischia (Italy), Calosi *et al.* [64] provide evidence that both adaptation (genetic and physiological) and phenotypic plasticity are viable strategies to persist under elevated pCO_2; species overall showing elevated levels of metabolic control. Other species found only outside the CO_2 vent showed a marked departure from their 'original' metabolism under elevated pCO_2 conditions. These differences in metabolic control likely explain the distribution of polychaetes around the CO_2 vent, shedding light on how alteration in energetics may have caused species extinction during climate change events.

Marine microorganisms that drive many global ocean processes (e.g. oxygen production, primary productivity and biogeochemical cycling) are able to adapt to ocean acidification [49]. However, understanding of whether these organisms are also able to adapt to the combined changes in pCO_2 and temperature is still lacking. Benner *et al.* [65] consider this issue using over 703 cultured generations of the coccolithophore *Emiliania huxleyi*. They show that long-term acclimatization or adaptation to warm and acidified conditions could change or even reverse the negative calcification responses observed in short-term studies, and thus alter feedbacks to the global carbon cycle. Moreover, for the first time, they show that changes

in whole-organism phenotypic responses are accompanied by changes in the expression of genes related to intracellular regulatory processes rather than genes thought to be essential for calcification. Therefore observed increases in energetic costs are more likely linked to cell homeostasis rather than calcification as previously thought. Furthermore, even if organisms will be able to adapt to ocean acidification and warming, species-specific competitiveness might be modified. In the final paper of this issue, Tatters *et al.* [66] study the competitiveness of natural diatom communities incubated under future environmental conditions for two weeks, after which the dominant species were isolated and then incubated again for over a year before recombining the now conditioned species to reconstruct the original community. Inter-specific competition was found to be similar in both the unconditioned natural and the conditioned artificial community, suggesting that for diatom communities, short-term manipulative experiments may be used to predict the effects of long-term environmental forcing on community structure. Although both pCO_2 and temperature were found to affect community structure, elevated temperature was the main driver of change for reducing species richness in this study.

2. Conclusion

Ocean acidification and ocean warming are predicted to have substantial impacts not only on marine biodiversity [4,9,10] but also on ecosystem functioning and service provision [41,67]. Whilst much has been learned in the past decade about the potential implications of climate change on marine organisms and ecosystems, substantial knowledge gaps still exist.

In this issue, we have identified and addressed three major knowledge gaps of the organismal, ecological and ecosystem consequences of ocean acidification and ocean warming: (i) species interactions, (ii) biotic mediation of ecosystem functioning and (iii) capacity for phenotypic buffering and adaptation.

It has become clear that future empirical studies will need to incorporate longer incubation periods that allow to incorporate seasonal environmental processes, and, where possible, multiple generations, to enable organisms to fully express their phenotypic plasticity, as drawing conclusions based only on short-term exposures may over- or underestimate the consequences of future climate change. Combining results from laboratory studies with manipulative or observational studies conducted at naturally elevated pCO_2 sites will provide a more holistic view of the consequences environmental change. In addition, it is of fundamental importance that we refocus the current 'single stressor' focus to studies investigating the combined effects of multiple environmental and anthropogenic drivers (e.g. elevated temperature, pCO_2, pollution, overexploitation) in order to establish generality of the effects that complex interactions between drivers of change may have for organisms and ecosystems (see also [68]). In addition, this special issue highlights the importance of considering the capacity of organisms for phenotypic buffering and evolutionary adaptation in future predictions on community structure and ecosystem function, including the use of gene expression profiling, which will help to better understand the mechanisms underpinning organisms' responses to global change.

The contributions and recommendations in this issue substantially advance our knowledge of the likely organism and ecosystem consequences of ocean acidification and warming

that should be considered in future studies and will be important for the development and implementation of management and conservation strategies.

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