REVIEW, CONCEPT, AND SYNTHESIS

Biological impacts of ocean acidification: a postgraduate perspective on research priorities

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Abstract Research into the effects of ocean acidification (OA) on marine organisms has greatly increased during the past decade, as realization of the potential dramatic impacts has grown. Studies have revealed the multifarious responses of organisms to OA conditions, indicating a high level of intra- and interspecific variation in species' ability to accommodate these alterations. If we are to provide policy makers with sound, scientific input regarding the expected consequences of OA, we need a broader understanding of these predicted changes. As a group of 20 multi-disciplinary postgraduate students from around the globe, with a study focus on OA, we are a strong representation of 'next generation' scientists in this field. In this unique cumulative paper, we review knowledge gaps in terms of assessing the biological impacts of OA, outlining directions for future research.

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Introduction

Global oceans have absorbed over 500 billion tons of CO_2 since preindustrial times, which equates to over one-third of anthropogenic carbon emissions since the industrial revolution (Sabine and Feely 2007). If anthropogenic CO_2 emissions continue to increase, there is now little doubt that marine organisms will be impacted (Fabry et al. 2008), which could lead to an overall reduction in biodiversity (Hall-Spencer et al. 2008; Fabricius et al. 2011). Experimental exposures of organisms to ocean acidification (OA) conditions indicate a high level of intra- and interspecific variation in species' ability to accommodate these alterations. For example, positive adaptations that may enable the survival of some calcifying organisms have been shown, whilst other species appear less able to adapt (Sunday et al. 2011). The effects of OA conditions are not always deleterious, but may be advantageous such as increased growth in calcifying organisms (e.g. the sea star *Crossaster papposus*, see Dupont et al. 2010b) or enhanced biological carbon fixation in phytoplankton (Riebesell et al. 2007). Due to such variability of results, it has been difficult to provide sound scientific input regarding the expected environmental, social and economic consequences of OA.

As a group of 20 multi-disciplinary postgraduate students from around the globe, we participated in a workshop on 'Acidification in aquatic environments' held at the Fram Centre, Tromsø, Norway from 27th to 29th September 2011. In this paper, we review the previous OA research relating to the impacts on biogeochemistry, organisms and ecosystems, detailing the knowledge gaps and unanswered questions of these subjects. From this, we aim to cumulatively provide a fresh outlook to current OA scientists regarding priorities for future research. Overall, we conclude that wider collaboration and communication between institutions and disciplines will increase awareness of current OA research amongst the whole community and provide potential opportunities for large-scale multi-disciplinary projects. This will be vital if we are to provide policymakers and stakeholders with the information required for the effective development of successful mitigation and adaptation measures.

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Biogeochemistry

Under the IS92a 'business-as-usual' scenario, the surface seawater concentration of carbonate (CO_3^{2-}), and therefore the saturation state of calcite and aragonite, is expected to decrease by 48 %, whilst carbonic acid will increase by 178 % (Fabry et al. 2008). These changes in carbonate chemistry will not only impact organisms but may lead to changes in biogeochemical cycling in the oceans (Doney et al. 2009).

The biological pump

The biological pump, whereby carbon is biologically fixed and exported from the productive zone to the ocean interior, may be affected by a drop in pH. Vertical fluxes of organic matter are dominated by the gravitational sinking of particles (Gardner 2000) and minerals, of which calcium carbonate forms a large component (Francois et al. 2002). Reduced pH can directly affect adsorption of ions to surface-charged particles, resulting in a reduced adsorption coefficient. Aggregation and adsorption are two important processes in the interaction between particulate and dissolved compounds, and therefore organic matter cycling and export (Fowler and Knauer 1986). Changes in mineral ballast may weaken the biological pump and enhance the production of hypoxic zones, particularly in shallow waters (Hofmann and Schellnhuber 2009). Together with other stressors, such as eutrophication and increased stratification, this could have severe effects on the marine environment.

However, the effects of OA on the biological pump may not be entirely negative, and the vertical flux of organic matter may be enhanced through other mechanisms. Transparent exopolymeric particles (TEPs), primarily consisting of acidic polysaccharides, support coagulation processes and aggregate formation (marine snow) (Passow 2002) facilitating vertical carbon flux to the deep sea. Increased primary productivity under OA conditions may lead to amplification of the exudation rates of TEPs by phytoplankton and therefore increase particle sinking (Engel et al. 2010). If we are to understand the effect of OA on the biological pump and associated processes, then further investigation of the impacts on transport interactions (e.g. particle sinking and physical mixing of dissolved and particulate compounds) is strongly needed. In order to be able to predict future scenarios, quantification of positive and negative feedbacks is necessary.

Subpolar and polar regions are particularly sensitive to enhanced CO_2 due to its high solubility in cold, low salinity waters. In these areas, deep water formations draw down CO_2, which is further promoted by brine caused by sea ice formation. In this context, future research should focus on the role of the sea ice in vertical carbon transport and

addressing knowledge gaps regarding the extent that changing sea ice conditions in the polar regions will affect CO_2 uptake, $CaCO_3$ dissolution and precipitation, brine rejection and thus the fate of increased atmospheric CO_2.

Metal and toxicant bioavailability

Whilst studying biogeochemical responses to ocean acidification, it is essential to take into consideration the resulting indirect effects of a decrease in pH, such as changes in the speciation of metals and therefore their bioavailability or toxicity (Millero et al. 2009). The effects of OA on metal availability will have implications for marine primary producers and could affect fundamental biogeochemical processes, such as the biological pump. Iron limitation controls biological productivity in 30 % of the world's oceans (Ardelan and Steinnes 2010); therefore, assessing the potential effects of OA on iron biogeochemistry is crucial. Millero et al. (2009) showed that a decrease in pH from 8.1 to 7.4 will increase the solubility of Fe(III) by approximately 40 %, whilst Breitbarth et al. (2010) showed a similar pH decrease could cause a 10-fold increase in the half-life of Fe(II). In comparison, other studies have suggested that the bioavailability of iron will decrease under acidified conditions (Martin and Fitzwater 1988; Shi et al. 2010). Metals such as manganese, iron, nickel, cobalt, copper, zinc and cadmium are biochemically significant as they are required for the growth and survival of photosynthetic organisms; however, small increases in their concentration can turn these necessary metals into toxic stressors. Metals may be present in both soluble and particulate forms within the water column. Soluble species are comprised of free metal ions, inorganic and organic complexes (Allen 1993). As a consequence of OA, the concentration of hydroxide (OH^-) and carbonate (CO_3^{2-}) ions will decrease, and metals with speciation schemes dominated by carbonate complexation will be strongly affected (Millero et al. 2009). For example, the free-ion form of Cu increases as pH decreases (Pascal et al. 2010). This could cause negative effects under OA conditions as concentrations as low as 10^{-12} M of the free-ion form of Cu (II) would be toxic to marine phytoplankton (Brand et al. 1986). Furthermore, bioavailability of other toxicants such as emergent pollutants (nanomaterials and pharmaceuticals), xenobiotics and hydrocarbons may also change in availability.

Studies on marine trace metal chemistry and how it may be altered by OA conditions have increased in the last decade, although we still have little understanding of how this will affect marine organisms (Byrne 2002; Riba et al. 2010). Preliminary studies suggest that bioaccumulation of metals will change with decreased pH (Lacoue-Labarthe et al. 2009; Lacoue-Labarthe et al. 2011) with some metals

incorporated more (i.e. Ag) and others less (i.e. Cd) at low pH. The response of exposed species to contaminants under OA conditions will depend on the intensity and duration of exposure, as well as the ability of an organism to overcome the stress (Vasseur and Leguille 2004). Future experiments should focus on metal incorporation and detoxifying pathways under chronic exposure to an acidified environment. Detoxifying systems in organisms consist of eliminating reactive chemical species (e.g. xenobiotics), neutralizing their effects, repairing initial lesions, or compensating deficient metabolic pathways (Winston and Di Giulio 1991; McFarland et al. 1999; Wright and Welbourn 2002; Vasseur and Cossu-Leguille 2003). To evaluate detoxifying system activity (e.g. changes in enzymatic activity), the application of biomarkers is recommended (Solé et al. 1995; Van der Oost et al. 2003; Gagné et al. 2006), as they can detect sublethal effects before deeper alterations to the animal body start to manifest (Peakall and Walker 1994; Martín-Díaz et al. 2004).

Future research should incorporate two different approaches that, together, will enable us to more precisely assess the implications of CO_2-induced changes in the bioavailability of trace metals and toxic organic compounds under various scenarios. Firstly, a physio-mechanistic approach should be taken to unravel the mechanisms behind the responses of organisms to CO_2-induced changes in contaminant availability and how these changes may interact with predicted changes in other physico-chemical parameters (Portner 2008). Secondly, we suggest that this is complimented by a field-based approach utilizing natural situations (e.g. caged organisms in an area of natural pH variability) to understand how multiple stressors interact in a natural environment.

Benthic remineralization

Very little is known about how sediments, the organisms that live there and the processes that occur in them will react to changes in the acidity of seawater. Sediments are largely responsible for marine processes including nutrient cycling in key coastal areas and continental shelves. In coastal areas (<50 m deep), 80 % of nitrogen consumed by phytoplankton originates from bacterial regeneration of organic matter in sediments (Dale and Prego 2002). Although this activity is carried out primarily by microbial communities, nutrient cycling (including transformations and transport across the sediment–water interface) is significantly influenced by the activity of multi-cellular organisms, which live and feed in the sediment (Widdicombe and Austen 1998; Tuominen et al. 1999).

The effect of acidification on sediment geochemistry is unknown. Bioturbation as a result of building and ventilating burrows reduces the sediment pH (Soetaert et al.

2007) due to the enhancement in organic matter degradation and turnover. Whilst decreasing seawater pH to 5.6 in mesocosms did not affect mortality of the burrowing annelid Nereis virens (Widdicombe and Needham 2007), other studies of OA conditions highlight a range of tolerances amongst different infaunal organisms (Zhu et al. 2006; Widdicombe et al. 2009). Meiofauna plays a crucial role in nutrient cycling and energy flow from lower to higher trophic levels in the marine sediments. Most taxonomic groups of meiofauna were not negatively affected by increased CO_2 concentrations during a 56-day study near the Kii Peninsula, Japan (Kurihara et al. 2007). In a 30-day in situ deep sea CO_2 experiment in California (USA), a reduction in pH of 1.3 units below ambient increased nematode abundance (Barry et al. 2004), possibly because ecological pressure was reduced with the loss of other more vulnerable species. This has further implications for a shift in infaunal biodiversity and species abundance under ocean acidification.

The loss of key species in sediment communities can potentially alter sediment biogeochemical processes and also lead to the reduction of structural complexity and hence habitat for associated organisms. The decrease in degradation of organic matter in sediments due to the reduction of benthic biodiversity can directly affect the accumulation of organic carbon and cause the possible emergence of anoxic regions, with a rapid increase in the carbon flux to the sediments (Blackford and Gilbert 2007). Thus, much research is needed on the effects of OA on infaunal species and interactions. Benthic remineralization responses to changes in pH and CO_2 concentrations can be better understood by combining in situ and manipulated examinations of metabolic measurements across a range of different trophic levels alongside research on how OA impacts organic matter degradation and, consequently, nutrient fluxes from the benthos to the water column. The use of long-term mesocosm experiments focussing on sediment–water interface measurements and benthic metabolism would be able to investigate likely changes in sediment biogeochemistry. This proposed research will allow us to predict the impacts of OA on the viability of benthic remineralization and therefore the future changes of biogeochemical processes in marine sediments.

Regional and temporal modelling

In addition to understanding changes in carbonate chemistry and biogeochemical cycling on a global scale, it is important to undertake regional and seasonal modelling. Currently, the majority of OA research is based on the IS92a 'business-as-usual' scenario of CO_2 emissions for 2100 (e.g. Andersson et al. 2009; Connell and Russell 2010; De Bodt et al. 2010; Holcomb et al. 2010) and

standardized changes in calcite and aragonite saturation states. Carbonate parameters will vary regionally (Steinacher et al. 2009), seasonally (McNeil and Matear 2008), with latitude (Orr et al. 2005), with depth (Caldeira and Wickett 2003) and with habitat (Striegl et al. 2007). Greater impacts may be seen on a local scale depending on hydrographical and environmental factors, particularly in northern near-shore waters. Upwelling of low pH waters in regions such as the coast of Northern California should be modelled, as these areas are increasing in size through the anthropogenic uptake of CO_2 (Feely et al. 2008). An increase in monitoring efforts through the designation of open-ocean and coastal monitoring stations for the collection of time-series data on carbonate parameters is urgently required. To reduce costs, these parameters should be monitored at existing stations where other biological and chemical data are collected for time-series analysis. The use of coupled carbon cycle-climate models incorporating relevant parameters of natural variability alongside climate change parameters will be important for determining how regional and seasonal variations in factors such as CO_2 air-sea fluxes, temperature, salinity, ventilation and upwelling will cause changes in ocean carbonate chemistry. These models will be invaluable in ensuring that realistic carbonate parameters are used for OA research.

Organisms

Calcification is widespread in marine organisms (Brennan et al. 2004) and is thought to be particularly susceptible to future changes in ocean carbonate chemistry (Orr et al. 2005; Fabry et al. 2008). Although a large number of studies have focused on this process (e.g. Gazeau et al. 2007; Brennand et al. 2010; Gutowska et al. 2010), numerous questions remain unanswered. The molecular process of calcification is unknown for most species; we are yet to understand what carbon source is used, how OA impacts calcification-associated enzymes (e.g. carbonic anhydrase), where $CaCO_3$ molecules are created and how they are transported or stored. One particularly interesting factor is that some organisms appear to be able to switch between biomineralization of calcite and aragonite (e.g. Thompson et al. 2000). As calcite is less soluble than aragonite, this may provide a key advantage to some species under OA conditions. The vulnerability and commercial nature of many calcifying organisms makes these questions key areas for continued research. However, in the light of recent evidence indicating that physiological processes other than calcification may be altered in high pCO$_2$ conditions (Fabry et al. 2008) and variations in acid base/ regulatory mechanisms may influence the degree of impact, we feel the future of OA research at the organism level

must be directed towards both calcifying and non-calcifying species if we are to fully understand the ecological impacts of these predicted changes. Here, for both microorganism and metazoan species groups, we discuss further priorities for future OA research.

Phytoplankton and bacteria

Research into the effects of OA on phytoplankton species is extensive. It has shown that future ocean changes in carbonate chemistry can affect growth, photosynthesis, calcification and nitrogen fixation rates of different species (e.g. Iglesias-Rodriguez et al. 2008; Czerny et al. 2009; Kranz et al. 2009; De Bodt et al. 2010; Wu et al. 2010), although considerable intra- and interspecific variation in species' OA sensitivity has been found (Lau et al. 2007; Iglesias-Rodriguez et al. 2008; Rost et al. 2008). The majority of monoculture and community perturbation experiments show increased rates of primary productivity in response to OA conditions (Riebesell et al. 1993; Tortell et al. 2008), whilst variable calcification responses (Iglesias-Rodriguez et al. 2008) and changes in elemental ratios (Barcelos e Ramos et al. 2007; Hutchins et al. 2007) have also been observed.

Changes in pCO_2 can alter the competitive interactions between species and their ability to take up and use CO_2. The resulting shifts in community composition will lead to modifications in the relative abundance of functional groups (Riebesell et al. 2007; Tortell et al. 2008), which could have significant consequences on the structure and dynamics of the marine food web, and biogeochemical cycling (Engel et al. 2008; Guinotte and Fabry 2008). Recent work of Low-Décarie et al. (2011) highlighted that differential responses may result in competitive advantages or disadvantages for some species that could drive significant changes in phytoplankton communities. However, an increase in long-term multi-species manipulation experiments (e.g. Müller et al. 2010) incorporating grazers and viruses is needed to assess the adaptive evolutionary responses of phytoplankton species and to predict future changes with greater confidence.

In comparison with research on phytoplankton, the effects of OA on marine microbes, microbial processes and their interactions with higher organisms are greatly understudied (Weinbauer et al. 2011). Prokaryotes and viruses and their interactions are crucial for the functioning of large proportions of the global ocean, influencing biogeochemical cycling (Danovaro et al. 2008). Moreover, prokaryotes and microalgae play a critical role in the health and fitness of many eukaryotic organisms (Rosenberg et al. 2007).

Joint et al. (2011) stated that predicted changes in pH are unlikely to affect microbial-related biogeochemical processes, due to their ability to accommodate pH alterations. Although this appears to be true for some studies (e.g. Allgaier et al. 2008), many positive (e.g. Grossart et al. 2006; Riebesell et al. 2007; Kranz et al. 2009) or negative (e.g. Czerny et al. 2009; Piontek et al. 2010) effects have been found therefore more robust experimentation is required (Liu et al. 2010). Ubiquitous photoproteins (proteorhodopsins) found in bacteria in the photic zone are particularly sensitive to changes in pH (Fuhrman et al. 2008), which could lead to reduced survival of bacteria under low pH conditions. Indirect effects must also be taken into consideration, such as cascade effects through the response of higher organisms (Liu et al. 2010).

Future research needs to give more attention to the effects on microbial diversity because alteration of pH may change the dominant species with subtle but potentially important consequences for biogeochemical processes and food webs (Joint et al. 2011). Adaptation rates for microbes may be faster than for multi-cellular marine organisms because the likely mechanisms of adaptation for microbes are lateral gene transfer and viral infection (Joint et al. 2011). Knowledge of the response of viruses to pH change is particularly poor (Larsen et al. 2008). It should be a priority for microbial experiments to investigate whether changing pH will influence the transfer of genetic information and the interactions between viruses and their host.

As of yet, the effects of OA on the interactions between eukaryotic organisms and their microbial community are largely unknown. Corals exposed to reduced pH exhibit strong shifts in their bacterial community composition towards bacterial groups indicative of diseased colonies (Vega Thurber et al. 2009; Meron et al. 2011). As an adaptive strategy, the holobiont appears to increase stress resistance by increasing the production of secondary metabolites (Vega Thurber et al. 2009). On the other hand, photosymbiotic relationships may benefit from a decrease in pH. The acoel worm *Symsagittifera roscoffensis* showed increased growth and fertility under CO_2-induced acidification, which is thought to be due to increased algal metabolism (Dupont et al. 2012b).

Witt et al. (2011) found that bacterial biofilm communities rapidly adapt and reorganize in response to high pCO_2, allowing the community to maintain activities such as oxygen production. Furthermore, previous mesocosm experiments suggest that heterotrophic planktonic free-living bacterial communities shifted in response to high CO_2 levels, whilst the abundance and activity of communities of particle-attached bacteria remained unaffected by high CO_2 and were rather linked to a phytoplankton bloom (Allgaier et al. 2008). Understanding how OA effects bacterial biofilm community composition may determine whether they act as facilitators or inhibitors of invertebrate settlement (Dahms et al. 2004).

Whilst several studies to date have highlighted the importance of invertebrate–microbial interactions for key ecosystem engineering functions and for influencing biogeochemical element cycles (Mouchka et al. 2010; Webster and Taylor 2012), the majority have focused on coral–microbial interactions. These studies have overlooked viral-associated assemblages (Hewson et al. 2011), the in situ activity and function of microbes associated with other possible hosts (Webster and Taylor 2012), or the ecological consequences of environmental stressors (Garren and Azam 2011). Future research efforts should be driven to understanding the effects of future pCO_2 conditions, in combination with other possible local or global stressors (e.g. nutrient overloading, temperature) on these fundamental macro–micro relationships. Whole-genome amplification or functional metagenomics analyses could help by revealing unprecedented insights into their functions in a changing ocean.

Traits for ecological success

In metazoans, physiological processes that may be affected by low pH conditions include calcification, growth, survival, metabolism, pH balance, reproduction and development (Fabry et al. 2008). Experimental results have highlighted a strong level of variation in species' response to increased pCO_2 (Ries et al. 2009; Dupont et al. 2010a). If we are to predict how species may react to future changes in OA, we need to understand which physiological, behavioural and morphological traits or life history strategies will reduce species vulnerability to OA. Some populations or strains appear to be less vulnerable than others to OA conditions (Parker et al. 2011), and these differences may provide important insights into which traits prove advantageous. There appears to be little correlation between taxonomic groups and OA sensitivity, although headway has been made in discovering certain morphological traits (Rodolfo-Metalpa et al. 2011) or life history strategies (Dupont et al. 2010b) that may reduce vulnerability to OA. The ability of a species to regulate the pH of internal fluids has been implicated as a key factor in OA response (Melzner et al. 2009), although regulation may come at an energetic cost (Portner et al. 2004). We need to understand the mechanisms behind pH regulation and their efficiency if we are to understand why some processes/stages/organisms may be more or less vulnerable.

Gene/protein expression is a rapid way an organism can respond to an environmental stressor, so genomics and transcriptomics tools may be useful in uncovering mechanisms conferring physiological plasticity (Gracey 2007). Gene expression analysis has revealed that calcification genes are down-regulated in the larvae of the sea-urchin

Strongylocentrotus purpuratus (Stumpp et al. 2011), show some signs of up-regulation in the larvae of the sea-urchin *Paracentrotus lividus* (Martin et al. 2011) and do not change in different life stages of the red abalone *Haliotis rufescens* (Zippay and Hofmann 2010) under low pH. These studies show the high degree of species-specific variation in molecular responses to low pH, comparable to variation found in physiological studies. Future OA research should explore why these differences exist and whether they are beneficial to the organism. Is it good to up-regulate calcification or is it better to conserve energy for other purposes and stand the 'stress' of OA? The study of proteins may also be important in providing insight into the molecular response of marine organisms to OA, particularly when monitoring the activity of enzymes such as carbonic anhydrase.

Using a combination of molecular and physiological research will give us a broader understanding of physiological plasticity and how species may be able to acclimate to future OA conditions. When determining which parameters to test for, a priority should be given to how the fitness (i.e. survival and reproduction) of an organism is affected, as this is the parameter that ultimately decides whether a species can endure future conditions. Furthermore, this parameter will have the strongest carry-over effects for the population.

Acclimation and adaptation potential

The duration of experiments is a further important consideration, and an increase in the number of entire life history (e.g. McDonald et al. 2009) trans-generational (e.g. Donelson et al. 2011) and multi-generational (e.g. Kurihara and Ishimatsu 2008) studies is needed. Many negative effects of OA have been documented for marine larvae (Arnold et al. 2009), but, for most species, we are unaware of how this affects their ability to perform the energetically demanding process of metamorphosis, or how impacts at the larval stage translate to the adult. Documenting the full development process may also expose particularly vulnerable stages and provide necessary information for effective protection of the species (Gaylord et al. 2011).

We are currently unsure whether species may be able to acclimate or adapt to future conditions (Piazzi et al. 2001), as the majority of experiments subject organisms to acute acidification. Extrapolating from the results of these studies can be difficult, as organisms may acclimate to OA through phenotypic or physiological plasticity when exposed to chronic acidification. Trans-generational acclimation studies will reduce our uncertainty on whether and how species will cope with future conditions (Kerrison et al. 2011). Parker et al. (2011) recently highlighted the carry-over effects of parental OA exposure on offspring growth,

development and survival in the Sydney rock oyster (*Saccostrea glomerata*), whilst Dupont et al. (2012a) showed that acclimation to OA in adult green sea urchins (*Strongylocentrotus droebachiensis*) leads to negative carry-over effects on juvenile settlement success and survival. These results indicate the importance of extending studies between generations as well as throughout life cycles.

We further need to understand the variation and heritability (e.g. adaptability) of tolerance to OA within populations (Dupont and Thorndyke 2009). Adaptation through contemporary evolution can occur quickly; directional selection due to changing environmental conditions can act on standing genetic variation, producing progeny with a greater mean fitness than the previous generation (Bijlsma and Loeschcke 2005; Carroll et al. 2007). Quantifying the standing genetic variation, that is genetically determined variation in a trait (in this case in response to OA), will enable more accurate predictions of how species will respond to OA over time and give a higher-resolution picture of future ecosystem structure. This line of research involves comparing the response of many different highly related (e.g. siblings or clones) groups to OA and examining the variation in response to OA between and within those groups, finally allowing the calculation of the heritability associated with tolerance to high pCO_2 (Becker 1984).

To date, very few studies have attempted to quantify the variation and heritability of OA responses. Pistevos et al. (2011) found variation between bryozoan colonies, and Sunday et al. (2011) found significant maternal effect in sibling groups of urchins and mussels. Studies such as these must overcome a variety of challenges including 'disentangling' maternal effects, non-additive phenotypic plasticity and additive genetic effects (Gienapp et al. 2008). Whilst multi-generation experiments are difficult in higher organisms with slow generation turnover, parental genotypes can be tested to identify those that predispose their offspring with greater OA tolerance. Depending on the design, an experiment can also quantify the contribution of each source of variation (maternal effect, phenotypic plasticity and additive genetic effect). Despite the technical challenges of the experimental set-up, the information provided by experiments addressing this issue will, no doubt, provide insight into the inevitable evolutionary shifts that will occur as OA progresses. Evolution is a very real but under-studied possibility in organisms with short generation times (i.e. <3 years) and a wide range of studies that address this issue would point researchers towards animals of special interest, either due to their potential for adaptation and the investigation of underlying genes or due to their low adaptation potential and consequential increased necessity for research aiming to assist ailing populations.

Species choice

Species composition and ecosystem functioning are tightly linked (e.g. nutrient and carbon cycling, provision of refugium and nursery habitats, primary and secondary productivity). These ecosystem functions determine which goods and services an ecosystem provides (e.g. food production, climate and nutrient regulation) (de Groot et al. 2002), and values can be placed on these (e.g. Costanza et al. 1997).

Species loss as a result of OA could cause a reduction in community stability and ecosystem function (Lehman and Tilman 2000; Worm et al. 2006), therefore reducing the value of the goods and services that ecosystem provides. This said, ecosystem function is not related to taxonomic diversity but to the diversity of the functional characteristics of the organisms found within that system (Grime 1997). When a species is lost, the proliferation of functionally similar species may buffer any impacts (Tilman 1996), and this is particularly relevant for fast growing, species-rich communities (Vinebrooke et al. 2003). On the other hand, loss of a key species will lead to disproportionate impacts on a habitat or ecosystem and therefore reductions in ecosystem function. Whilst hard corals are a good example of a group of well-studied key structural species (e.g. Albright et al. 2008; Crawley et al. 2010; Hofmann et al. 2011), there is little or no literature on the effects of OA on many other key species. For example, the horse mussel *Modiolus modiolus* is a key structural species in the Northern hemisphere, and its loss could lead to the disappearance of its associated community (Hiscock et al. 2004), whilst the triton *Charonia* spp. is a key functional species that feeds on the crown of thorns starfish *Acanthaster planci* and prevents this species from removing the hard corals of the Indo-Pacific (Barnes 1966), and yet no available information can be found on how these species may be impacted.

We are now under little doubt that marine diversity will be reduced under future changes in carbonate chemistry, but there is a clear requirement to prioritize species in terms of their importance commercially or in terms of their role within an ecosystem, rather than focusing on model or sensitive species. In particular, for commercial species, it may be more beneficial to focus on relevant parameters (e.g. the edible tissue of molluscs, rather than their calcification) (Hilmi et al. 2012). Invasive species should also be prioritized as if they proliferate under low pH conditions, this could lead to devastating impacts to marine ecosystems. For example, some invasive species of algae appear abundant in low pH areas surrounding the submerged CO_2 vents of Ischia, Italy (Hall-Spencer et al. 2008), suggesting that these species are highly tolerant and deleterious effects from their proliferation may be greatly

enhanced in future. This prioritization will allow us to produce societal relevant science that will lead to predictions of direct/indirect human impacts.

Ecosystems

It is important that the impacts of future acidification be scaled up to the ecosystem level in order to provide policy makers with robust scientific evidence of expected environmental impacts. With respect to proposed future acidification, species abilities to adapt or tolerate these changes will be important in determining survival success, but accurate predictions must take into consideration a complex array of both biotic and environmental interactions (Russell et al. 2011). Whilst OA will occur simultaneously with changes in other physical parameters such as temperature, salinity and oxygen, the interaction between species may change as well, as winners and losers arise. Marine organisms will therefore face the challenge of coping with multiple changes at all levels. Understanding the ecosystem-level effects of OA is a priority and as techniques and expertise in the field of OA have developed, this has become increasingly attainable. Here, we highlight three areas where we feel research should be directed.

Multi-stressor interactions

Many stressors are causing changes in our seas such as ocean warming, coastal hypoxia and open-ocean deoxygenation, changes in salinity, rising nitrogen levels, contaminants, physical disturbance and stratification amongst others. These stressors may have synergistic, antagonistic or additive effects when combined with OA and influence an organism's sensitivity to decreases in pH accordingly. If we disregard the nature of these multiple stressor interactions, we may under- and/or overestimate the effects of OA.

Recent studies have begun to take this into consideration and increase our understanding of the combined effects of OA with other stressors, but are mostly limited to single species experiments (e.g. De Bodt et al. 2010; Dissard et al. 2010; Holcomb et al. 2010). Increases in temperature and pCO_2 can have synergistic (e.g. Findlay et al. 2008) or additive (e.g. Talmage and Gobler 2010) effects on physiological processes such as growth or survival. A combination of changes in seawater temperature and pH may affect marine biodiversity and the geographical distribution of some species (Findlay et al. 2010; Hale et al. 2011). For example, a physiological study of the jumbo squid *Dosidicus gigas* suggests that in the absence of adaption, the synergism between OA, global warming and expanding hypoxia may compress the habitable depth of the species (Rosa and Seibel 2008).

These studies highlight the importance of studying combined effects of global change on ecosystems in order to predict and model impacts of global change, such as OA, although the majority of current research has focused on the interaction between CO_2 and temperature. Multifactorial experiments that combine a number of different stressors are complex, although they may be a key to understanding the relationship between different environmental stressors in future. For example in a terrestrial system, Shaw et al. (2002) found that the enhanced effects of increased temperature, nitrogen deposition and precipitation on primary production were dampened by CO_2 enrichment.

Multi-stressor experiments with complex experimental designs will require increased collaboration and joint funding initiatives to allow the manpower, expertise and funding to successfully carry them out. In terrestrial systems, combined efforts have resulted in tremendous global change experiments that have successfully provided important data for over two decades, for example free-air carbon dioxide enrichment (FACE) experiments. As an ocean equivalent, free-ocean carbon dioxide enrichment (FOCE) experiments are being developed and may provide fundamental information about OA in natural environments. Although a water environment complicates the design of such an experiment, it serves as an excellent example of how complex tasks can be approached by combining the efforts of multiple disciplines such as engineers, biologists and chemists.

Species interactions

Another consideration is that species do not exist as isolated elements of an ecosystem, but through a complex range of biotic interactions. Food availability may change through altered composition of primary producers (e.g. Kuffner et al. 2008; Wootton et al. 2008), loss of nutritional value of the prey species (e.g. Rossoll et al. 2012), or decline of important prey species (e.g. Lischka et al. 2011), whilst predator–prey interactions may change through loss of sensory capabilities (e.g. Dixson et al. 2010; Ferrari et al. 2011a), changes in metabolism (e.g. Gooding et al. 2009) or reductions in shell defence (e.g. Bibby et al. 2007; Comeau et al. 2010). Changes in competitive interactions through the differential responses of species in the same trophic guild will also be important for determining future OA scenarios (e.g. Jokiel et al. 2008; Cigliano et al. 2010). Deep sea vents provide an excellent example of how fitness can be a relative concept dependant on the biotic interactions present. For example, bivalves found at deep sea vents with low pCO_2 (pH 5.36–7.29) show a sharp reduction in calcification. Although shell defences are greatly

reduced, this species continues to thrive due to the absence of predators (Tunnicliffe et al. 2009).

Other behavioural interactions need to be considered as well. In some species, for example, much energy is expended on sexual behaviour such as mate finding, display and nest building. In species that brood their offspring, the amount of energy invested in brood care must be prioritized and balanced with the energy invested in coping with high pCO_2. Behavioural studies are limited to homing and predator avoidance (e.g. Munday et al. 2009; Cripps et al. 2011; Ferrari et al. 2011b), whilst reproductive studies focus on fertilization success (e.g. Havenhand et al. 2008; Parker et al. 2009). Studies that incorporate behavioural aspects of reproductive performance, such as those mentioned above, would provide important further insight into whether OA will impact organisms at the behavioural level.

Classic ecological and more recent aquatic acidification literature offers valuable insight into changes in species interactions as an ecosystem becomes stressed. Increased species dominance, more negative species interactions (e.g. parasitism, predation) and less positive interactions (e.g. mutualism) have been documented (Odum 1985). However, it has been shown that, generally, the impact of stress may be buffered through the facilitative interactions of ecosystem 'engineers' such as marsh plants (Bertness and Hacker 1994) or bivalves (reviewed in Gutierrez et al. 2003). Much ecological work has focused on the strength of species interactions and subsequent changes in community dynamics (e.g. Paine 1992; Novak and Wootton 2010; Sala and Dayton 2011), and this experience can be utilized in the experimental design of OA research. Initial studies suggest that OA may impact species directly by altering their immune response (Dupont and Thorndyke 2012). This could lead to extreme consequences in terms of the interaction between a pathogen and their host. In order to gain an understanding of the effects of OA at the ecosystem level, it is important to incorporate multi-species experimentation (e.g. competition mediated by a predator or trophic interactions mediated by a competitor species) to determine how species interactions will change under low pH conditions.

Species interactions, especially competition and trophic dynamics, are responsible for biodiversity at the local scale, and it is thus imperative to document the responses of those interactions to OA in order to reasonably make predictions for future biodiversity. Furthermore, extensive previous work in this area not only provides an experimental context for determining changes in species interactions, but also provides a valuable baseline of community function as well as predictions for ecological impacts of species removals (e.g. Paine 1966; Dayton 1971).

Natural pH gradients

Exploiting natural pH gradients in space or time, to help unravel the ecosystem-level effects of OA by seeing how species, communities and ecosystems react to a decrease in pH in a natural environment is an alternative method for studying OA (Barry et al. 2010). Ecological research at CO_2 vent sites in Italy (e.g. Hall-Spencer et al. 2008), Greece (e.g. Vizzini et al. 2010), Papua New Guinea (e.g. Fabricius et al. 2011) and Mexico (Crook et al. 2012) has flourished over recent years. Although attempts have been made to characterize some of these sites through the placement of stationary pH sensors (Kroeker et al. 2011) and the analysis of gas emissions (Hall-Spencer et al. 2008), the quality of this research could be improved by collaborations with physical oceanographers and other disciplines to gain in depth of knowledge of the physical and chemical attributes of these vent sites, and their temporal and spatial variation (e.g. under different atmospheric pressures or hydrodynamic conditions). This would aid in determining their suitability for OA research and potentially allow for the minimization of confounding factors.

Many of these vent sites show a high degree of pH variation (Kroeker et al. 2011), and further effort should be placed into understanding how pH variation, alongside pH reduction, impacts organisms. Some organisms live in areas of high pH variation such as estuarine habitats and areas of upwelling, whilst those in the open ocean deal with very little variation (Hofmann et al. 2011). Are perturbation experiments, whereby pH is maintained at a constant level, truly indicative of future oceans or should pH variation be taken into consideration during experimental periods? At vent sites is it acceptable to note the mean or median value as an indicator of pH or should lowest values be taken into greater consideration? Laboratory experiments should be designed to improve methodology in this field and understand the impact of high or little pH variation on organisms.

Natural gradients and lowered pH can be found at sites other than vents, although these have perhaps received less recognition. Some regions are particularly vulnerable to the effects of our changing climate and seas and are already experiencing lowered pH and saturation states. These are set to expand in range and magnitude over the forthcoming years and can be used as important indicators of the ecosystem-level effects of OA (Fabry et al. 2009). Future research should include gaining understanding of changes in species, communities and ecosystems through monitoring of vulnerable habitats such as (1) polar and subpolar seas where sea ice melt has altered carbon chemistry parameters, such as surface waters of the Canadian Basin which show aragonite undersaturation (Yamamoto-Kawai et al. 2009), (2) coastal waters where seasonal upwelling

causes decreased pH and saturation states such as the coast of Northern California, Oregon and Washington (Feely et al. 2008), (3) zones where strong riverine inputs decrease the pH of estuarine waters such as the Yukon River in the Bering Sea (Striegl et al. 2007), including areas exhibiting mixed effects (i.e. Puget Sound: Feely et al. 2010) and (4) areas of high microbial activity and respiration combined with little exchange with other water bodies, depleting oxygen and enriching CO_2 such as the Baltic Sea (Frommel et al. 2012). Increasing sampling effort for monitoring these systems, including carbonate chemistry and observed species composition, will be important, and increased funding for time-series monitoring is strongly suggested. Not only do these examples of apparent 'vulnerable habitats' function as important indicators of environmental change, but also will aid in our understanding of how the direct and indirect effects of climate change, OA and other anthropogenic stressors will interact to cause changes in our future oceans.

On global and regional scales, most patterns of biological diversity can be explained by macroecological and macroevolutionary patterns (Whitman and Roy 2009). We recommend that research looks to the boundaries of defined large biological provinces, which are typically delineated by physical factors, and pay close attention to regions where macroecological boundaries overlap with zones where we expect large effects of OA, and even areas with multiple stressors. These areas, especially, are locales where we would expect a small physical change to have larger biological and ecological consequences.

It is also important to note that natural pH gradients can be found over time, as well as spatially. Paleoclimate proxies have been shown to be valuable tools for understanding changes in ocean chemistry over time, with emphasis on the stable isotopes of carbon and boron ($\delta^{13}C$ and $\delta^{11}B$) for elucidating changes in seawater carbon chemistry (Honisch et al. 2009). These tools can be particularly useful for extending our understanding of very recent climate and carbon chemistry, given the paucity of coastal ocean environmental datasets (Pfister et al. 2011). Furthermore, this approach can be combined with historical ecological datasets or abundances and used for traditional comparisons between historical and current patterns of species diversity and abundance. With corresponding laboratory studies, relevant ecological changes and their underlying mechanisms can be identified in the appropriate historical and ecological contexts.

Methodological approach

As with any emerging field of study, methods for investigating the effects of high pCO_2 have evolved greatly over the past decade. This has been aided by the collaborative provision of the EPOCA 'Guide to best practices for ocean acidification research and data reporting' (Riebesell et al. 2010). However, we would like to mention that there are still considerations for future research techniques in terms of pCO_2 manipulation and experimental design. A number of different techniques may be used to alter the pCO_2 or pH of seawater, and the advantages and drawbacks to each method have been extensively reviewed (Gattuso and Lavigne 2009). Care must be taken when considering which method of pCO_2 manipulation to use, particularly when studying OA at the microbial scale (Hurd et al. 2009). Most experiments take place in a laboratory setting (e.g. Piontek et al. 2010; Yamada and Suzumura 2010), and the majority of these manipulate pH by bubbling CO_2 gas into seawater. This is an effective method of altering carbonate chemistry (Gattuso et al. 2010), but it is currently unclear how the bubbling affects microbial and phytoplankton communities in terms of formation of transparent exopolymers or cellular lysis (Engel 2002). Furthermore, it is unclear what degree of experimental variation is caused by the specific method of pCO_2 manipulation. Increasing the degree of collaboration between different research institutes will enhance knowledge transfer and method standardization, therefore reducing variation between studies.

Experimental designs must also account for possible confounding sources of variation, to ensure our conclusions about species are robust. Variations in temperature, nutrient limitation, UV radiation, exposure time, culture density, acclimation time and other factors can also cause divergence in results. For example, saturation can mask OA effects, most notably in sperm and food concentrations. Water supersaturated with sperm and providing exaggerated sperm-egg contact times does not reflect natural conditions for broadcast spawners and could overestimate fertilization success. Therefore, experiments looking at fertilization success should utilize a range of sperm concentrations and realistic sperm-egg contact times in order to determine whether acidified treatments result in an increase in fertilization success (Reuter et al. 2011). Marshall (2006) suggests that serial 10-fold dilutions should be used during experimentation to estimate maximum fertilization. The quantity of available energy from food will have a similar effect, as organisms with an unnaturally abundant food source are likely to better withstand the energy requirements imposed by increased pCO_2, although some species have exhibited reduced feeding rates under OA conditions (Stumpp et al. 2012). Exposures of early life stages would benefit from increasing the number of male–female combinations to ensure individual compatibility is not a factor. Additionally, for all life stages, sampling animals from multiple sites and at various times throughout the

year would reduce the potential of spatial and temporal effects on the organism's response to OA. It should also be noted that food quality may vary if grown under OA conditions, and this should be investigated.

Discussion

This paper highlights the vast scope of environmental impacts that are predicted to occur in future oceans as a consequence of increased CO_2 emissions and proposes areas for future research from the perspective of early career researchers in this field. From biogeochemistry, species and onwards to entire ocean ecosystems, changes in seawater chemistry will have numerous and highly varied consequences for global oceans and the life within them and, as can be seen, there are many areas where our knowledge is lacking in terms of understanding these impacts. Unfortunately, it is not possible to understand how all species and ecosystems may be affected, capturing the complexity of their environment and the differing potential scenarios. In order to provide evidence of the expected consequences of OA to the marine environment within a reasonable timeline (i.e. 5-10 years), we need to prioritize where research efforts are placed. The three topics agreed upon by the authors which should be given greatest priority are: (1) understanding how OA will interact with other anthropogenic and climatic stressors, (2) understanding whether species may adapt or acclimate to future OA conditions and how this will affect species interactions and ecosystem stability and (3) monitoring and modelling temporal, spatial and habitat variability in carbonate chemistry in order to more accurately predict future changes at the regional and local scale. Whilst these topics are seen as particular priorities, in answering questions regarding the expected consequences of OA, many of the topics we have listed are interlinked, providing background and context for other research areas. If we are going to understand the biological impacts of OA at different ecological levels, then we must utilize a number of different approaches. For example, to investigate how a key species may react to future conditions, we need to understand the temporal and spatial variations in carbonate chemistry (with the use of observational data) in order to design experiments. We need to understand what traits may give it the potential to acclimate or adapt to future conditions, and how interactions with other species or stressors may affect this. Investigations may include short-term acute laboratory experiments in conjunction with mesocosm or field experiments to observe long-term consequences of chronic exposure.

Ocean acidification has become a priority area in marine science; the number of papers published in this field has grown exponentially in recent years (Kroeker et al. 2010),

and funding for this area of science is generally substantial due to the urgent necessity to understand the impacts. As a result, the European Project on Ocean Acidification (EPOCA) has developed a blog site (http://oceanacidification.wordpress.com) in order to centralize our information on OA research. This has been invaluable for research scientists in coordinating research activities and organizing joint projects and cruises. Furthermore, the project Biological Impacts of Ocean Acidification (BIOACID), funded by the German Ministry for Education and Research (BMBF), has implemented a marketplace serving a similar purpose of informing scientists of current and planned OA research with possibilities for collaboration (http://www.bioacid.de/) whilst the database PANGEA (http://www.pangaea.de/) offers access to raw data from experiments, cruises, field data, etc. and scientists funded by European projects such as EPOCA are required to submit their data there upon publication for storage and quality control. This website serves as a platform to compound data on lots of ocean acidification research that can easily be searched for and it is suggested that collection of data on this platform could be expanded to projects worldwide. Alternatively, we suggest that a central database is developed where OA scientists may input their current research plans and results for wider use by the OA community. Whilst there is a trend for research to edge towards joint international projects between institutes, such as large-scale mesocosm experiments like the pelagic ecosystem CO_2 enrichment studies (e.g. Bellerby et al. 2008; Engel et al. 2008; Tanaka et al. 2008) and the Svalbard campaign 2010, 50 % of the authors of this paper had no collaboration with other research institutes during their postgraduate studies. This suggests that, even for a well-organized community of researchers such as those involved in OA, for some institutions, collaboration in OA research is minimal and should be expanded where possible.

If we are to mitigate OA impacts through the development of climate change policies, it is essential that we bridge the gap between scientists and economists, as climate change policies are often driven by economic evaluation. Although socio-economic research was not within the scope of this paper, we would like to state that integration of socio-economic and ecological research has been beneficial for other research areas (e.g. Cooke et al. 2009) and is a priority area if we are to provide policymakers with the information required regarding future ocean changes. Finally, we would like to highlight the importance of workshops such as 'Acidification in Aquatic Environments' held in Tromsø, Norway. This provided insight into the many different facets of OA through lectures from experts within the field, whilst allowing opportunity for discussion of research and creating a platform for possible future collaborations. As 'next-generation' OA scientists,

we benefitted greatly from the level of knowledge transfer and advice gained at this workshop and strongly promote such integrative events in future to benefit the advancement of OA research.

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