The Effect of Ocean Acidification on Calcifying Organisms in Marine Ecosystems: An Organism to Ecosystem Perspective

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Abstract

Ocean acidification (OA), a consequence of anthropogenic carbon dioxide emissions, poses a serious threat to marine organisms in tropical, open-ocean, coastal, deep-sea, and high-latitude sea ecosystems. The diversity of taxonomic groups that precipitate calcium carbonate from seawater are at particularly high risk. Here we review the rapidly expanding literature concerning the biological and ecological impacts of OA on calcification, using a cross-scale, process-oriented approach. In comparison to calcification, we find that areas such as fertilization, early life-history stages, and interaction with synergistic stressors are understudied. Although understanding the long-term consequences of OA are critical, available studies are largely short-term experiments that do not allow for tests of long-term acclimatization or adaptation. Future research on the phenotypic plasticity of contemporary organisms and interpretations of performance in the context of current environmental heterogeneity of pCO_2 will greatly aid in our understanding of how organisms will respond to OA in the future.

INTRODUCTION

Ocean acidification (OA), a reduction in ocean pH due to the uptake of anthropogenic carbon dioxide (CO_2) by surface waters, has recently emerged as a major research area in the marine science. Since the first publications about OA and its potential impact on calcifying marine organisms (e.g., Kleypas et al. 1999), there has been an emergence of experimental work designed to examine the effect of altered seawater chemistry—elevated pCO_2, decreased saturation states for various mineral forms of calcium carbonate, and low pH—on marine calcifying organisms. The goal of this review is to explore the responses of key marine calcifers at the organismal level and extend these observations, where possible, to potential outcomes at the ecosystem level.

Ocean Acidification: An Overview

The atmospheric global average level of CO_2 has increased from preindustrial levels of ∼280 ppm to nearly 385 ppm and is projected to increase to 500–1,000 ppm CO_2 by the end of the 21st century (Meehl et al. 2007, Smith et al. 2009). A great deal of anthropogenic CO_2 has been absorbed by the ocean; estimates are that ∼30% of recently emitted CO_2 has been absorbed to date (Feely et al. 2009). Chemically, this absorbed CO_2 reacts with seawater, resulting in a net increase in proton ions (H+), which is measured as a reduction in pH, and decreases the levels of carbonate ion (CO_3^2). This process results in OA and is projected to decrease the pH of oceanic surface waters by 0.14 to 0.35 pH units by 2,100 (Meehl et al. 2007, Orr et al. 2005). These changes in future ocean chemistry may cross thresholds in saturation states that support biogenic calcification (e.g., aragonite and calcite) and could therefore drive net dissolution of carbonate structures. Thus, OA poses significant problems to marine organisms that form calcium carbonate shells, skeletons, or internal structures (e.g., otoliths and statoliths) (Andersson et al. 2008, Cohen & Holcomb 2009). Currently, many OA studies report experimental conditions that are framed by the emission scenarios in the Intergovernmental Panel on Climate Change (IPCC) [for a detailed description of studies, see **Supplemental Table 1** (follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**) with the pCO_2 levels employed and treatment outcomes. Although calcification is a central focus of OA research, there is growing evidence from CO_2 perturbation experiments that OA may alter other processes, notably aspects of reproduction and development (Kurihara 2008), acid-base regulation (Pörtner 2008), photosynthesis (Anthony et al. 2008, Crawley et al. 2010, Iglesias-Rodriguez et al. 2008), respiration (Rosa & Seibel 2008), aspects of behavior (Munday et al. 2009), and tolerances of other stressors (Hoegh-Guldberg et al. 2007, Hutchins et al. 2009, Pörtner et al. 2005).

The impacts of future CO_2 levels on marine ecosystems are expected to be dramatic. For example, some models indicate that even if atmospheric CO_2 is stabilized at 450 ppm, only 8% of coral reefs will be surrounded by seawater that supports calcification (Cao & Caldeira 2008). For Arctic surface waters, conditions that are corrosive to aragonite are likely if atmospheric CO_2 is not stabilized below 450 ppm (Steinacher et al. 2009), and aragonite undersaturation has already been reported in areas of the Arctic Ocean influenced by rapidly melting sea ice (Yamamoto-Kawai et al. 2009). Thus, tropical corals are particularly threatened (Hoegh-Guldberg et al. 2007) as are the marine invertebrate fauna of high-latitude seas (Fabry et al. 2009). However, although high-latitude seas and tropical reef ecosystems are threatened first in time, there is strong evidence that coastal regions that are characterized by episodic upwelling events are also operating near physiological thresholds for calcifying marine organisms (Hauri et al. 2009).

OA: Ocean acidification

pCO_2: partial pressure of CO_2

Calcium carbonate ($CaCO_3$): the main component of the shells and skeletons of marine organisms, occurring in the form of aragonite, calcite, and high-Mg calcite.

CO_3^{2-}: carbonate ion

Considerations for Ocean Acidification Research on Contemporary Organisms

As the study of OA develops, there are issues and complexities that are noteworthy. First, for historical reasons the study of OA is more advanced in some ecosystems than others, leaving a gap in mechanistic understanding when various ecosystems are compared. For example, the biological consequences of OA were brought to the forefront by coral biologists (e.g., Kleypas et al. 1999), and researchers from this field published some of the first manipulative experiments exploring the influence of pCO_2 on calcification (e.g., Gattuso et al. 1998, Langdon et al. 2000). In contrast, data on calcification rates in calcifying organisms from benthic environments (e.g., Ries et al. 2009) and for polar regions (e.g., Comeau et al. 2009) are only recently published. Thus, in this review the coverage for each ecosystem is different and serves to highlight critical needs for research in some parts of the world's oceans. Second, much of the published information on marine calcifiers comes from short-term laboratory-based manipulative experiments whose results may not be ultimately comparable. Thus, we face challenges in making firm conclusions about physiological responses for species that are collected from different locations, at different times of year (e.g., at different times in a growth phase) and without much regard for whether there is local adaptation of populations that are studied, that is, there may be differences in performance across large spatial scales that are significant (Chown & Gaston 2008). Furthermore, the short-term experiments do not allow for tests of long-term acclimatization or adaptation. Finally, attention to OA as an issue related to anthropogenic CO_2 was first introduced by models that predicted changes in seawater chemistry based upon IPCC emission scenarios (e.g., Orr et al. 2005). From an ecological standpoint, heterogeneity in the pCO_2 environment exists now. Some coastal regions experience episodic upwelling that result in large fluctuations in pCO_2 (e.g., Feely et al. 2008), and diurnal fluctuations in pH are found in waters surrounding coral reefs (J.E. Smith, N.N. Price, and T.R. Martz, unpublished observations). Such natural environmental variation needs to be considered in the framework of forecasting the long-term response of species to OA because adaptation to a particular environmental regime may influence how populations ultimately respond to future pH declines. Thus, a core issue in the study of OA is to what extent can contemporary organisms tolerate future acidification, that is, what is the acclimatization capacity within populations? Notably, because environmental conditions are changing rapidly in climate change scenarios and will likely outpace the ability of many organisms to adapt to new conditions (Bell & Collins 2008, Gienapp et al. 2008, Visser 2008), inherent physiological and phenotypic plasticity in contemporary populations may be critical to the ability of many organisms to respond to rapid environmental change (Bradshaw & Holzapfel 2010, Hofmann & Todgham 2010).

Adaptation: genetic change in a population due to natural selection, leading to improved function with respect to some aspect of the environment

Acclimatization: phenotypic adaptation to environmental fluctuations; a usually reversible adjustment of physiology or morphology to several simultaneously changing environmental factors

Phenotypic plasticity: the ability of an individual organism to change its physiological, behavioral, developmental, or morphological phenotype, usually in response to a variable environment

CORAL REEF ECOSYSTEMS

Corals calcify to form the massive three-dimensional structures that define coral reefs and that create habitat supporting an extraordinarily high biodiversity. As such, coral reef ecosystems are contextualized by calcification and are highly vulnerable to conditions that impact this process or promote dissolution of $CaCO_3$. Simulations of climate models project that at a level of 550 ppm CO_2, net dissolution of reefs worldwide is possible (Silverman et al. 2009). As such, dramatic impacts to the integrity of these globally important ecosystems are likely to occur within the current century (Veron et al. 2009). Although there remains a pressing need to elucidate large-scale responses of reef communities to OA (Hoegh-Guldberg et al. 2007, Przeslawski et al. 2008), such studies should be founded on a clear understanding of the physiological response of scleractinian corals to perturbed seawater chemistry.

HCO₃⁻: bicarbonate ion

DIC: dissolved organic carbon

From a geochemical perspective, declining seawater pH reduces coral calcification rates because it depletes CO_3^{2-} and depresses Ω_a, a scenario that potentially explains the near-linear relationship between calcification and Ω_a for corals and coral reefs (Langdon & Atkinson 2005). It is, however, hard to reconcile this interpretation with the biological reality that coral calcification occurs inside an animal, in a space between the calicoblastic ectoderm and the skeletal surface (the subcalicoblastic space). Here the fluid is spatially isolated and likely chemically different from seawater (Cohen & McConnaughey 2003), and to be utilized directly for calcification in this microenvironment, the CO_3^{2-} would need to be actively transported into the subcalicoblastic space by transcellular pathways (Allemand et al. 2004). Although the direct use of CO_3^{2-} is considered unlikely (Herfort et al. 2008, Jury et al. 2010, Marubini et al. 2008), there is a need to better understand the chemical milieu within this cavity and to resolve whether the subcalicoblastic space itself is an artifact of the preparations for microscopy. In contrast to CO_3^{2-}, exogenous HCO_3^- stimulates coral calcification to at least 18 mM (Herfort et al. 2008) and is reportedly actively transported to the subcalicoblastic space (Allemand et al. 2004), supporting the hypothesis that HCO_3^- is the preferred dissolved organic carbon (DIC) species for calcification.

The importance of biology is also highlighted by the fact that calcification in corals is enhanced in the light compared to the dark. Corals form obligate endosymbioses with dinoflagellates in the genus *Symbiodinium*, a union that plays a pivotal role in the nutrition and physiology of the coral host. It has long been thought that calcification and the photosynthetic activity of *Symbiodinium* are functionally intertwined, with the by-products of calcification stimulating photosynthesis and/or photosynthesis driving calcification (Allemand et al. 2004). Although direct evidence supporting these scenarios is lacking, it is feasible that photosynthetically fixed carbon translocated from the *Symbiodinium* contributes to the cost of calcification (Anthony et al. 2002) or to the formation of the organic matrix into which aragonite crystals are deposited (Tambutté et al. 2007). It is difficult to evaluate how this might occur given that *Symbiodinium* are restricted to the oral endoderm and spatially removed from the calcifying surface. Despite this separation, areas of intense photosynthetic carbon fixation correspond with intense calcium deposition across the coral surface, confirming the association between these processes in situ (Al-Horani et al. 2005).

The *Symbiodinium* also use HCO_3^- to supply CO_2 for photosynthesis and this results in the production of OH^-, which potentially neutralizes protons released during $CaCO_3$ deposition (Allemand et al. 2004). This reaction is important, because it reconciles the association between photosynthesis and calcification and presents the processes as complementary rather than dependent (Allemand et al. 2004). As with calcification, coral photosynthesis is stimulated by exogenous HCO_3^-, although it saturates at a lower $[HCO_3^-]$ (≈6 mM) (Herfort et al. 2008). If HCO_3^- rather than CO_3^{2-} determines the rate of coral calcification, this creates a dilemma in explaining how OA inhibits calcification when it increases $[HCO_3^-]$ as it depresses $[CO_3^{2-}]$ (Kleypas et al. 1999). Although there is no solution to this dilemma, it has been speculated that a decline in seawater pH might directly affect calcification by impeding the active transport of H^+ or Ca^{2+} within the sub calicoblastic space (Jury et al. 2010).

The challenges of unraveling the biological processes driving coral calcification remain significant, but regardless of these challenges, the concept of biological control raises two important questions that are relevant to evaluating the effects of OA. First, what innate biological capacity exists in corals to tolerate geochemical constraints on calcification, and second, is there potential for corals to acclimatize or adapt to OA?

The internal environment in corals, as well as the habitats in which they are found, provide clues to the range of OA drivers that corals can tolerate. These features are best evaluated relative to the changes in seawater expected by the year 2100 under a conservative climate change scenario (S650 IPCC 2007), which predicts that pH should decline from 8.15 (currently) to 7.3, with

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[$CO_3{}^{2-}$] declining from 270 μmol kg^{-1} to 195 μmol kg^{-1} (Orr et al. 2005). Relative to these predictions, physical variations within corals and over reefs, are large. Inside coral cells containing *Symbiodinium*, pH varies from 7.4 to 7.1 (Venn et al. 2009), and in the subcalicoblastic space, it has been speculated that Ω_a may exceed 100 (Cohen & McConnaughey 2003). At the community scale, seawater pH varies diurnally over reef flats from 8.56 to 7.84, and Ω_a from 5.54 to 1.83 (Ohde & van Woesik 1999), with coral reefs in the Galapagos Islands enduring the lowest Ω_a (ca. 2.27) recorded for any reef location (Manzello 2010). Some corals can be grown for months under high pCO_2 (≈1147 μatm) and low Ω_a (ca. 1.4) (Andersson et al. 2009), and at the Waikiki Aquarium, multiple coral species have been grown for years under such conditions (Atkinson et al. 1995). Further, on a centurial scale, the boron isotope compositions of cores from massive *Porites* show evidence of interdecadal pH oscillations of 0.3 pH units, during which colony growth remained ≥1 g cm^{-2} year^{-1} and was unrelated to pH or Ω_a (Pelejero et al. 2005).

The identification of situations in which corals experience conditions similar to those expected from OA does not diminish the threat that OA poses to coral reefs, nor does it demonstrate that corals can tolerate the conditions that will occur. Further, in evaluating the significance of corals apparently thriving in extreme "OA-like" conditions, it is important to identify the issues that distinguish such occurrences from the OA context, such as the extent to which short-term transgressions of low pH and low Ω_a have impacts that are similar to those occurring through long-term exposure to the same conditions. Nevertheless, tolerance by corals to short exposures of OA-like conditions is important, because it suggests that they possess mechanisms that can respond in beneficial ways to low pH and conceivably could play a role in reducing the consequences of OA for coral reefs. Currently, there is little known of the mechanisms that corals use to resist low pH, although there are observations that such resistance is associated with high nutrient concentrations (Manzello 2010) and heterotrophy (Cohen & Holcomb 2009). Indeed, the corals grown in low-pH/low-Ω_a conditions at the Waikiki Aquarium were also exposed to elevated nutrient concentrations (Atkinson et al. 1995), and manipulations of N and P over experimental reef communities suggest that nutrients reduce the inhibitory effects of low Ω_a on calcification, and, at very high nutrient loading, may be able to completely neutralize the effect (Atkinson & Cuet 2008).

Given the role of biology in coral calcification, and the clear threat posed to corals by OA, it is germane to ask whether corals have the capacity to acclimatize or adapt to the impending changes. Although there is no evidence to support adaptation to low pH/low Ω_a in corals, it is important to note that there have been no explicit tests of this hypothesis. Based on the pervasive presence of acclimatization in metazoans and in corals challenged by a variety of conditions including light and temperature (Edmunds & Gates 2008), it is likely that corals can and will acclimatize to OA to some extent.

Acclimatization in corals is complex, because they not only possess the suite of molecular and physiological mechanisms normally associated with acclimatization, but they also live in symbioses with a diversity of eukaryotic and prokaryotic taxa. The chimeric nature of corals thus provides an opportunity for rapid changes in physiological performance through qualitative and quantitative changes in the symbiotic assemblage. The eukaryotic dinoflagellate genus *Symbiodinium* is the best-studied group of coral symbionts in this context and contains tremendous taxonomic diversity associated with a range of phenotypic traits (Stat et al. 2006). The emergence of this taxonomic landscape paved the way in the 1990s for the idea that coral bleaching could be adaptive if it provided corals the opportunity to optimize the physiology of the symbiotic partnership to new environmental conditions. This could be accomplished by either switching existing with new *Symbiodinium* types culled from the environment or by changing the relative abundance of types within existing *Symbiodinium* communities (adaptive bleaching hypothesis;

Buddemeier & Fautin 1993). Although still controversial, some elements of the hypothesis are correct (Stat et al. 2006); corals host diverse endosymbiont communities (Apprill & Gates 2007) whose composition is temporally dynamic with respect to environment and, most importantly, some *Symbiodinium* types perform better under certain environmental conditions than others (e.g., Jones et al. 2008).

Symbiosis: a close interaction or association between evolutionarily distinct organisms

In the context of OA, there is very little direct research evaluating the role of *Symbiodinium* in the response of corals to reduced pH. This is, however, an important research direction given how fundamentally linked the photosynthetic activity of *Symbiodinium* community is with coral calcification and the fact that *Symbiodinium* types exhibit a range of photophysiological performance (Hennige et al. 2009). We also know that exposure of corals to low pH induces bleaching (Anthony et al. 2008) and that photorespiration in *Symbiodinium* can be affected by high pCO_2 (Crawley et al. 2010). Therefore, it is quite feasible that the taxonomic nature and flexibility of the unions between corals and *Symbiodinium* could influence responses to OA. The capacity to potentially acclimatize or adapt to OA through modifications to coral symbiotic communities, of course, extends far beyond *Symbiodinium* to the diversity of bacteria and other microeukaryotes that inhabit the cells, extracellular spaces, tissues, skeletons, and surface microlayer of corals (Ainsworth et al. 2010).

Central to whether corals can adapt to OA is the extent to which biology can override geochemical constraints on carbonate deposition and the juxtaposition of the timescale necessary for adaptation versus the speed with which the environment is changing. Assuming that the biology of corals can ameliorate the geochemical consequences of OA, at least within their tissues and at the tissue-skeleton interface, then the consensus opinion remains that atmospheric CO_2 (the driver of OA) is rising at an unprecedented rate for the last 650,000 years (Siegenthaler et al. 2005). Importantly, it is occurring at a rapid rate relative to the slow generation times of cnidarians, therefore it is unlikely that OA will act as a strong selective force to modify gene frequencies in corals. However, the compositionally dynamic, diverse, and high turnover communities of microorganisms hosted by corals may be subject to strong selection by OA, and as such, these symbioses represent an avenue for rapid change in the functional range of the coral holobiont. Similar processes have a long history of creating evolutionary novelty within the metazoa (Moran 2007), and perhaps this offers a means by which scleractinians might alter their physiology to better tolerate the effects of OA.

THE OPEN OCEAN

The vast expanses of the open ocean central gyre ecosystems are among the largest contiguous biomes on the planet, reaching from the temperate latitudes to the tropics. Biological production here is usually constrained by the supply rate of "new" limiting nutrients, especially nitrogen, which arrives in surface waters either from underlying deepwater sources or from the activity of N_2-fixing prokaryotes such as cyanobacteria. Increasing seawater pCO_2 may especially favor these cyanobacteria such as the ubiquitous warm-water genera *Trichodesmium* and *Crocosphaera*, which exhibit dramatically increased N_2 fixation and photosynthetic rates under projected future CO_2 conditions (Fu et al. 2008, Hutchins et al. 2007). Thus, OA has the potential to profoundly alter present day nutrient cycling and biological communities throughout these oceanic regimes (Hutchins et al. 2009).

Despite the immense areal extent of the open ocean, calcification here is dominated by just three planktonic groups; pteropods, coccolithophores, and foraminiferans. Pteropods are the major metazoan calcifiers in the pelagic realm and are most prominent in the high-latitude oceans. As such, the potential impact of OA on this group is discussed in the high-latitude ocean section below. Coccolithophores are unicellular haptophyte algae (Prymnesiophyceae) covered by overlapping

calcite plates called coccoliths. They are found throughout the world's oceans with the exception of the polar seas and produce massive spring blooms in some temperate regimes like the North Atlantic. Their calcification reaction converts two bicarbonate ions (HCO_3^-) to one CO_2 and one $CaCO_3$, so despite being photoautotrophs, their blooms may sometimes be net sources of CO_2 to the atmosphere (Boyd et al. 2010). Coccolithophores seem to be extending their latitudinal range limits, possibly in response to ongoing sea surface warming. Unprecedented regional blooms have occurred recently in the Bering Sea (Merico et al. 2004), as well as new range extensions into sub-Antarctic waters (Cubillos et al. 2007).

Because of their ecological and biogeochemical importance, coccolithophores were the subject of early investigations into the effects of carbonate undersaturation on calcification. A laboratory culture study using the cosmopolitan species *Emiliania huxleyi* showed that calcification can be significantly reduced by CO_2 levels expected over the next century (Riebesell et al. 2000). These results were supported by other culture experiments, as well as by CO_2 manipulation studies using natural coccolithophore assemblages (reviewed in Zondervan 2007). In contrast to these negative impacts of high pCO_2 on calcification, photosynthetic carbon fixation in *E. huxleyi* could be significantly stimulated by future OA because it is undersaturated at current atmospheric pCO_2 (Rost et al. 2003). Thus, either decreased calcite production, increased organic carbon production, or both, could lower the particulate inorganic (PIC)-to-particulate organic carbon (POC) ratio of coccolithophores with increasing pCO_2.

Subsequent work has suggested that the responses of coccolithophore calcification to a high-CO_2 ocean may be more complex than originally suggested. Two recent experiments show a contrary trend of increased calcification in *E. huxleyi* at elevated pCO_2 (Iglesias-Rodriguez et al. 2008, Shi et al. 2009). One potentially confounding issue is the tremendous intraspecific variability in genetics, physiology, and calcification within this commonly cultured model coccolithophore species (Ridgwell et al. 2009) and the fact that the various studies have used different isolates. Langer et al. (2009) reported differing responses of calcification to pCO_2 increases in four *E. huxleyi* strains, including decreases, slight increases, or no change. This intraspecific diversity in the pCO_2 responses of *E. huxleyi* strains is echoed by major differences between coccolithophore species. Calcification in two other species shows either a nonlinear relationship (*Calcidiscus leptoporus)* or no change (*Coccolithus pelagicus*) across a pCO_2 gradient (Langer et al. 2006). Ridgwell et al. (2009) suggest that future global decreases in coccolithophore calcification may occur not from species-specific physiological changes, but rather from community composition shifts from heavily to lightly calcified species.

An additional layer of complexity is added by the fact that pCO_2 effects on calcification can be strongly modulated by simultaneous changes in other environmental variables. Sciandra et al. (2003) reported that unlike nutrient-replete cultures, nitrogen-limited *E. huxleyi* showed no reduction in PIC:POC production ratios with higher CO_2 levels (Sciandra et al. 2003). Feng et al. (2008) found that calcification of a Sargasso Sea *E. huxleyi* isolate was not altered by pCO_2 increases under low light conditions, but was strongly inhibited by high pCO_2 under saturating light levels (Feng et al. 2008). A shipboard incubation study using a natural North Atlantic spring bloom community showed that coccolithophore calcification rates were insensitive to increased pCO_2 at ambient temperature (690 ppm and 12°C), but decreased markedly when pCO_2 and temperature were increased together (690 ppm and 16°C). In this combined "greenhouse" treatment, reduced calcification was accompanied by large increases in coccolithophore abundance, suggesting the possibility of denser blooms of very lightly calcified cells under future ocean conditions (Feng et al. 2009). Numerous other key environmental factors will undergo major shifts in the future, changing oceans along with rising pCO_2, including sea surface temperature, water column stratification, and light and nutrient availability—formulating accurate predictions requires

PIC: particulate inorganic carbon

POC: particulate organic carbon

accounting for the complex synergistic and antagonistic interactions of all of these many co-variables (Boyd et al. 2010, Hutchins et al. 2009).

Foraminiferans are amoeboid zooplankton that secrete calcite shells. By comparison to coccolithophores, fewer studies have addressed acidification effects in this group, perhaps reflecting the difficulty of maintaining and propagating laboratory cultures of these delicate heterotrophic protozoans. A rigorous assessment of pCO_2 effects on foraminifera calcification is especially critical, because their calcite shells in ocean sediment deposits are widely employed by paleoceanographers as proxies for past climate changes. The limited number of available foraminifera studies suggest that, as with many other marine calcifiers, the chemistry changes associated with OA will result in reduced calcification (Bijma et al. 1999, Russell et al. 2004). For instance, calcification rates of two common planktonic species are reduced by 6–13% under projected year 2100–pCO_2 conditions (Lombard et al. 2010). Clearly, more work is needed to quantify OA impacts on this important calcifying group, which is responsible for 25–50% of pelagic calcium carbonate export (Moy et al. 2009).

One important caveat is that nearly all of the published pCO_2 studies using coccolithophores and foraminifera have been relatively short-term experiments, and so the potential for long-term acclimation and adaptation of their growth and calcification to OA remains untested. Casareto et al. (2009) showed that calcification decreased in all CO_2 treatments in very short incubations (<39 h) using a natural bloom of the coccolithophore *Pleurochrysis carterae*, but it increased at high pCO_2 in longer (7-day) experiments (Casareto et al. 2009). In contrast, Barcelos e Ramos et al. (2010) found that the decreases in *E. huxleyi* calcification observed in response to abruptly increased pCO_2 during very short incubations (hours) were similar to those seen in cultures that had been preacclimated over 20 generations to the same carbonate system conditions. Langer et al. (2006) examined coccoliths collected from sediment cores spanning large variations in past atmospheric pCO_2 and found no evidence for the malformed coccolith morphologies they observed in high CO_2–grown modern cultures. They interpreted this as offering possible evidence for adaptation to changing pCO_2 over geological timescales. However, the fact that modern foraminiferal shells weigh about one-third less than those of the same species in sedimentary deposits from preindustrial times suggests that reductions in calcification, possibly due to recent OA, have not been compensated for through adaptation (Moy et al. 2009). Currently, several laboratories are carrying out long-term high-CO_2 evolution experiments with coccolithophore cultures similar to the 1,000-generation adaptation experiments using freshwater green algae presented by Collins & Bell (2004), but the results of these efforts have not yet been published.

THE COASTAL OCEAN

Coastal oceans are likely to exhibit early signs of OA. Acidification associated with seasonal upwelling has already been detected in the California Current System (CCS) (Feely et al. 2008, Hauri et al. 2009). Aragonite saturation horizons, which in the North Pacific are shallow due to natural respiration processes, are subject to further shoaling due to uptake of anthropogenic CO_2, with the result that saturation horizons can reach the surface during upwelling events. Such waters are characterized by pCO_2 levels of about 1,100 μatm (Feely et al. 2008). Although the intermittent nature of upwelling and mesoscale eddy formation causes variation in the acidification signal, surface waters in the CCS could become permanently undersaturated with respect to aragonite in the foreseeable future (Hauri et al. 2009). Other eastern boundary current systems are likely to be at similar risk (Wootton et al. 2008). This finding is significant given the importance of coastal upwelling systems to nearshore productivity.

Processes other than dissolution of atmospheric CO_2 add to acidification of coastal oceans. Deposition of reactive nitrogen and sulfur from fossil-fuel combustion and agriculture can reduce alkalinity in coastal waters (Doney et al. 2007). Inputs of river water, which typically are more acidic than receiving waters, further reduce alkalinity, as can interactions with bottom sediments (Salisbury et al. 2008). Oxidation of organic matter from upland areas can reduce pH and influence carbonate system variables (Gattuso et al. 1998). In tide pools, pCO_2 is elevated by respiration when pools are isolated at low tide. In combination, these sources amplify the OA signal in coastal systems. Notably, several drivers of coastal acidification exist independent of fossil-fuel contributions and have operated over evolutionary timescales, but virtually all are now influenced by human activities.

Coastal organisms show diverse responses to elevated seawater pCO_2 (Hendriks et al. 2010, Ries et al. 2009). Among calcifiers, six patterns of response in net calcification rate were observed across four pCO_2 levels (409, 606, 903, and 2,856 ppm). Responses varied from strictly increasing to strictly decreasing, with several taxa showing highest net calcification at intermediate levels of pCO_2 (Ries et al. 2009). Among noncalcifying taxa, both positive and negative responses in growth, reproduction, and survivorship have been observed in response to increasing pCO_2 from 477 to 2,000 ppm (Hendriks et al. 2010).

Due to metabolic and physiological constraints, the lower invertebrates may be especially vulnerable to OA (Pörtner 2008). Furthermore, early life-history stages may be disproportionately susceptible to OA. Fertilization rates in echinoderms declined as pCO_2 levels increased from 360 to 10,360 µatm (Kurihara 2008). Rates of successful cleavage in fertilized eggs of an echinoderm declined by 20% as pH dropped from 8.1 to 7.7 (Havenhand et al. 2008). Abnormalities in larval morphologies were observed in bivalves and echinoderms reared at 1,000 and 2,000 ppm CO_2 (Kurihara 2008) and in brittlestar larvae reared at three levels of pH between 8.1 and 7.7 (Dupont et al. 2008). Mortality in brittlestar larvae increased from 30% at pH 8.1 to 100% at pH 7.9 and 7.7 (Dupont et al. 2008), respectively. Metamorphosis, growth, and survivorship of clam, scallop, and oyster larvae all were negatively impacted at 650 ppm pCO_2 compared with controls (Talmage & Gobler 2009).

Among coastal taxa, variation in response to acidification could reflect differences in calcification mechanisms (Ries et al. 2009) as well as underlying variation in genes that code for these responses. Because of their history of exposure to low-alkalinity waters, coastal taxa may have greater capacity for adaptation than other marine organisms. Physiological tolerance to low pH and carbonate saturation state could already have evolved in response to repeated exposure to such conditions during and prior to the industrial era and could account for positive responses to acidification reported for some taxa (Gooding et al. 2009). Compensatory or adaptive responses to acidification can also be inferred from studies of urchins (Todgham & Hofmann 2009) and barnacles (McDonald et al. 2009). Because of their prior history of exposure, coastal regions may be hot spots for local adaptation to OA. Tide pools, in particular, could provide useful natural settings in which to examine short-term responses to variation in pH and pCO_2 occurring over the tidal cycle.

Variation in response to OA is observable in key habitat-forming species. Experiments suggest that seagrass growth increases as pCO_2 levels increase from 477 to 2,000 ppm (Hendriks et al. 2010), perhaps because increased DIC reduces carbon limitation in these primary producers. There are hints that other primary producers in coastal systems—seaweeds and phytoplankton—could respond similarly. Alternatively, calcification rates in key habitat-forming bivalves (Pacific oysters and edible mussels) declined linearly as pCO_2 increased from about 600 to 2,000 ppm (Gazeau et al. 2007). Growth and calcification were lower in larvae of eastern oysters grown at 800 µatm compared with 280 µatm (Miller et al. 2009, Talmage & Gobler 2009). Generally, we

might expect calcified biogenic habitat to contract under conditions of OA, whereas noncalcified biogenic habitat could expand.

Acidification is only one of several physical changes occurring in coastal systems. Temperature, stratification, and hypoxia all are increasing with climate change (Bograd et al. 2008, Meehl et al. 2007), and all will interact with acidification. Multiple stressors produce biological responses that are not predictable from single-factor experiments. Synergistic interactions have been observed in response to combinations of elevated pCO_2 and temperature (Connell & Russell 2010, Martin & Gattuso 2009) and to elevated pCO_2 and UV light (Gao & Zheng 2010, Swanson & Fox 2007).

Indirect effects of OA will occur through intensification of, or release from, competition or predation as species change in distribution and abundance. Feedbacks between biological and physical systems also will occur. In shelf and slope ecosystems, calcification among echinoids contributes substantially to the marine carbon cycle. Changes in pCO_2 are likely to alter calcification rates in echinoids, thereby influencing the carbon cycle, but the direction of change is unclear (Lebrato et al. 2010). Feedbacks to nutrient cycling are likely, for example, through changing rates of microbial degradation (Swanson & Fox 2007). Additional feedbacks, both stabilizing and destabilizing, undoubtedly will be revealed as acidification proceeds and as our understanding grows.

In coastal areas, linkages between the natural and social systems are readily apparent. Coastal systems are intensively managed because the goods and services they provide are essential to human well-being. Managers now must address the potential impacts of OA and associated stressors on coastal resources. Impacts are likely to include changes in the distribution and abundance of finfish and shellfish resources (Cooley & Doney 2009), reductions in the yield and profitability of wild-capture fisheries and shellfish aquaculture (Cheung et al. 2009, Cooley & Doney 2009), suppression of recovery of species and stocks already depleted through overfishing or habitat loss, and the expansion of taxa now considered undesirable, for example non-native invasive species or those causing harmful algal blooms. In the United States, the shift toward ecosystem management and marine spatial planning could assist managers in responding to the challenges of acidification by promoting consideration of multiple taxa at relevant spatial scales (Miles 2009, Ruckelshaus et al. 2008). The evolutionary potential that likely exists in coastal populations argues forcefully for careful and conservative management in the near term, because biological adaptation to changing ocean chemistry is the sole mechanism (absent engineering) by which taxa will persist and ecosystem goods and services will be retained. The loss of evolutionary potential forecloses options for biological and human adaptation to the threat of OA.

THE DEEP SEA

The influx of anthropogenic CO_2 to deep-sea waters is reducing the saturation states for aragonite (Ω_A) and calcite (Ω_C); this has profound implications for the global distribution of deep-sea corals and other calcifiers. In many areas, the deep waters of the oceans are already undersaturated with respect to aragonite and calcite and appear to constrain the distribution of corals and perhaps other calcifiers. Present day distribution of deep-sea scleractinian corals (aragonite-forming) is correlated strongly with the depth of the aragonite saturation boundary, suggesting that Ω_A imposes limits on their bathymetric range (Guinotte et al. 2006). Measurements of reduced growth rates of shallow-water scleractinian corals under lower Ω_A (Kleypas et al. 1999), and the similar pattern observed for the single deep-sea coral examined to date (*Lophelia pertusa*, Maier et al. 2009), support the notion that Ω_A regulates coral distributions. Similar studies for calcite-forming taxa are not yet available.

Rapid shoaling of the saturation boundaries (where $\Omega = 1$) for aragonite and calcite through this century (Orr et al. 2005) may drive a massive change in habitat quality for a variety of deep-sea

calcifiers, leading to a reshuffling of faunal composition and changes in community function. The consequences for coral-dominated bioherms and seamounts at depths that will become undersaturated over this century are uncertain, but likely to be negative. For aragonite-forming corals (scleractinians) the largest changes may occur in the North Atlantic, where the saturation boundary is expected to rise 1–2 km by the year 2100. Shoaling of Ω_A in the Pacific should be milder only because the saturation boundary is already near the surface ($\sim$0.5 km depth) in the oldest waters of the N.E. Pacific. The effects of reduced Ω_C for calcitic deep-sea corals (e.g., gorgonians) are less well understood, but are also likely to include changes in bathymetric ranges. Corals throughout the deep sea, particularly slow growing taxa that can range in age from centuries to millennia (Roark et al. 2009) may be unable to survive as their present habitat becomes corrosive, particularly considering the relatively rapid change in carbonate saturation. Some deep-living corals may resist dissolution because tissues protect their carbonate skeletons. The octocorallian gorgonian *Paragorgia arborea* (bubblegum coral) has calcite sclerites embedded in tissue and can reach 10 m in height (Roberts et al. 2009).

Calcification rates have been measured in temperate, shallow-water taxa (e.g., Fabry et al. 2008, Ries et al. 2009). Although no studies of calcification are yet available for deep-sea taxa, the bathymetric distributions of some taxa are coupled closely to depth-related changes in calcite saturation. Echinoderms, including five classes with magnesium-calcite skeletons, are found throughout the world's oceans, but are far less abundant or absent from undersaturated waters (Lebrato et al. 2010). Calcification also appears weak in deep, low-pH waters. Abyssal echinoids in the N.E. Pacific typically are weakly calcified (e.g., *Cystochinus* sp.) or uncalcified (e.g., *Tromikosoma* sp.), and are sensitive to mild pH reductions (Barry et al. 2003). Calcification is also reduced in larvae of shallow-living urchins, bivalves, and shrimp exposed to low-pH waters (Kurihara et al. 2008), but mixed results are reported for adults, including increased calcification in an ophiuroid (Wood et al. 2008) and crustaceans (Ries 2005). A handful of studies indicate that molluscs generally have reduced rates of growth and calcification under high-pCO_2 conditions (Doney et al. 2009). Although no direct experiments concerning the impacts of OA on calcification in deep-living molluscs have been performed, field studies of mussels (*Bathymodiolus brevior*) from deep-sea hydrothermal venting sites indicate that growth and calcification is reduced at more acidic locations, even though calcification occurs in waters with pH $\sim$ 5.4–7.3 as long as the proteinaceous periostracum covering the carbonate shell remains intact (Tunnicliffe et al. 2009).

Calcite-forming foraminifera are also a common constituent of deep-sea sediment communities, where they play an important trophic role. The bathymetric distribution of foraminifera is constrained, at least partially by the calcite saturation horizon, and in situ experiments simulating deep-sea carbon dioxide sequestration have shown that high CO_2 levels are lethal for most foraminifera examined (Bernhard et al. 2009).

The potential impacts of OA on planktonic and pelagic calcifiers in the deep sea are almost completely unknown. Otoliths used for balance in fishes are aragonitic and have been shown to increase in size in juvenile sea bass exposed to CO_2-rich waters (Checkley et al. 2009), but it remains unclear if there is any cost in metabolism or performance. Statocysts are also important balance organs in a number of invertebrates, including many gelatinous plankton, crustacean zooplankton, and benthic invertebrates. The composition of statoliths varies among taxa, but they are calcium carbonate in several groups (Fabry et al. 2008). Potential effects of OA on biomineralization of statoliths are not understood. The consequences of statolith dissolution, however, could include an inability of various taxa to orient to gravity as well as include behavioral abnormalities as has been shown for marine fish (Munday et al. 2009).

Calcification in marine animals is linked intimately to other physiological processes that are also likely to be affected by OA, particularly for deep-sea animals, which are generally adapted to

having a low-energy lifestyle with a high percentage of water and low protein content in tissues, low enzyme levels, reduced rates of metabolism, and slower growth than related shallow-water taxa (Drazen 2007). These adaptations are suited to the reduced food availability of the deep sea and are linked to colder temperatures and (for mobile organisms) the reduced energetic requirements for visual predator-prey interactions with depth (Seibel & Drazen 2007). Elevated environmental pCO_2 levels can disrupt internal pH balance (acidosis), which may be partially restored by passive (nonbicarbonate) or active buffering (Melzner et al. 2009). Passive buffering occurs through the binding of excess protons on partially protonated proteins in internal fluids (e.g., histidine), but is far less effective in organisms with low tissue protein content (e.g., deep-sea animals). Passive pH buffering in response to a doubling of intracellular pCO_2 in a shallow-living squid resulted in a ΔpH of only -0.02 units, whereas similar conditions caused a ΔpH of -0.2 in a deep-sea squid (Seibel & Walsh 2003). Active pH buffering may be invoked to compensate pH disturbance through the use of energetically expensive ion exchangers and proton pumps, which for deep-sea animals may increase total energy costs considerably.

Together, the combined impacts of OA on a variety of physiological and metabolic processes are likely to limit animal performance in many areas, including calcification. For example, failure to preserve or restore pH balance in extracellular fluids following acidosis can lead to metabolic depression (Pörtner 2008); this can potentially have large impacts on all cellular functions. Similarly, uncompensated acidosis of extracellular fluids can limit gas transport and exchange for animals with respiratory proteins, further reducing metabolic efficiency (Melzner et al. 2009). Expansion of hypoxia related to OA in surface waters could intensify acidosis by limiting further the ability of some species (e.g., deep-sea crabs, *Chionoecetes bairdi*) to compensate pH disturbance (Pane & Barry 2007). For many deep-sea animals, limited physiological capacity for coping with pH-related stresses may have broad-ranging consequences for individual performance including calcification, behavior, growth, reproduction, and ultimately survival.

Ocean acidification, along with climate-related stressors (that is, warming, hypoxia), is likely to affect the performance of many deep-sea animals directly or indirectly, with cascading consequences that modify the composition and function of deep-sea ecosystems on local to global scales. For marine calcifiers in the deep sea, shoaling of the aragonite and calcite saturation boundaries may redefine fundamental boundaries of habitability in the deep sea, leading to reduced calcification or dissolution of exposed carbonate for many populations throughout the deep sea and having wide-ranging impacts for communities and ecosystems. Coral mounds and seamounts that currently have expansive coral assemblages supporting complex assemblages of invertebrates and fishes may lose the three-dimensional structure provided by corals, reducing habitat quality for many species, potentially promoting the collapse of these communities (Andersson et al. 2008, Roberts et al. 2009). For pelagic communities, the impacts of OA for calcifying taxa are unclear, but could be significant due to shifts in the carbonate rain, hypoxia, and altered trophic relationships. Ecosystem changes caused by OA are not yet evident in the deep sea, perhaps in part to the weak existing baseline concerning the current status (that is, distribution, abundance, and biodiversity) of deep-sea ecosystems (Kaiser & Barnes 2008). Because calcification is coupled strongly to the carbonate chemistry of seawater, baseline information concerning the distribution and calcification rates for key calcifiers may be an important first step in detecting and understanding the future impacts of OA in the deep sea.

HIGH-LATITUDE SEAS

Models project that high-latitude seas will be the "first in time" to experience significant undersaturation of surface waters—as early as 2050 for the Southern Ocean when atmospheric levels reach

~560 ppm, and by 2020 in the Arctic Ocean (Orr et al. 2005, Steinacher et al. 2009). Seasonal winter undersaturation is predicted for the Southern Ocean by 2030 (McNeil & Matear 2008), a mere 20 years from now. From a physiological perspective, the sensitivity of polar organisms to OA is only beginning to be explored and as such we have a very incomplete view of how biota may respond. However, the low to subzero temperatures of high-latitude seas presents an already challenging environment in which to perform calcification (Andersson et al. 2008), with increased CO_2 gas solubility due to low temperatures driving carbonate saturation states to levels already naturally lower than in tropical and temperate systems. Characteristics of polar metazoans, in particular, increase the susceptibility to OA and climate change in general because life-history traits and long generation times reduce the potential for the appearance of phenotypes that are tolerant of the new environmental conditions (see Visser 2008). Overall, the rapid pace of environmental change predicted for polar regions heightens the need for research in this area.

Data regarding calcification rates for polar organisms are extremely limited at this stage. Manipulative experiments on polar calcifying organisms have generally hypothesized that OA conditions (as simulated in the laboratory) would result in decreased rates of calcification and dissolution of calcium carbonate structures (e.g., Fabry et al. 2009, Orr et al. 2005). Available data suggest that this is the case. Arctic pteropods (*Limacina helicina*) exposed to 765 ppm CO_2 exhibited a 28% decline in calcification rates as compared to control (385 ppm CO_2) during a short-term laboratory experiment (5 day) (Comeau et al. 2009). Research on Antarctic populations of the pteropod (*L. helcina*) found that oxygen consumption was relatively unchanged in response to elevated pCO_2 (B.A. Seibel, unpublished observations). This suggests that, if there are compensatory changes to support calcification, extra metabolic cost was not detectable using this measure of organismal performance. Notably, Melzner et al. (2009) has hypothesized that organisms with relatively lower metabolic rates, a trait of ectothermic polar metazoans, may render these species more sensitive to OA. At present, there is insufficient data to conclude whether polar benthic invertebrates or fish are more vulnerable to OA stress than their temperate or tropical counterparts.

In other polar calcifiers, a comparative study of a Southern Ocean planktonic foraminifera (*Globigerina bulloides*) showed a 30–35% reduction in shell weight of those collected from sediment traps (industrial era) with preindustrial shells preserved in Holocene sediment cores (Moy et al. 2009). As foraminifera and pteropods are numerically dominant members of the zooplankton, are important components of polar food webs, and contribute to both organic carbon and $CaCO_3$ flux to the benthos, declines in numbers and/or northward shifts in distribution as a result of aragonite undersaturation are therefore likely to produce broad-scale ecosystem effects (Hunt et al. 2008). Recent research on Antarctic benthic invertebrates found a significant dissolution of the weakly calcified calcite and aragonite shells on a timescale of 14–35 days at a seawater pH expected by the year 2300, pH 7.4 (McClintock et al. 2009). However, these studies were performed on postmortem shells; and in nature the periostracum may provide some protection from dissolution and the physiology at the site of calcification may mechanistically compensate for altered external conditions, as shown in shell-forming invertebrates in other extreme environments (Tunnicliffe et al. 2009). The observations by McClintock et al. (2009) are, however, ecologically noteworthy. Shell or skeletal thinning may result in these species being more vulnerable to the impacts of disturbance, particularly on Antarctic shelves that, under global climate change (GCC), may see a greater frequency of iceberg scouring (Barnes & Peck 2008) or predation from recently invasive shell-crushing predators such as the deep-water king crab (Aronson et al. 2007).

In contrast to other calcification studies, developmental studies on larvae of the benthic Antarctic sea urchin (*Sterechinus neumayeri*) found that a calcification index was not reduced in

GCC: global climate change

CO_2-acidified seawater at low pHs (pH 7.0–7.5) as compared to skeletal formation in larvae of tropical and temperate sea urchins (Clark et al. 2009). Clark and colleagues suggest that *S. neumayeri* may be preadapted to low saturation states; these data also may suggest that Antarctic sea urchins may possess greater mechanistic control over the chemical nature of the extracellular space that surrounds the site of calcification of the larval endoskeleton. Such variation in cellular capacity and mechanistic variation has been discussed for temperate invertebrates that exhibited variable responses to CO_2 perturbation in the laboratory (Ries et al. 2009). Although data do not yet exist, gametes of polar invertebrates, which in temperate species can be sensitive to OA conditions (Havenhand et al. 2008), may be a particularly vulnerable life-history stage in Antarctic species where higher sperm concentrations are required for successful fertilization (Powell et al. 2001). In general, slow development times and extended pelagic larval duration (Pearse et al. 1991) may also result in exposure to OA conditions and/or warmer seawater temperatures for timescales from months to years.

Marine organisms in high-latitude seas may also be exposed to a suite of multistressors, including changes in salinity, seawater temperature, sea-ice coverage, and UV exposure (Aronson et al. 2007, Barnes & Peck 2008, Turner & Overland 2009). Early development in a dominant benthic invertebrate, the sea urchin *S. neumayeri* was found to be perturbed by small reductions in salinity (Cowart et al. 2009). This suggests that OA and increased influx of freshwater from melting ice shelves may impact larval organisms in the plankton and the interaction of these stressors is worth further investigation. Shallowing of saturation horizons in the Arctic and Antarctic are likely to restrict the lower bathymetric ranges of slope and deep sea fauna, while the climate change multistressors will be acting from the shallows to push organisms deeper. This "double-whammy" of GCC effects from both the shallows and from the deep is likely to impact many heavily calcified members of the macrofauna, including the sea urchins (M.A. Sewell and G.E Hofmann, unpublished data). Loss, or reduction, of populations of individual species may then have carryover effects to ecosystem biodiversity and function. As an example, cidaroid sea urchins have spines directly exposed to seawater and are an important settlement surface for encrusting endosymbionts (e.g., sponge, bryozoan, hydroid) in Antarctic environments where there is a low availability of hard substrate (Hétérier et al. 2008). Local extinction of a single species, therefore, has the potential to severely impact population numbers of associated species.

Of particular importance when considering OA effects in high-latitude seas is that both the Arctic and Antarctic will show distinctive environmental heterogeneity. In particular, the Arctic is influenced by local differences in riverine input and the inflow of water from the Atlantic and Pacific Oceans. The more isolated Antarctic shows different responses to climate change between the Western Antarctic Peninsula, which is one of the most rapidly changing ecosystems on the planet, and the geographically larger Antarctic continent (Barnes & Peck 2008). In the Arctic, loss of sea ice and greater open water area should result in greater upwelling at the shelf-break, increasing nutrients available for primary production (Bates & Mathis 2009). This is predicted to result in a shift from a "sea ice algae-benthos"- to a "phytoplankton-zooplankton"-dominated ecosystem with concomitant reductions in export of organic carbon from surface waters and altered bentho-pelagic coupling (Bates & Mathis 2009). Additionally, in a bioclimate envelope model it was shown that the Arctic and subpolar Southern Ocean will be subject to the greatest global biodiversity changes by 2050, with overall increases in species richness due to poleward expansion of species ranges (Cheung et al. 2009). In the Arctic, range shifts have already been reported in marine mammals, benthic clams, and zooplankton (reviewed in Fabry et al. 2009), and are also predicted to occur in Antarctic seaweeds (Müller et al. 2009), which would result in major structural impacts on the ecosystems that they invade.

SUMMARY POINTS

1. Although OA is occurring on a global scale, coral reefs, the open ocean, the deep sea, coastal oceans, and high-latitude seas differ in their vulnerability to OA. The knowledge base regarding responses to OA for taxa in each ecosystem varies, with a distinct data deficit on calcifying organisms in the deep sea and high-latitude seas.

2. Studies that document the effect of OA conditions on calcification by key calcifiers in each ecosystem generally show a deleterious impact, although, with greater taxonomic coverage, there is an emerging variation in response to OA. Numerous other physiological processes are understudied. Notably, more studies that integrate the response to OA across life-history transitions are needed, as are studies that further explore the metabolic costs of function under OA conditions.

3. Multiple interactive stressors imposed by GCC will modulate the biological impacts of OA. Although we know very little about how such interactions will be manifest, we can expect that in some or many cases, multiple interactive stressors will impair biological function beyond the influence of any single variable.

4. Adaptation and levels of phenotypic plasticity are in need of empirical research in marine organisms. Given the rapid rate of environmental change, studying the phenotypic plasticity of contemporary populations and the potential to acclimatize to coming OA conditions will aid in forecasting the ecosystem-level impact of OA.

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LITERATURE CITED

Ainsworth TD, Thurber RV, Gates RD. 2010. The future of coral reefs: a microbial perspective. *Trends Ecol. Evol.* 25:233–40

Al-Horani FA, Ferdelman T, Al-Moghrabi SM, de Beer D. 2005. Spatial distribution of calcification and photosynthesis in the scleractinian coral *Galaxea fascicularis*. *Coral Reefs* 24:173–80

Allemand D, Ferrier-Pages C, Furla P, Houlbreque F, Puverel S, et al. 2004. Biomineralisation in reef-building corals: from molecular mechanisms to environmental control. *C. R. Palevol.* 3:453–67

Andersson AJ, Kuffner IB, Mackenzie FT, Jokiel PL, Rodgers KS, Tan A. 2009. Net loss of $CaCO_3$ from a subtropical calcifying community due to seawater acidification: mesocosm-scale experimental evidence. *Biogeosciences* 6:1811–23

Andersson AJ, Mackenzie FT, Bates NR. 2008. Life on the margin: implications of ocean acidification on Mg-calcite, high latitude and cold-water marine calcifiers. *Mar. Ecol. Prog. Ser.* 373:265–73

Anthony KRN, Connolly S, Willis BL. 2002. Comparative analysis of energy allocation to tissue and skeletal growth in corals. *Limnol. Oceanogr.* 47:1417–29

Anthony KRN, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O. 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proc. Natl. Acad. Sci. USA* 105:17442–46

Apprill AM, Gates RD. 2007. Recognizing diversity in coral symbiotic dinoflagellate communities. *Mol. Ecol.* 16:1127–34

Aronson RB, Thatje S, Clarke A, Peck LS, Blake DB, et al. 2007. Climate change and invasibility of the Antarctic Benthos. *Annu. Rev. Ecol. Evol. Syst.* 38:129–54

Atkinson MJ, Carlson B, Crow GL. 1995. Coral growth in high-nutrient, low-pH seawater: a case study of corals cultured at the Waikiki Aquarium, Honolulu, Hawaii. *Coral Reefs* 14:215–23

Atkinson MJ, Cuet P. 2008. Possible effects of ocean acidification on coral reef biogeochemistry: topics for research. *Mar. Ecol. Prog. Ser.* 373:249–56

Barcelos e Ramos J, Mueller MN, Riebesell U. 2010. Short-term response of the coccolithophore *Emiliania huxleyi* to an abrupt change in seawater carbon dioxide concentrations. *Biogeosciences* 7:177–86

Barnes DKA, Peck LS. 2008. Vulnerability of Antarctic shelf biodiversity to predicted regional warming. *Climate Res.* 37:149–63

Barry JP, Seibel BA, Drazen JC, Tamburri MN, Buck KR, et al. 2003. *Deep-sea field experiments on the biological impacts of direct deep-sea CO_2 injection.* Presented at Proc. 2nd Annu. Conf. Carbon Seq., Alexandria, VA

Bates NR, Mathis JT. 2009. The Arctic Ocean marine carbon cycle: evaluation of air-sea CO_2 exchanges, ocean acidification impacts and potential feedbacks. *Biogeosciences* 6:2433–59

Bell G, Collins S. 2008. Adaptation, extinction and global change. *Evol. Appl.* 1:3–16

Bernhard JM, Barry JP, Buck KR, Starczak VR. 2009. Impact of intentionally injected carbon dioxide hydrate on deep-sea benthic foraminiferal survival. *Glob. Change Biol.* 15:2078–88

Bijma J, Spero HJ, Lea DW. 1999. Reassessing foraminiferal stable isotope geochemistry: impact of the oceanic carbonate system (Experimental results). In *Use of Proxies in Paleoceanography: Examples From the South Atlantic*, ed. G Fischer, G Wefer, pp. 489–521. New York: Springer

Bograd SJ, Castro CG, Di Lorenzo E, Palacios DM, Bailey H, et al. 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. *Geophys. Res. Lett.* 35:L1 2607

Boyd PW, Strzepek R, Fu F-X, Hutchins DA. 2010. Environmental control of open ocean phytoplankton groups: now and in the future. *Limnol. Oceanogr.* 55:1353–76

Bradshaw WE, Holzapfel CM. 2010. Light, time and the physiology of biotic response to rapid climate change in animals. *Annu. Rev. Physiol.* 72:147–66

Buddemeier R, Fautin D. 1993. Coral bleaching as an adaptive mechanism: a testable hypothesis. *Bioscience* 43:320–26

Cao L, Caldeira K. 2008. Atmospheric CO_2 stabilization and ocean acidification. *Geophys. Res. Lett.* 35:L19609

Casareto BE, Niraula MP, Fujimura H, Suzuki Y. 2009. Effects of carbon dioxide on the coccolithophorid *Pleurochrysis carterae* in incubation experiments. *Aquat. Biol.* 7:59–70

Checkley DM Jr, Dickson AG, Takahashi M, Radich JA, Eisenkolb N, Asch R. 2009. Elevated CO_2 enhances otolith growth in young fish. *Science* 324:1683

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D. 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish.* 10:235–51

Chown SL, Gaston KJ. 2008. Macrophysiology for a changing world. *Proc. R. Soc. B* 275:1469–78

Clark D, Lamare M, Barker M. 2009. Response of sea urchin pluteus larvae (Echinodermata: Echinoidea) to reduced seawater pH: a comparison among a tropical, temperate, and a polar species. *Mar. Biol.* 156:1125–37

Cohen AL, Holcomb M. 2009. Why corals care about ocean acidification. *Oceanography* 22:118–27

Cohen AL, McConnaughey TA. 2003. Geochemical perspectives on coral mineralization. *Rev. Mineral. Geochem.* 54:151–87

Collins S, Bell G. 2004. Phenotypic consequences of 1,000 generations of selection at elevated CO_2 in a green alga. *Nature* 431:566–69

Comeau S, Gorsky G, Jeffree R, Teyssie JL, Gattuso JP. 2009. Impact of ocean acidification on a key Arctic pelagic mollusc (*Limacina helicina*). *Biogeosciences* 6:1877–82

Connell SD, Russell BD. 2010. The direct effects of increasing CO_2 and temperature on noncalcifying organisms: increasing the potential for phase shifts in kelp forests. *Proc. R. Soc. B* 277:1409–15

Cooley SR, Doney SC. 2009. Anticipating ocean acidification's economic consequences for commercial fisheries. *Environ. Res. Lett.* 4:024007

Cowart D, Ulrich P, Miller D, Marsh A. 2009. Salinity sensitivity of early embryos of the Antarctic sea urchin, *Sterechinus neumayeri*. *Polar Biol.* 32:435–41

Crawley A, Kline D, Dunn S, Anthony K, Dove S. 2010. The effect of ocean acidification on symbiont photorespiration and productivity in *Acropora formosa*. *Glob. Change Biol.* 16:851–63

Cubillos JC, Wright SW, Nash G, de Salas MF, Griffiths B, et al. 2007. Calcification morphotypes of the coccolithophorid *Emiliania huxleyi* in the Southern Ocean: changes in 2001 to 2006 compared to historical data. *Mar. Ecol. Prog. Ser.* 348:47–54

Doney SC, Fabry VJ, Feely RA, Kleypas JA. 2009. Ocean acidification: the other CO_2 problem. *Annu. Rev. Mar. Sci.* 1:169–92

Doney SC, Mahowald N, Lima I, Feely RA, Mackenzie FT, et al. 2007. Impact of anthropogenic atmospheric nitrogen and sulfur deposition on ocean acidification and the inorganic carbon system. *Proc. Natl. Acad. Sci. USA* 104:14580–85

Drazen JC. 2007. Depth related trends in proximate composition of demersal fishes in the eastern North Pacific. *Deep-Sea Res. I* 54:203–19

Dupont S, Havenhand J, Thorndyke W, Peck L, Thorndyke M. 2008. Near-future level of CO_2-driven ocean acidification radically affects larval survival and development in the brittlestar *Ophiothrix fragilis*. *Mar. Ecol. Prog. Ser.* 373:285–94

Edmunds PJ, Gates RD. 2008. Acclimatization in tropical reef corals. *Mar. Ecol. Prog. Ser.* 361:307–10

Fabry VJ, McClintock JB, Mathis JT, Grebmeier JM. 2009. Ocean acidification at high latitudes: the bellwether. *Oceanography* 22:160–71

Fabry VJ, Seibel BA, Feely RA, Orr JC. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES J. Mar. Sci.* 65:414–32

Feely RA, Doney SC, Cooley SR. 2009. Ocean acidification: present conditions and future changes in a high-CO_2 world. *Oceanography* 22:37–47

Feely RA, Sabine CL, Hernandez-Ayon JM, Ianson D, Hales B. 2008. Evidence for upwelling of corrosive "acidified" water onto the continental shelf. *Science* 320:1490–92

Feng Y, Hare CE, Leblanc K, Rose JM, Zhang Y, et al. 2009. Effects of increased pCO_2 and temperature on the North Atlantic spring bloom. I. The phytoplankton community and biogeochemical response. *Mar. Ecol. Prog. Ser.* 388:13–25

Feng Y, Warner ME, Zhang Y, Sun J, Fu F-X, et al. 2008. Interactive effects of increased pCO_2, temperature and irradiance on the marine coccolithophore *Emiliania huxleyi* (Prymnesiophyceae). *Eur. J. Phycol.* 43:87–98

Fu F-X, Mulholland MR, Garcia N, Beck A, Bernhardt PW, et al. 2008. Interactions between changing pCO_2, N_2 fixation, and Fe limitation in the marine unicellular cyanobacterium *Crocosphaera*. *Limnol. Oceanogr.* 53:2472–84

Gao K, Zheng Y. 2010. Combined effects of ocean acidification and solar UV radiation on photosynthesis, growth, pigmentation and calcification of the coralline alga *Corallina sessilis* (Rhodophyta). *Glob. Change Biol.* 16:2388–98

Gattuso JP, Frankignoulle EM, Wollast R. 1998. Carbon and carbonate metabolism in coastal aquatic systems. *Annu. Rev. Ecol. Syst.* 29:405–34

Gazeau F, Quibler C, Jansen JM, Gattuso J-P, Middelburg JJ, Heip CHR. 2007. Impact of elevated CO_2 on shellfish calcification. *Geophys. Res. Lett.* 34:L07603

Gienapp P, Teplitsky C, Alho JS, Mills JA, Merila J. 2008. Climate change and evolution: disentangling environmental and genetic responses. *Mol. Ecol.* 17:167–78

Gooding RA, Harley CDG, Tang E. 2009. Elevated water temperature and carbon dioxide concentration increase the growth of a keystone echinoderm. *Proc. Natl. Acad. Sci. USA* 106:9316–21

Guinotte JM, Orr J, Cairns S, Freiwald A, Morgan L, George R. 2006. Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? *Front. Ecol. Environ.* 4:141–46

Hauri C, Gruber N, Plattner G-K, Alin S, Feely RA, et al. 2009. Ocean acidification in the California current system. *Oceanography* 22:60–71

Havenhand JN, Buttler FR, Thorndyke MC, Williamson JE. 2008. Near-future levels of ocean acidification reduce fertilization success in a sea urchin. *Curr. Biol.* 18:R651–52

Hendriks IE, Duarte CM, Alvarez M. 2010. Vulnerability of marine biodiversity to ocean acidification: a meta-analysis. *Estuar. Coast. Shelf Sci.* 86:157–64

Hennige S, Suggett D, Warner M, McDougall K, Smith D. 2009. Photobiology of *Symbiodinium* revisited: bio-physical and bio-optical signatures. *Coral Reefs* 28:179–95

Herfort L, Thake B, Taubner I. 2008. Bicarbonate stimulation of calcification and photosynthesis in two hermatypic corals. *J. Phycol.* 44:91–98

Hétérier V, David B, De Ridder C, Rigaud T. 2008. Ectosymbiosis is a critical factor in the local benthic biodiversity of the Antarctic deep sea. *Mar. Ecol. Prog. Ser.* 364:67–76

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, et al. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–42

Hofmann GE, Todgham AE. 2010. Living in the now: physiological mechanisms to tolerate a rapidly changing environment. *Annu. Rev. Physiol.* 72:127–45

Hunt BPV, Pakhomov EA, Hosie GW, Siegel V, Ward P, Bernard K. 2008. Pteropods in Southern ocean ecosystems. *Prog. Oceanogr.* 78:193–221

Hutchins DA, Fu F-X, Zhang Y, Warner ME, Feng Y, et al. 2007. CO_2 control of *Trichodesmium* N_2 fixation, photosynthesis, growth rates, and elemental ratios: implications for past, present, and future ocean biogeochemistry. *Limnol. Oceanogr.* 52:1293–304

Hutchins DA, Mulholland MR, Fu F-X. 2009. Nutrient cycles and marine microbes in a CO_2-enriched ocean. *Oceanography* 22:128–45

Iglesias-Rodriguez MD, Halloran PR, Rickaby REM, Hall IR, Colmenero-Hidalgo E, et al. 2008. Phytoplankton calcification in a high-CO_2 world. *Science* 320:336–40

Jones A, Berkelsman R, van Oppen M, Mieog J, Sinclair W. 2008. A community change in the algal endosymbionts of a scleractinian coral following a natural bleaching event: field evidence of acclimatization. *Proc. R. Soc. B* 275:1359–65

Jury CP, Whitehead RF, Szmant AM. 2010. Effects of variations in carbonate chemistry on the calcification rates of *Madracis auretenra* (= *Madracis mirabilis* sensu Wells, 1973): bicarbonate concentrations best predict calcification rates. *Glob. Change Biol.* 16:1632–44

Kaiser S, Barnes DKA. 2008. Southern ocean deep-sea biodiversity: sampling strategies and predicting responses to climate change. *Clim. Res.* 37:165–79

Kleypas JA, Buddemeier RW, Archer D, Gattuso J-P, Langdon C, Opdyke BN. 1999. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284:118–20

Kurihara H. 2008. Effects of CO_2-driven ocean acidification on the early developmental stages of invertebrates. *Mar. Ecol. Prog. Ser.* 373:275–84

Kurihara H, Matsui M, Furukawa H, Hayashi M, Ishimatsu A. 2008. Long-term effects of predicted future seawater CO_2 conditions on the survival and growth of the marine shrimp *Palaemon pacificus*. *J. Exp. Mar. Biol. Ecol.* 367:41–46

Langdon C, Atkinson MJ. 2005. Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *J. Geophys. Res.* 110:C09S07

Langdon C, Takahashi T, Sweeney C, Chipman D, Goddard J, et al. 2000. Effect of calcium carbonate saturation state on the calcification rate of an experimental reef. *Glob. Biogeochem. Cycles* 14:639–54

Langer G, Geisen M, Baumann K-H, Klaus J, Riebesell U, et al. 2006. Species-specific responses of calcifying algae to changing seawater carbonate chemistry. *Geochem. Geophys. Geosyst.* 7:Q09006

Langer G, Nehrke G, Probert I, Ly J, Ziveri P. 2009. Strain-specific responses of *Emiliania huxleyi* to changing seawater carbonate chemistry. *Biogeosciences* 6:2637–46

Lebrato M, Iglesias-Rodriguez D, Feely R, Greeley D, Jones D, et al. 2010. Global contribution of echinoderms to the marine carbon cycle: a reassessment of the oceanic CaCO$_3$ budget and the benthic compartments. *Ecol. Monogr.* 80:441–67

Lombard F, da Rocha RE, Bijma J, Gattuso JP. 2010. Effect of carbonate ion concentration and irradiance on calcification in planktonic foraminifera. *Biogeosciences* 7:247–55

Maier C, Hegeman J, Weinbauer MG, Gattuso JP. 2009. Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. *Biogeosciences* 6:1671–80

Manzello DP. 2010. Ocean acidification hot spots: Spatiotemporal dynamics of the seawater CO$_2$ system of eastern Pacific coral reefs. *Limnol. Oceanogr.* 55:239–48

Martin S, Gattuso JP. 2009. Response of Mediterranean coralline algae in ocean acidification and elevated temperature. *Glob. Change Biol.* 15:2089–100

Marubini F, Ferrier-Pagès C, Furla P, Allemand D. 2008. Coral calcification responds to seawater acidification: a working hypothesis towards a physiological mechanism. *Coral Reefs* 27:491–99

McClintock JB, Angus RA, McDonald MR, Amsler CD, Catledge SA, Vohra YK. 2009. Rapid dissolution of shells of weakly calcified Antarctic benthic macroorganisms indicates high vulnerability to ocean acidification. *Antarct. Sci.* 21:449–56

McDonald MR, McClintock JB, Amsler CD, Rittschof D, Angus RA, et al. 2009. Effects of ocean acidification over the life history of the barnacle *Amphibalanus amphitrite*. *Mar. Ecol. Prog. Ser.* 385:179–87

McNeil BI, Matear RJ. 2008. Southern Ocean acidification: a tipping point at 450-ppm atmospheric CO$_2$. *Proc. Natl. Acad. Sci. USA* 105:18860–64

Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, et al. 2007. In *Climate Change 2007: The Physical Science Basis. Contribution Working Group I 4th Assessment Report of the Intergovernmental Panel in Climate Change*, ed. S Solomon, D Qin, M Manning, Z Chen, M Marquis, et al. pp. 747–845. Cambridge, UK: Cambridge Univ. Press

Melzner F, Gutowska MA, Langenbuch M, Dupont S, Lucassen M, et al. 2009. Physiological basis for high CO$_2$ tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? *Biogeosciences* 6:2313–31

Merico A, Tyrrell T, Lessard EJ, Oguz T, Stabeno PJ, et al. 2004. Modelling phytoplankton succession on the Bering Sea shelf: role of climate influences and trophic interactions in generating *Emiliania huxleyi* blooms 1997–2000. *Deep-Sea Res. I* 51:1803–26

Miles EL. 2009. On the increasing vulnerability of the world ocean to multiple stresses. *Annu. Rev. Environ. Resour.* 34:17–41

Miller AW, Reynolds AC, Sobrino C, Riedel GF. 2009. Shellfish face uncertain future in high CO$_2$ world: influence of acidification on oyster larvae calcification and growth in estuaries. *PLoS One* 4:e5661

Moran NA. 2007. Symbiosis as an adaptive process and source of phenotypic complexity. *Proc. Natl. Acad. Sci. USA* 104:8627–33

Moy AD, Howard WR, Bray SG, Trull TW. 2009. Reduced calcification in modern Southern Ocean planktonic foraminifera. *Nat. Geosci.* 2:276–80

Müller R, Laepplea T, Bartsch I, Wiencke C. 2009. Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. *Bot. Mar.* 52:617–38

Munday PL, Dixson DL, Donelson JM, Jones GP, Pratchett MS, et al. 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proc. Natl. Acad. Sci. USA* 106:1848–52

Ohde S, van Woesik R. 1999. Carbon dioxide flux and metabolic processes of a coral reef, Okinawa. *Bull. Mar. Sci.* 65:559–76

Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, et al. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681–86

Pane EF, Barry JP. 2007. Extracellular acid-base regulation during short-term hypercapnia is effective in a shallow-water crab, but ineffective in a deep-sea crab. *Mar. Ecol. Prog. Ser.* 334:1–9

Pearse J, McClintock JB, Bosch I. 1991. Reproduction of Antarctic benthic marine invertebrates: tempos, modes and timing. *Am. Zool.* 31:65–80

Pelejero C, Calvo E, McCulloch MT, Marshall JF, Gagan MK, et al. 2005. Preindustrial to modern inter-decadal variability in coral reef pH. *Science* 309:2204–7

Pörtner HO. 2008. Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. *Mar. Ecol. Prog. Ser.* 373:203–17

Pörtner HO, Langenbuch M, Michaelidis B. 2005. Synergistic effects of temperature extremes, hypoxia, and increases in CO_2 on marine animals: from Earth history to global change. *J. Geophys. Res.* 110:C09S10

Powell DK, Tyler PA, Peck LS. 2001. Effect of sperm concentration and sperm ageing on fertilisation success in the Antarctic soft-shelled clam *Laternula elliptica* and the Antarctic limpet *Nacella concinna*. *Mar. Ecol. Prog. Ser.* 215:191–200

Przeslawski R, Ahyong S, Byrne M, Worheide G, Hutchings P. 2008. Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. *Glob. Change Biol.* 14:2773–95

Ridgwell A, Schmidt DN, Turley C, Brownlee C, Maldonado MT, et al. 2009. From laboratory manipulations to Earth system models: scaling calcification impacts of ocean acidification. *Biogeosciences* 6:2611–23

Riebesell U, Zondervan I, Rost B, Tortell PD, Zeebe RE, Morel FMM. 2000. Reduced calcification of marine plankton in response to increased atmospheric CO_2. *Nature* 407:364–67

Ries JB. 2005. Aragonite production in calcite seas: effect of seawater Mg/Ca ratio on the calcification and growth of the calcareous alga *Penicillus capitatus*. *Paleobiology* 31:445–58

Ries JB, Cohen AL, McCorkle DC. 2009. Marine calcifiers exhibit mixed responses to CO_2-induced ocean acidification. *Geology* 37:1131–34

Roark E, Guilderson TP, Dunbar RB, Fallon SJ, Mucciarone DA. 2009. Extreme longevity in proteinaceous deep-sea corals. *Proc. Natl. Acad. Sci. USA* 106:5204–8

Roberts J, Wheeler AJ, Freiwald A, Cairns S. 2009. *Cold-Water Corals*. Cambridge, UK: Cambridge Univ. Press. 334 pp.

Rosa R, Seibel BA. 2008. Synergistic effects of climate-related variables suggest future physiological impairment in an oceanic predator. *Proc. Natl. Acad. Sci. USA* 105:20776–80

Rost B, Riebesell U, Burkhardt S, Sültemeyer D. 2003. Carbon acquisition of bloom-forming marine phytoplankton. *Limnol. Oceanogr.* 48:55–67

Ruckelshaus M, Klinger T, Knowlton N, DeMaster DP. 2008. Marine ecosystem-based management in practice: scientific and governance challenges. *BioScience* 58:53–63

Russell AD, Honisch B, Spero HJ, Lea DW. 2004. Effects of seawater carbonate ion concentration and temperature on shell U, Mg, and Sr in cultured planktonic foraminifera. *Geochim. Cosmochim. Acta* 68:4347–61

Salisbury J, Green M, Hunt C, Campbell J. 2008. Coastal acidification by rivers: a threat to shellfish? *Eos* 89:513–28

Sciandra A, Harlay J, Lefevre D, Lemee R, Rimmelin P, et al. 2003. Response of coccolithophorid *Emiliania huxleyi* to elevated partial pressure of CO_2 under nitrogen limitation. *Mar. Ecol. Prog. Ser.* 261:111–22

Seibel BA, Drazen JC. 2007. The rate of metabolism in marine animals: environmental constraints, ecological demands and energetic opportunities. *Philos. Trans. R. Soc. B* 362:2061–78

Seibel BA, Walsh PJ. 2003. Biological impacts of deep-sea carbon dioxide injection inferred from indices of physiological performance. *J. Exp. Biol.* 206:641–50

Shi D, Xu Y, Morel FMM. 2009. Effects of the pH/pCO_2 control method on medium chemistry and phytoplankton growth. *Biogeosciences* 6:1199–207

Siegenthaler U, Stocker T, Monnin E, Lüthi D, Schwander J, et al. 2005. Stable carbon cycle-climate relationship during the late Pleistocene. *Science* 310:1313–17

Silverman J, Lazar B, Cao L, Caldiera K, Erez J. 2009. Coral reefs may start dissolving when atmospheric CO_2 doubles. *Geophys. Res. Lett.* 36:L05606

Smith JB, Schneider SH, Oppenheimer M, Yohe GW, Hare W, et al. 2009. Assessing dangerous climate change through an update of the Intergovernmental Panel on Climate Change (IPCC) "reasons for concern". *Proc. Natl. Acad. Sci. USA* 106:4133–37

Stat M, Carter D, Hoegh-Guldberg O. 2006. The evolutionary history of *Symbiodinium* and scleractinian hosts—symbiosis, diversity, and the effect of climate change. *Perspect. Plant Ecol. Evol. Syst.* 8:23–43

Steinacher M, Joos F, Frölicher TL, Plattner GK, Doney SC. 2009. Imminent ocean acidification in the Arctic projected with the NCAR global coupled carbon cycle-climate model. *Biogeosciences* 6:515–33

Swanson AK, Fox CH. 2007. Altered kelp (Laminariales) phlorotannins and growth under elevated carbon dioxide and UV-B treatments can influence associated intertidal food webs. *Glob. Change Biol.* 13:1696–709

Talmage SC, Gobler CJ. 2009. The effects of elevated carbon dioxide concentrations on the metamorphosis, size and survival of larval hard clams (*Mercenaria mercenaria*), bay scallops (*Argopecten irradians*), and Eastern oysters (*Crassostrea virginica*). *Limnol. Oceanogr.* 54:2072–80

Tambutté E, Allemand D, Zoccola D, Meibom A, Lotto S, et al. 2007. Observations of the tissue-skeleton interface in the scleractinian coral *Stylophora pistillata*. *Coral Reefs* 26:517–29

Todgham AE, Hofmann GE. 2009. Transcriptomic response of sea urchin larvae, *Strongylocentrotus purpuratus*, to CO_2-driven seawater acidification. *J. Exp. Biol.* 212:2579–94

Tunnicliffe V, Davies KTA, Butterfield DA, Embley RW, Rose JM, Chadwick WW Jr. 2009. Survival of mussels in extremely acidic waters on a submarine volcano. *Nat. Geosci.* 2:344–48

Turner J, Overland J. 2009. Contrasting climate change in the two polar regions. *Polar Res.* 28:146–64

Venn AA, Tambutté E, Lotto S, Zoccola D, Allemand D, Tambutté S. 2009. Imaging intracellular pH in a reef coral and symbiotic anemone. *Proc. Natl. Acad. Sci. USA* 106:16574–79

Veron JEN, Hoegh-Guldberg O, Lenton TM, Lough JM, Obura DO, et al. 2009. The coral reef crisis: the critical importance of <350 ppm CO_2. *Mar. Pollut. Bull.* 58:1428–36

Visser ME. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc. R. Soc. B* 275:649–59

Wood HL, Spicer JI, Widdicombe S. 2008. Ocean acidification may increase calcification rates, but at a cost. *Proc. R. Soc. B* 275:1767–73

Wootton JT, Pfister CA, Forester JD. 2008. Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. *Proc. Natl. Acad. Sci. USA* 105:18848–53

Yamamoto-Kawai M, McLaughlin FA, Carmack EC, Nishino S, Shimada K. 2009. Aragonite undersaturation in the Arctic Ocean: effects of ocean acidification and sea ice melt. *Science* 326:1098–100

Zondervan I. 2007. The effects of light, macronutrients, trace metals and CO_2 on the production of calcium carbonate and organic carbon in coccolithophores–a review. *Deep-Sea Res. II* 54:521–37