The Threat of Acidification to Ocean Ecosystems

By John Guinotte and Victoria J. Fabry

SEAWATER CHEMISTRY IS CHANGING RAPIDLY BECAUSE HUMANS ARE *burning fossil fuels and releasing carbon dioxide into the atmosphere at unprecedented levels. Since the Industrial Revolution, the oceans have become 30% more acidic and are predicted to become up to 150% more acidic by the end of this century. These chemical changes are occurring so rapidly that many marine species, particularly those that build structures out of calcium carbonate, may have a difficult time adapting quickly enough to survive these changes. This paper reviews known responses of select marine organisms to ocean acidification and potential ecosystem-level impacts.*

THE PROBLEM OF HIGH CO_2

For the past 200 years, the rapid increase in atmospheric CO_2 has been, and continues to be, caused by the burning of fossil fuels (e.g., oil and gas), deforestation, industrialization, cement production, and other land-use changes. The oceans absorb much of this excess CO_2 through air-sea gas exchange, which results in changes in seawater chemistry (through changes in the partial pressure of CO_2, pH, alkalinity, and calcium carbonate saturation states). Ocean acidification describes the relative decrease in seawater pH that is caused by oceanic uptake of specific compounds from the atmosphere. Today, the overwhelming cause of ocean acidification is the absorption of human produced CO_2, although in some coastal regions, nitrogen and sulfur are also important (Doney et al. 2007).

Presently, atmospheric CO_2 concentration is approximately 383 parts per million by volume (ppmv), and is projected to increase by 0.5% per year throughout the 21st century, a rate of change that is approximately 100-times faster than has occurred in the past 650,000 years (Meehl et al. 2007). In recent decades, only half of human-produced CO_2 has remained in the atmosphere, the other half has been taken up by the terrestrial biosphere (ca. 20%) and the oceans (ca. 30%) (Sabine et al. 2004). This increase in atmospheric CO_2 has caused a decrease in seawater pH. Since the Industrial Revolution, a time span of less than 250 years, the pH of surface oceans has dropped by 0.1 pH units and is projected to drop another 0.3-0.4 pH units by the end of this century (Figure 1) (Feely et al. 2008).

The absorption of excess atmospheric CO_2 impacts the ocean's carbonate system with important consequences for calcifying marine plants and animals. Many marine organisms use carbonate minerals ($CaCO_3$) to form shells, skeletons, and tests, including crustose coralline algae, planktonic organisms (e.g., foraminifera, coccolithophores, and pteropods), warm-water corals, cold-water corals, and a range of benthic organisms (e.g., oysters, clams, sea urchins, and sea stars). When carbon dioxide dissolves in seawater, it forms carbonic acid and several dissociation products (Figure 2). The net effect of changes in this chemical equilibrium (driven by increased absorption of CO_2) is both an increase in the acidity of seawater and a decrease in the availability of carbonate ions, which make it more difficult for marine organisms to build and maintain carbonate structures.

The impacts of these changes in seawater chemistry are further complicated by ocean temperature. The solubility of both calcite and aragonite (which are different forms of calcium carbonate used by marine organisms) is affected by the amount of CO_2 in seawater, which is partially determined by temperature: colder waters naturally hold more CO_2 and are more acidic than warmer waters. The sum of these differences leads to "saturation horizons" in the oceans, which represent the transition depth between waters that are either under- or over-saturated

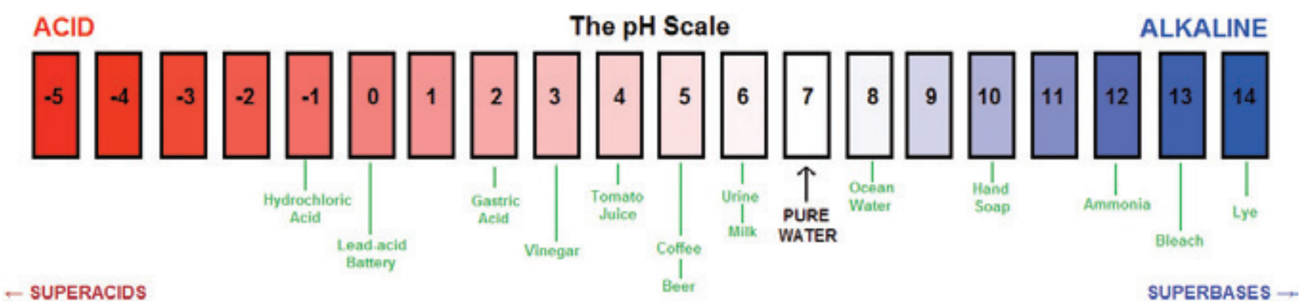


Figure 1. The pH scale. The pH scale is logarithmic, and as a result, each whole unit decrease in pH is equal to a 10-fold increase in acidity. Ocean surface water now has an average pH of 8.1 and is predicted to decrease rapidly with projected rises in atmospheric CO_2.

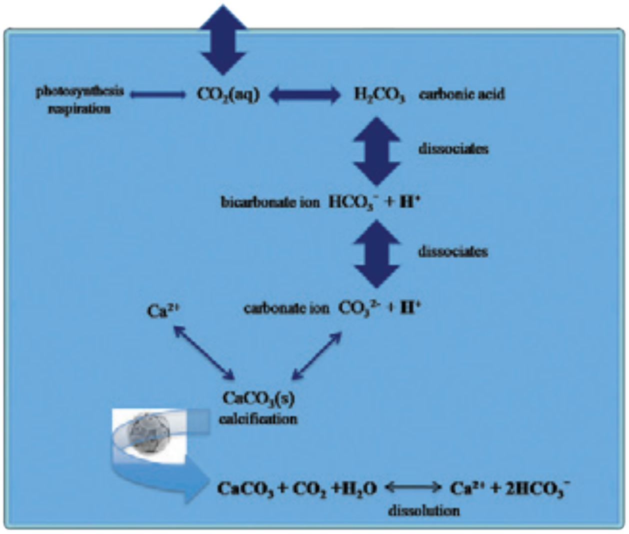


Figure 2. Simplified diagram of the seawater carbonate system. Carbonate chemistry in the oceans involves a complex series of chemical equilibria that are driven by the concentration of various carbon species and are influenced by factors such as temperature and pressure. The dissolution of CO_2 into seawater generates carbonic acid which, in turn, dissociates to release hydrogen ions (H^+). In addition to reducing pH, the excess hydrogen ions bind with available carbonate ions (CO_3^{2-}), thereby reducing the bioavailability of this compound for marine organisms and favoring the dissolution of existing carbonate structures. The net effect of these changes is more corrosive seawater (due to a lowering of pH) and a decrease in the carbonate saturation state of the waters decrease (making it more difficult for organisms to build and maintain carbonate structures).

with respect to calcite and aragonite. In areas that are undersaturated, calcite and aragonite will tend to dissolve. The depth of the ocean's aragonite and calcite saturation horizons determines where calcium carbonate formation by marine organisms is favored (above the saturation horizon) and where dissolution will occur (below the saturation horizon).

The aragonite and calcite saturation horizons of the world's oceans are becoming shallower (i.e., shoaling) due to the rapid uptake of human-produced CO_2 (Feely et al. 2004). Future estimates of aragonite saturation horizon depth, for example, indicate that shoaling will occur in the North Pacific and Southern Ocean within the century (Orr et al. 2005). Many of these areas are highly productive and support some of the world's most important and economically lucrative commercial fisheries.

ACIDIFICATION MAY SPELL TROUBLE FOR MANY CALCIFYING PLANTS AND ANIMALS

Warm-water reef-building corals: The calcification (or growth) response of reef-building corals to ocean acidification has been documented for a handful of species. Current evidence indicates that the calcification rates of warm-water corals will be reduced by 20-60% at double preindustrial atmospheric CO_2 concentrations (Kleypas et al. 2006). A reduction in calcification of this magnitude could fundamentally alter reef structure (and ultimately, its function as habitat), as growth is dependent on the ability of reef-building corals to accrete (build skeleton) at rates faster than erosional processes can break them down. Weaker coral skeletons will probably result from decreasing aragonite saturation states, which makes the colonies more susceptible to storms and heavy wave action, and increases the erosion rate of the reef foundation (Kleypas et al. 2006).

Crustose coralline algae: Corals are not the only calcifying organisms that are sensitive to ocean acidification. Crustose coralline algae are a critical player in the ecology of coral-reef systems as they provide the "cement" that helps stabilize reefs and are important food sources for sea urchins, parrot fish, and several species of mollusks (Figure 3; Littler and Littler 1984). Laboratory experiments exposing these algae to elevated CO_2 (two-times present-day values), indicated up to a 40% reduction in growth rates, a 78% decrease in recruitment of new larvae, and a 92% reduction in areal coverage (Kuffner et al. 2007).

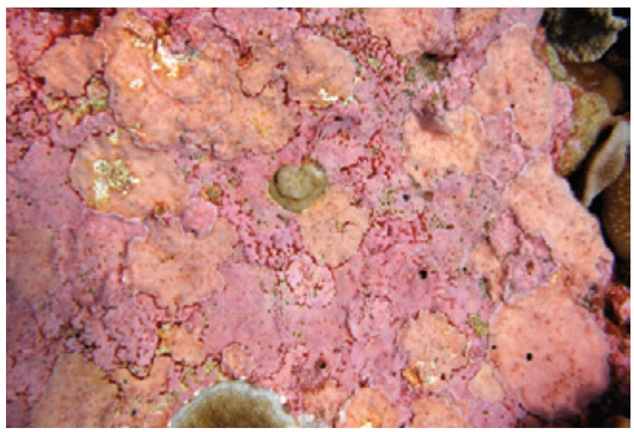


Figure 3. Crustose coralline algae with a new coral recruit (see center of photo). Crustose coralline algae are ubiquitous red algae that belong to the division Rhodophyta in the order of Corallinales. It is common in rocky tidal areas and in coral reef communities, where it provides food for invertebrates and some fish, and serves as a form of biological "cement." Crustose coralline algae are some of the first organisms to appear on exposed hard substrate, and studies have shown that coral larvae use its presence as a cue to settle and form new colonies. This suggests that these calcified algae are indicators of good habitat for reef corals.

Cold-water corals: Cold-water corals are found throughout the world's oceans and can form biologically-rich ecosystems that provide habitat and nursery areas for many deep-sea organisms, including several commercially-important fish species (Figure 4; see *Current*, Vol. 21, No. 4, 2005, special edition on Deep-sea corals). These ecosystems are bathed in waters that have naturally high levels of CO_2; however, more than 95% of cold-water coral reefs occur in waters that are supersaturated with respect to aragonite. Future projections of ocean acidification, however, indicate that 70% of cold-water corals could experience corrosive water conditions by the end of the century (Guinotte et al. 2006).

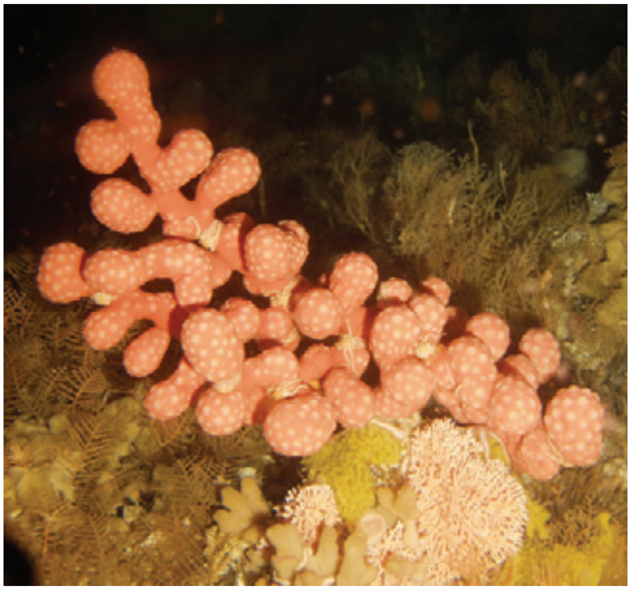


Figure 4. Bubblegum coral in the waters off Alaska. Bubblegum corals (*Paragoria* spp.) are cold water corals that inhabit the deep waters of the oceans, well beyond the reach of sunlight. Although they belong to the same phylum (*Cnidaria*) as tropical corals, cold water corals lack symbiotic algae and instead use their small tentacles to feed on plankton and drifting pieces of organic material. Slow growing and incredibly long lived (200 years+), these ancient animals are easily damaged by human activities and are at risk from ocean acidification.

Figure 5. Blue mussel bed in the intertidal of the coast of Cornwall England. The blue mussel (*Mytilus edulis*) is a ubiquitous member of intertidal communities in temperate and polar waters around the world. Able to withstand the dramatically fluctuating conditions of the intertidal realm, blue mussels often form dense mussel beds that provide important physical habitat for a range of other intertidal organisms and serve as an important source of food for intertidal predators such as starfish and dogwhelk. Blue mussels are an important source of food for humans, too, as mussel middens have been found in kitchens dating back to 6000 B.C.

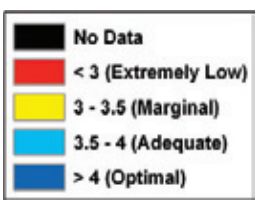
Benthic invertebrates: The effects of CO_2 on benthic invertebrates such as mollusks and echinoderms are currently not well known. Gazeau and colleagues (2007) found that calcification rates of the mussel (*Mytilus edulis*) and Pacific oyster (*Crassostrea gigas*) can be expected to decline by 25% and 10% respectively, by the end of the century. Both species are important to coastal ecosystems and represent a significant portion of global aquaculture production (Figure 5; Gazeau et al. 2007). Early life stages of these species appear to be more sensitive to environmental disturbances than adults. For example, Kurihara et al. (2004) found that ocean acidification affects the fertilization rates of sea urchin embryos and the size and formation of sea urchin larvae.

Plankton: Marine plankton are an important part of the marine food chain upon which all other life in the ocean depends. Several important plankton groups produce calcium carbonate, including coccolithophores (single-celled algae), foraminifera (protists), and pteropods (planktonic snails). The likely effect of ocean acidification has been investigated in only a few species. Experiments with coccolithophores (Figure 6) have demonstrated decreases in calcification rates ranging from 25-66% (associated with partial pressure values of CO_2 of 560 and 840 ppmv, respectively). However, in experiments with *Coccolithus pelagicus*, Langer et al. (2006) found that calcification did not change appreciably with increased CO_2. Further complicating the issue, experiments with *Calcidiscus leptoporus* suggest that this coccolithophore has the highest calcification rates at present-day CO_2 levels, with malformed structures at both lower and higher CO_2 levels (Langer et al. 2006). In lab experiments with two species of foraminifera, shell mass decreased as water became more acidic (Spero et al. 1997; Bijma et al. 1999), while data for shelled pteropods suggest that shell dissolution occurs in live pteropods within 48 hours under high CO_2 conditions (Fabry et al. 2008).

Figure 6a. This is a scanning electron micrograph of a coccolithophore, (*Coccolithus pelagicus*), which is a single-celled marine planktonic alga that creates a calcified shield as a series of ornate plates. These tiny creatures (usually 10-40 μm diameter and much smaller than a grain of sand) are important primary producers in open ocean ecosystems.

Figure 6b. Coccolithophore bloom in English Channel off the coast of Cornwall. Despite their small individual size, blooms of coccolithophores can be extensive, as illustrated by this LANDSAT satellite image. The species responsible for this bloom is *Emiliana huxleyi*, a common and widespread (cosmopolitan) coccolithophore. The shedding of coccoliths into the surface water scatters sunlight, yielding the milky-white turquoise color of the waters seen here, which were called "white waters" by seafarers.

Interestingly, the response of planktonic calcifying organisms to acidifying waters may not be uniform among species or over time. Although current research indicates that most calcareous plankton have reduced calcification in response to higher CO_2 conditions, these have been short-term experiments, ranging from hours to weeks. Little is known about the long-term impacts of chronically high CO_2, and such experiments may yield complex effects on the growth and reproduction or may induce adaptations that are absent from short-term experiments.



PHYSIOLOGICAL RESPONSES OF MARINE ORGANISMS TO HIGHER CO_2

In addition to impacts on calcification processes, elevated concentrations of CO_2 in seawater affects the physiology of certain marine organisms. In water-breathing animals such as fish, ocean acidification may reduce the pH of tissues and body fluids resulting in short-term effects on respiration, blood circulation, and nervous system functions and long-term effects on metabolism, growth, and reproduction (Ishimatsu et al. 2004, 2005). Fish in early developmental stages are more sensitive to environmental change than adults, and a small number of studies have shown an adverse negative effect of acidified seawater on fish throughout their entire life cycle (eggs, larvae, juveniles, and adults: Ishimatsu et al. 2004).

Not all marine organisms will be negatively impacted by elevated seawater CO_2. Short-term experiments with eelgrass indicate that elevated CO_2 increased photosynthetic rates and reduced light requirements (Zimmerman et al. 1997). Longer-term (one year) experiments exposing seagrasses to high CO_2 concentrations resulted in higher reproduction when light was in abundant supply (Palacios and Zimmerman 2007).

COMMUNITY-LEVEL IMPACTS

Seagrasses, coral reefs, and fishes: Seagrass meadows and mangroves provide important nursery areas for juvenile fishes, many of which migrate to coral reefs as adults, and enhance fish diversity and abundance on coral reefs adjacent to these ecosystems (Mumby et al. 2004; Dorenbosch et al. 2005). The net effect of increasing CO_2 on seagrass ecosystems will probably be increased seagrass biomass and productivity. It is probable that an increase in total seagrass area will lead to more favorable habitat and conditions for associated invertebrate and fish species. However, the net effect of ocean acidification on coral reef ecosystems will probably be negative as many warm-water corals will be heavily impacted by the combined effects of increasing sea-surface temperatures (coral bleaching) and decreasing carbonate saturation states of surface waters in the coming decades (Figure 7) (Guinotte et al. 2003). The magnitude of both ecosystem responses to ocean acidification and other environmental changes working together is difficult to predict as are the effects on fish populations and diversity. Predicting the net effects on fish populations is further complicated by the great number of unknowns surrounding the

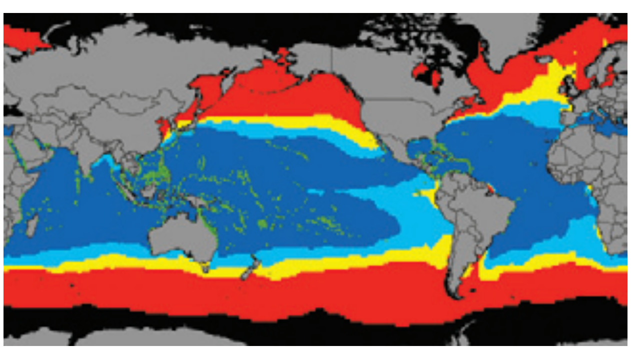


Figure 7a. Surface aragonite saturation state calculated for pre-industrial (year 1870) values of atmospheric CO_2 (280 ppmv). Green dots represent present-day distribution of shallow coral reefs.

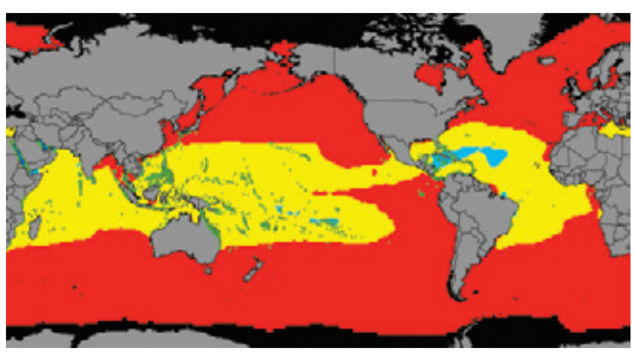


Figure 7b. Surface aragonite saturation state projected for expected increase in atmospheric CO_2 (517 ppmv) for years 2060-2069.

long-term effects of increasing CO_2 on fish physiology, metabolism, and probable shifts in their ranges from ocean warming.

Cold-water corals and fishes: The ecology and species relationships of cold-water coral ecosystems are not as advanced as the state of knowledge for warm-water coral reef systems; however, cold-water coral ecosystems are thought to provide important habitat, feeding grounds, and nursery functions for many deep-water species, including several commercially-important fish species (Mortensen 2000; Fossa et al. 2002). Ocean acidification could have significant effects on fishes and other deep-sea organisms that rely on cold-water coral ecosystems for protection and nutritional requirements. Documenting ocean acidification impacts on coral-associated fishes will be difficult because the ecology of these systems is not well known, but the net effects are likely to be negative as cold-water coral growth, distribution, and area decrease with increasing ocean acidification. Understanding coral-fish associations and the sensitivity of cold water corals to ocean acidification are top priorities for future research.

Plankton: If reduced calcification decreases a calcifying organism's fitness or survivorship, then some planktonic species may undergo shifts in their distributions as ocean acidification progresses. Calcifying species that are sensitive to CO_2 could potentially be replaced by noncalcifying species and/or those species that are not sensitive to elevated pCO_2. If high-latitude surface waters become increasingly more acidic as predicted, pteropods could eventually be eliminated from some regions, with consequences to food web dynamics and other ecosystem processes (Fabry et al. 2008). In the subarctic Pacific, for example, pteropods can be important prey for juvenile pink salmon, as well as chum and sockeye salmon, pollock, and other commercially-important fishes (Aydin pers. comm.). Because Pacific pink salmon have a short, two-year life cycle, prey quality and abundance during the salmon's juvenile stage may strongly influence the pink salmon's adult population size and biomass (Aydin et al. 2005). Ocean acidification may also favor undesirable species. Attrill et al. (2007) reported a significant correlation of increasing jellyfish numbers in the North Sea from 1971-1995 with decreased pH of surface waters and suggest that projected climate change and declining ocean pH will cause jellyfish numbers to increase over the next century. Jellyfish are both predators and potential competitors of fish and may substantially affect ocean ecosystems (Purcell et al. 2007).

CONCLUSIONS

The scientific knowledge base surrounding the biological effects of ocean acidification is in its infancy and the long-term consequences of changing seawater chemistry on marine ecosystems can only be theorized. Most is known about the calcification response for warm-water corals. The potential effects of ocean acidification on the vast majority of marine species are not known. Research into the combined effects of ocean acidification and other human induced environmental changes (e.g., increasing sea temperatures) on marine food webs and the potential transformative effects these changes could have on marine ecosystems is urgently needed. It is important to have a firm understanding of the degree to which ocean acidification influences critical physiological processes such as respiration, photosynthesis, and nutrient dynamics, as these processes are important drivers of calcification, ecosystem structure, biodiversity, and ultimately the health of the ocean.

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Figure 7a: Modified from Guinotte et al. (2003)
Figure 7a-7b Legend: Classification from Kleypas et al. (1999b)