

Ocean Acidification and Its Potential Effects on Marine Ecosystems

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Ocean acidification is rapidly changing the carbonate system of the world oceans. Past mass extinction events have been linked to ocean acidification, and the current rate of change in seawater chemistry is unprecedented. Evidence suggests that these changes will have significant consequences for marine taxa, particularly those that build skeletons, shells, and tests of biogenic calcium carbonate. Potential changes in species distributions and abundances could propagate through multiple trophic levels of marine food webs, though research into the long-term ecosystem impacts of ocean acidification is in its infancy. This review attempts to provide a general synthesis of known and/or hypothesized biological and ecosystem responses to increasing ocean acidification. Marine taxa covered in this review include tropical reef-building corals, cold-water corals, crustose coralline algae, *Halimeda*, benthic mollusks, echinoderms, coccolithophores, foraminifera, pteropods, seagrasses, jellyfishes, and fishes. The risk of irreversible ecosystem changes due to ocean acidification should enlighten the ongoing CO₂ emissions debate and make it clear that the human dependence on fossil fuels must end quickly. Political will and significant large-scale investment in clean-energy technologies are essential if we are to avoid the most damaging effects of human-induced climate change, including ocean acidification.

Key words: ocean acidification; climate change; carbonate saturation state; seawater chemistry; marine ecosystems; anthropogenic CO₂

Introduction

The carbonate system (pCO₂, pH, alkalinity, and calcium carbonate saturation state) of the world oceans is changing rapidly due to an influx of anthropogenic CO₂ (Skirrow & Whitfield 1975; Whitfield 1975; Broecker & Takahashi 1977; Broecker *et al.* 1979; Feely & Chen 1982; Feely *et al.* 1984; Kleypas *et al.* 1999a; Caldeira & Wickett 2003; Feely *et al.* 2004; Orr *et al.* 2005). Ocean acidification may be defined as the change in ocean chemistry driven by the oceanic uptake of chemical inputs to the atmosphere, including carbon, nitrogen, and sulfur compounds. Today, the

overwhelming cause of ocean acidification is anthropogenic atmospheric CO₂, although in some coastal regions, nitrogen and sulfur are also important (Doney *et al.* 2007). For the past 200 years, the rapid increase in anthropogenic atmospheric CO₂, which directly leads to decreasing ocean pH through air–sea gas exchange, has been and continues to be caused by the burning of fossil fuels, deforestation, industrialization, cement production, and other land-use changes. The current rate at which ocean acidification is occurring will likely have profound biological consequences for ocean ecosystems within the coming decades and centuries.

Presently, atmospheric CO₂ concentration is approximately 383 parts per million by volume (ppmv), a level not seen in at least 650,000 years, and it is projected to increase by 0.5% per year

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throughout the 21st century (Petit *et al.* 1999; Houghton *et al.* 2001; Augustin *et al.* 2004; Siegenthaler *et al.* 2005; Meehl *et al.* 2007). The rate of current and projected increases in atmospheric CO₂ is approximately 100× faster than has occurred in at least 650,000 years (Siegenthaler *et al.* 2005). In recent decades, only half of anthropogenic CO₂ has remained in the atmosphere; the other half has been taken up by the terrestrial biosphere (ca. 20%) and the oceans (ca. 30%) (Feely *et al.* 2004; Sabine *et al.* 2004). Since the Industrial Revolution, a time span of less than 250 years, the pH of surface oceans has dropped by 0.1 pH units (representing an approximately 30% increase in hydrogen ion concentration relative to the preindustrial value) and is projected to drop another 0.3–0.4 pH units by the end of this century (Mehrbach *et al.* 1973; Lueker *et al.* 2000; Caldeira & Wickett 2003; Caldeira *et al.* 2007; Feely *et al.* 2008). [Note: The pH scale is logarithmic, and as a result, each whole unit decrease in pH is equal to a 10-fold increase in acidity.] A pH change of the magnitude projected by the end of this century probably has not occurred for more than 20 million years of Earth's history (Feely *et al.* 2004). The rate of this change is cause for serious concern, as many marine organisms, particularly those that calcify, may not be able to adapt quickly enough to survive these changes.

A series of chemical reactions is initiated when CO₂ is absorbed by seawater. Ω is the calcium carbonate saturation state:

$$\Omega = [\text{Ca}^{2+}][\text{CO}_3^{2-}]/K_{\text{sp}}^*$$

where K_{sp}^* is the stoichiometric solubility product for CaCO₃ and [Ca²⁺] and [CO₃²⁻] are the *in situ* calcium and carbonate concentrations, respectively. The end products of these reactions are an increase in hydrogen ion concentration (H⁺), which lowers pH (making waters more acidic), and a reduction in the number of carbonate ions (CO₃²⁻) available. This reduction in carbonate ion concentration also leads to a reduction in calcium carbonate saturation state (Ω), which has significant impacts

on marine calcifiers. Table 1 lists carbon system parameters and temperature changes for surface waters based on the Intergovernmental Panel on Climate Change (IPCC) IS92a CO₂ emission scenario.

A reduction in the number of carbonate ions available will make it more difficult and/or require marine calcifying organisms to use more energy to form biogenic calcium carbonate (CaCO₃). Many marine organisms form biogenic calcium carbonate including: crustose coralline algae (the primary cementer that makes coral reef formation possible), *Halimeda* (macroalgae), foraminifera, coccolithophores, tropical reef-building corals, cold-water corals, bryozoans, mollusks, and echinoderms. The majority of marine calcifiers tested to date are sensitive to changes in carbonate saturation state and have shown declines in calcification rates in laboratory and mesocosm studies (Table 2). These organisms are affected and will continue to be affected by ocean acidification, but less well known are the ecosystem impacts on higher trophic-level organisms that rely on these calcifiers for shelter, nutrition, and other core functions.

Decreasing pH is not the only effect on the inorganic carbon system in seawater that results from the ocean's uptake of anthropogenic CO₂. Calcite and aragonite are the major biogenically formed carbonate minerals produced by marine calcifiers, and the stability of both minerals is affected by the amount of CO₂ in seawater, which is partially determined by temperature. Colder waters naturally hold more CO₂ and are more acidic than warmer waters. The depths of the aragonite and calcite saturation horizons are important to marine calcifiers because the depth of these horizons determines the limit at which precipitation of biogenic calcium carbonate by marine organisms is favored (shallower than the saturation horizon) and at which they will experience dissolution (deeper than the saturation horizons) in the absence of protective mechanisms.

TABLE 1. Projected changes in surface ocean carbonate chemistry based on IPCC IS92a CO₂ emission scenario (Houghton *et al.* 2001)^a

Parameter	Symbol	Unit	Glacial	Preindustrial	Present	2 × CO ₂	3 × CO ₂
Temperature	T	°C	15.7	19	19.7	20.7	22.7
Salinity	S		35.5	34.5	34.5	34.5	34.5
Total alkalinity	A _T	μmol kg ⁻¹	2356	2287	2287	2287	2287
pCO ₂ in seawater	pCO ₂	μatm	180	280	380	560	840
			(-56)	(0)	(35.7)	(100)	(200)
Carbonic acid	H ₂ CO ₃	μmol kg ⁻¹	7	9	13	18	25
			(-29)	(0)	(44)	(100)	(178)
Bicarbonate ion	HCO ₃ ⁻	μmol kg ⁻¹	1666	1739	1827	1925	2004
			(-4)	(0)	(5)	(11)	(15)
Carbonate ion	CO ₃ ²⁻	μmol kg ⁻¹	279	222	186	146	115
			(20)	(0)	(-16)	(-34)	(-48)
Hydrogen ion	H ⁺	μmol kg ⁻¹	4.79 × 10 ⁻³	6.92 × 10 ⁻³	8.92 × 10 ⁻³	1.23 × 10 ⁻²	1.74 × 10 ⁻²
			(-45)	(0)	(29)	(78)	(151)
Calcite saturation	Ω _{calc}		6.63	5.32	4.46	3.52	2.77
			(20)	(0)	(-16)	(-34)	(-48)
Aragonite saturation	Ω _{arag}		4.26	3.44	2.9	2.29	1.81
			(19)	(0)	(-16)	(-33)	(-47)
Dissolved inorganic carbon	DIC	μmol kg ⁻¹	1952	1970	2026	2090	2144
			(-1)	(0)	(2.8)	(6.1)	(8.8)
Total pH	pH _T		8.32	8.16	8.05	7.91	7.76

^aWe assume that PO₄ = 0.5 μmol L⁻¹ and Si = 4.8 μmol L⁻¹, and use the carbonic acid dissociation constants of Mehrbach *et al.* (1973) as refit by Dickson and Millero (1987). pH_T is based on seawater scale. Percent change from preindustrial values are in parentheses. After Feely *et al.* (2008).

The aragonite and calcite saturation horizons of the world's oceans are moving to shallower depths due to the rapid influx of anthropogenic CO₂ to the oceans (Fig. 1). This process has been well documented and modeled at the global scale (Skirrow & Whitfield 1975; Broecker & Takahashi 1977; Feely & Chen 1982; Feely *et al.* 1984, 1988; Kleypas *et al.* 1999a; Broecker 2003; Caldeira & Wickett 2003; Feely *et al.* 2004; Caldeira & Wickett 2005; Orr *et al.* 2005). Future estimates of aragonite saturation horizon depth indicate that shoaling will occur in the North Pacific, North Atlantic, and Southern Ocean within the century (Orr *et al.* 2005). The aragonite and calcite saturation horizons in the North Pacific are currently very shallow (Feely *et al.* 2004) and are moving toward the surface at a rate of 1–2 m per year (R.A. Feely pers. comm. 2007).

Many of the areas where shoaling is predicted to occur within the century are highly productive and home to many of the world's most important and economically lucrative commercial fisheries.

It is clear that human-induced changes in atmospheric CO₂ concentrations are fundamentally altering ocean chemistry from the shallowest waters to the darkest depths of the deep sea. The chemistry of the oceans is approaching conditions not seen in many millions of years, and the rate at which this is occurring is unprecedented (Caldeira & Wickett 2003). Caldeira and Wickett (2003, p. 365) state "Unabated CO₂ emissions over the coming centuries may produce changes in ocean pH that are greater than any experienced in the past 300 million years, with the possible exception of those resulting from rare,

TABLE 2. Changes in calcification in response to increased pCO₂ concentrations relative to calcification at present-day pCO₂ (~380 ppmv)^a

Organism/System	Mineralogy	Approx. % change in calcification when pCO ₂ is			References	Notes
		2 × preindustrial	3 × preindustrial	3 × preindustrial		
Coccolithophores						
<i>Emiliania huxleyi</i>	Calcite	-25			Sciandra <i>et al.</i> 2003	
<i>E. huxleyi</i>	"	-9	-18		Riebesell <i>et al.</i> 2000; Zondervan <i>et al.</i> 2001	Decrease in CaCO ₃ /cell
<i>E. huxleyi</i>	"		-40		Delille <i>et al.</i> 2005	Initial pCO ₂ = 713 ppmv. Decrease in net community calcification
<i>Gephyrocapsa oceanica</i>	"	-29	-66		Riebesell <i>et al.</i> 2000; Zondervan <i>et al.</i> 2001	Decrease in CaCO ₃ /cell
<i>Coccolithus pelagicus</i>	"	0	0		Langer <i>et al.</i> 2006	No change in CaCO ₃ /cell
<i>Calcidiscus leptoporus</i>	"		-25		Langer <i>et al.</i> 2006	Decrease in CaCO ₃ ; decrease also observed at 180 ppmv
Foraminifera						
<i>Orbulina universa</i>	Calcite	-8	-14		Spero <i>et al.</i> 1997; Bijma <i>et al.</i> 1999;	Decrease in shell weight
<i>Globigerinoides sacculifer</i>	"	-4 to -6	-6 to -8		Bijma <i>et al.</i> 2002 Bijma <i>et al.</i> 1999; Bijma <i>et al.</i> 2002	Decrease in shell weight
Scleractinian corals						
<i>Sylophora pistillata</i>	"	-14	-20		Gattuso <i>et al.</i> 1998	Curve was nonlinear; linear fit was made for Ω _{avg} from 2.0–3.9
<i>S. pistillata</i>	"	0 to -50			Reynaud <i>et al.</i> 2003	Level of response is temperature-dependent
<i>Acropora cervicornis</i>	Aragonite	-40	-59		Renegar & Riegl 2005	

TABLE 2.

Organism/System	Mineralogy	Approx. % change in calcification when pCO ₂ is		References	Notes
		2 × preindustrial	3 × preindustrial		
<i>Acropora eurystroma</i>	"	-55		Schneider & Erez 2006	
<i>Acropora verweyi</i>	"	-12	-18	Marubini <i>et al.</i> 2003	
<i>P. compressa</i> + <i>Montipora capitata</i>	"	-40	-59	Langdon & Atkinson 2005	
<i>Porites compressa</i>	"	-17	-25	Marubini <i>et al.</i> 2001	
<i>P. lutea</i>	"	-38	-56	Ohde & Hossain 2004	
<i>P. lutea</i>	"	-33	-49	Hossain & Ohde 2006	
<i>P. porites</i>	"	-16		Marubini & Thake 1999	
<i>Pavona cactus</i>	"	-14	-20	Marubini <i>et al.</i> 2003	
<i>Fungia</i> sp.	"	-47	-69	Hossain and Ohde 2006	
<i>Galaxea fascicularis</i>	"	-12	-18	Marubini <i>et al.</i> 2003	
<i>G. fascicularis</i>	"	-56	-83	Marshall & Clode 2002	
<i>Turbinaria reniformis</i>	"	-9	-13	Marubini <i>et al.</i> 2003	
Coralline red algae					
<i>Porolithon gardineri</i>	High-Mg calcite	-25		Agegian 1985	
Mesocosms and field studies					
<i>Biosphere 2</i>	Mixed	-56	-83	Langdon <i>et al.</i> 2000	Dominated by coralline red algae
<i>Monaco mesocosm</i>	"	-21		Leclercq <i>et al.</i> 2000	
<i>Monaco mesocosm</i>	"	-15		Leclercq <i>et al.</i> 2002	
<i>Bahamas Bank</i>	"	-57	-85	Broecker & Takahashi 1966	
<i>Rukau-sho, Okinawa</i>	"	-45	-67	Ohde & van Woessik 1999	
<i>Nature Reserve Reef, Red Sea</i>	"	-55		Silverman <i>et al.</i> 2007	

^aNearly all organisms tested to date show reduced calcification in response to elevated pCO₂ and decreased carbonate ion concentration and carbonate saturation state. Modified from Kleypas *et al.* (2006).

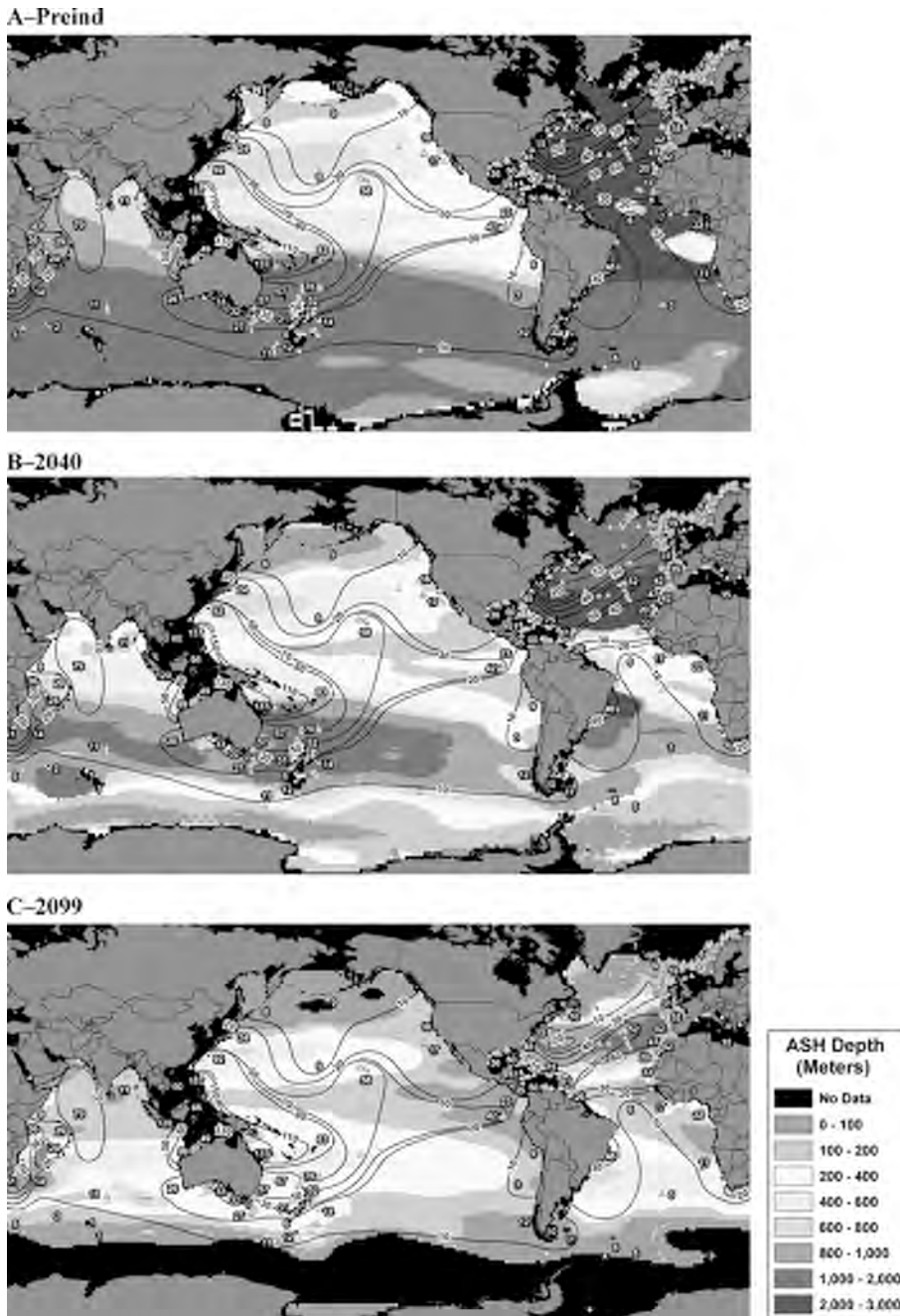


Figure 1. (A) Depth of the aragonite saturation horizon (ASH), locations of deep-sea bioherm-forming corals, and diversity contours for 706 species of azooxanthellate corals. Projected ASH depth for year 1765 (preindustrial); $p\text{CO}_2 = 278$ ppmv. Green triangles are locations of six deep-sea, scleractinian, bioherm-forming coral species (*Lophelia pertusa*, *Madrepora oculata*, *Goniocorella dumosa*, *Oculina varicosa*, *Enallopsammia profunda*, and *Solenosmilia variabilis*). Numerals not falling on diversity contours indicate number of azooxanthellate coral species. Reprinted with permission from Guinotte *et al.* (2006). (B) Projected ASH depth for year 2040; $p\text{CO}_2 = 513$ ppmv. (C) Projected ASH depth for year 2099; $p\text{CO}_2 = 788$ ppmv. Black areas appearing in the Southern Ocean and North Pacific indicate areas where the ASH depth has reached the surface. (In color in *Annals* online.)

catastrophic events in Earth history” (Caldeira and Rampino 1993; Beerling and Berner 2002). Recent evidence suggests ocean acidification was a primary driver of past mass extinctions and reef gaps, which are time periods on the order of millions of years that reefs have taken to recover from mass extinctions (Stanley 2006; Veron 2008). Zachos and colleagues (2005) calculated that if the entire fossil fuel reservoir (ca. 4500 GtC) were combusted, the impacts on deep-sea pH and biota would probably be similar to those in the Paleocene–Eocene Thermal Maximum (PETM), 55 million years ago. The PETM likely caused a mass extinction of benthic foraminifera (Zachos *et al.* 2005). Projected anthropogenic carbon inputs will occur within just 300 years, which is thought to be much faster than the CO₂ release during the PETM and too rapid for dissolution of calcareous sediments to neutralize anthropogenic CO₂. Consequently, the ocean acidification-induced impacts on surface ocean pH and biota will probably be more severe than during the PETM (Zachos *et al.* 2005).

While it is apparent changing seawater chemistry will have serious consequences for many marine calcifiers, the effects of ocean acidification on noncalcifiers and the ecosystem responses to these changes will be complex and difficult to quantify. Assessing whether ocean acidification is the primary driver of a species’ population decline will be difficult due to the multitude of ongoing physical and chemical changes currently occurring in the ocean. Ocean acidification is occurring in synergy with significant ongoing environmental changes (e.g., ocean temperature increases), and these cumulative impacts or interactive effects of multiple stressors may have more significant consequences for biota than any single stressor. Thus, research into the synergistic effects of these changes on marine organisms and the consequent ecosystem responses is critical but still in its infancy.

Calcification and Dissolution Response

Hermatypic Corals (Zooxanthellate)

The calcification response of reef-building corals to decreases in aragonite saturation state has been well documented for a handful of select species. These experiments have been conducted in laboratory tanks and mesocosms, but to date have not been conducted in *in situ* field experiments under “natural” conditions. Evidence from species tested to date indicate that the calcification rates of tropical reef-building corals will be reduced by 20–60% at double preindustrial CO₂ concentrations (pCO₂ ca. 560 ppmv) (Gattuso *et al.* 1998; Kleypas *et al.* 1999a; Langdon *et al.* 2000; Kleypas & Langdon 2002; Langdon *et al.* 2003; Reynaud *et al.* 2003; Langdon & Atkinson 2005; c.f. Royal Society 2005; c.f. Kleypas *et al.* 2006) (see Table 2). Figure 2 illustrates the projected reduction in surface-water aragonite saturation state through the year 2069. A reduction in calcification of this magnitude could fundamentally alter the current structure and function of coral-reef ecosystems, as their growth is dependent on their ability to accrete at faster rates than erosional processes can break them down. Reef accretion will become increasingly more critical in the coming decades, as global sea levels rise and available light for photosynthesis becomes a limiting factor for corals at the deepest reaches of the photic zone.

A substantial decrease in the number of carbonate ions available in seawater will have serious implications for coral calcification rates and skeletal formation. Weaker coral skeletons will probably result from a reduction in carbonate ions, enabling erosional processes to occur at much faster rates than have occurred in the past, and slower growth rates may also reduce corals’ ability to compete for space and light, though no studies have been conducted to test this hypothesis (reviewed in Kleypas *et al.* 2006). Biosphere II mesocosm experiments suggest that net reef dissolution will

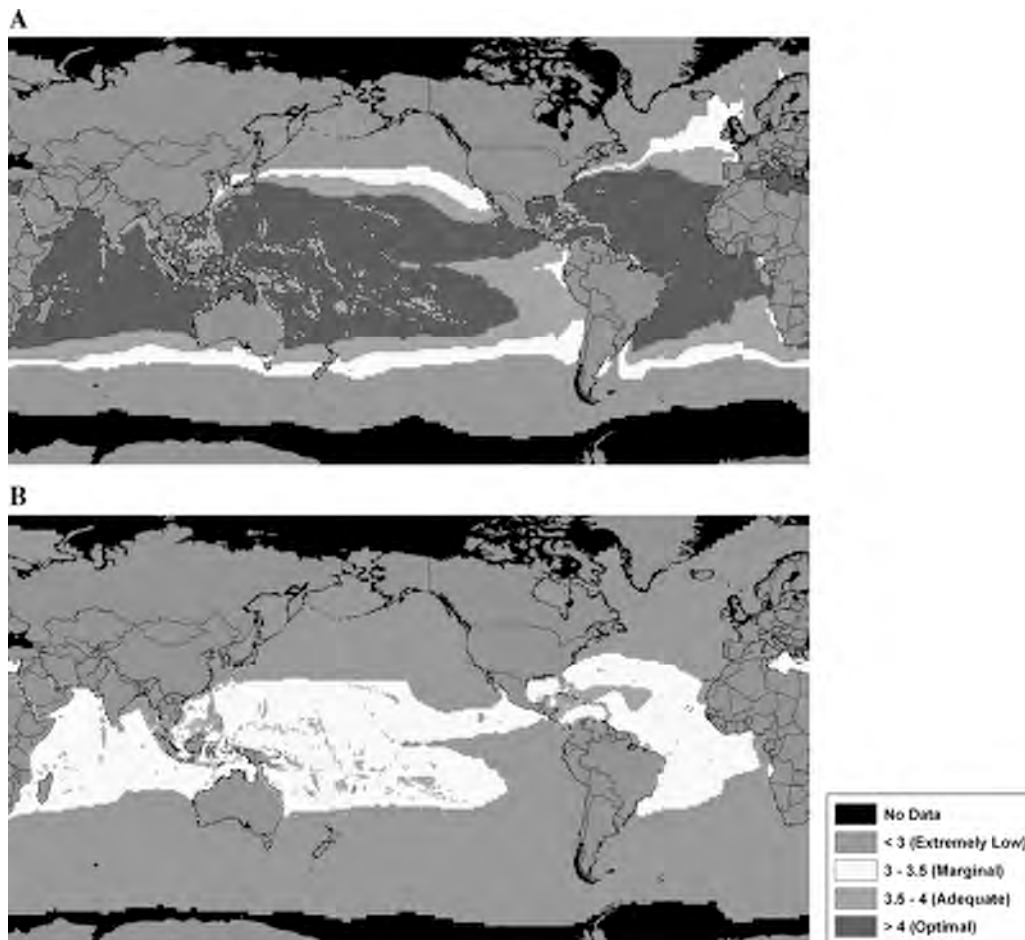


Figure 2. (A) Surface aragonite saturation state. Calculated preindustrial (1870) Ω_{arag} values; $p\text{CO}_2 = 280$ ppmv. Green dots represent present-day distribution of zooxanthellate coral reefs. Figure modified from Guinotte *et al.* (2003). Figure legend classification from Kleypas *et al.* (1999b). (B) Surface aragonite saturation state. Projected Ω_{arag} values, 2060–2069; $p\text{CO}_2 = 517$ ppmv. (In color in *Annals* online.)

outpace net reef calcification when carbonate ion concentration decreases to about 150 to 110 $\mu\text{mole kg}^{-1}$, a range that corresponds to atmospheric CO_2 concentrations of 560–840 ppmv (C. Langdon pers. comm. 2007). Hoegh-Guldberg and colleagues (2007) stated that aragonite saturation values will favor erosion when the carbonate ion concentration approaches 200 $\mu\text{mole kg}^{-1}$ (atmospheric CO_2 concentration = 480 ppmv). The effects of a reduction in calcification rates on recruitment, settlement, and juvenile life stages of most marine calcifiers, including the majority of scleractinian corals, are not well known. However,

Edmunds (2007) documented a decline in the growth rates of juvenile scleractinian corals in the U.S. Virgin Islands and raised the possibility that the effects of global climate change (increased seawater temperatures and decreasing aragonite saturation state) have already reduced the growth rate of juvenile corals.

Fine and Tchernov (2007a) reported two species of scleractinian corals were able to survive corrosive water conditions (pH values of 7.3–7.6), which caused their skeletons to dissolve completely, leaving the coral polyps exposed. When water chemistry returned to normal/ambient conditions, the coral polyps were

able to recalcify their skeletons without any obvious detrimental effects. These findings shed new light on the hypothesis that corals have a means of alternating between soft bodies and skeletal forms, which are absent from the fossil record during reef gaps (Stanley & Fautin 2001; Medina *et al.* 2006; Stanley 2006; Fine & Tchernov 2007a). Fine and Tchernov's results offer some hope for the future of corals in a high CO₂ world, but caution should be exercised as these manipulative experiments did not include the effects of predation on the "naked" coral polyps. Hard skeletons also provide another core function for coral polyps by protecting them from periodic natural events such as tsunamis and cyclones, which can cause significant damage to coral colonies and reef systems.

There is some discrepancy regarding the representativeness of the coral species used in the Fine and Tchernov calcification experiments. Stanley (2007) stated the experiments may not be representative of all coral species, particularly zooxanthellate reef-building species, which might have responded quite differently to the experiments because of the complex nature of their photosymbiosis. This assertion was challenged by Fine & Tchernov (2007b) in the statement that the evolution and physiology of the studied species are indistinguishable from tropical reef-building species. Representativeness aside, both parties agree that ocean acidification poses a significant threat to coral-reef ecosystems and the services they provide.

Calcifying Macroalgae

Coralline Algae

Scleractinian corals are not the only reef-calcifying organisms that are sensitive to decreasing saturation states. Crustose coralline algae (CCA) are a critical player in the ecology of coral-reef systems as they provide the "cement" that helps stabilize reefs, make significant sediment contributions to these systems, and are important food sources for sea urchins, par-

rot fish, and several species of mollusks (Littler & Littler 1984; Chisholm 2000; Diaz-Pulido *et al.* 2007). CCA also provide important hard settlement substrate for coral larvae (Heyward & Negri 1999; Harrington *et al.* 2005; Diaz-Pulido *et al.* 2007). Coralline algae produce calcium carbonate in the form of high-magnesium calcite, a more soluble form of calcium carbonate than either calcite or aragonite, which make these species particularly sensitive to decreasing carbonate saturation states.

Mesocosm experiments exposing CCA to elevated pCO₂ (2 × present day) indicate up to a 40% reduction in growth rates, 78% decrease in recruitment, 92% reduction in total area covered by CCA, and a 52% increase in noncalcifying algae (Buddemeier 2007; Kuffner *et al.* 2008). Agegian (1985) also reported a reduction in recruitment when CCA were exposed to elevated pCO₂ in aquarium experiments. Buddemeier (2007) states, "The combined effects of reduced carbonate production and diminished stabilization (cementation) of coasts and shallow seafloors by encrusting calcifiers are likely to lead to more rapid erosion and ecosystem transitions (macroalgal takeover) than would be expected on the basis of decreases in coral growth alone." The ecological importance of coralline algae to reef systems and the effects decreasing carbonate saturation state will have on these organisms have been overlooked to a significant degree, and more research is needed to document CCA response to reduced carbonate saturation states and in turn how these responses will impact reef ecosystems.

Halimeda

Halimeda is a genus of green, calcifying macroalgae that forms extensive beds in certain regions of the world's oceans. Some of the most well-developed *Halimeda* beds occur off the northeast coast of Australia, and estimates of total area covered by *Halimeda* in the Great Barrier Reef region are upwards of 2000 km² (reviewed by Diaz-Pulido *et al.* 2007). *Halimeda*, along with other calcareous algae (Udotea, Amphiroa, and Galaxaura), are

important producers of marine sediments and contribute to reef accretion by filling voids in the reef matrix with their sediments (Hillis-Colinvaux 1980; Davies & Marshall 1985; Drew & Abel 1988; Diaz-Pulido *et al.* 2007). Reefs and *Halimeda* bioherms have high calcification rates and are responsible for the majority of CaCO_3 production and accumulation on the continental shelf (Milliman & Droxler 1996; Kleypas *et al.* 2006).

The three-dimensional structures *Halimeda* form, which can be 20 m in height, provide important habitat for adult fishes and may serve as nursery grounds for juvenile fishes and invertebrates (Beck *et al.* 2003). Calcifying macroalgae produce biogenic calcium carbonate in three forms: high-magnesium calcite, aragonite, and calcite; all of these forms are susceptible to the negative effects of decreasing carbonate saturation states (Littler & Littler 1984). Few species of *Halimeda* have been exposed to high pCO_2 in lab experiments, but one species from the Great Barrier Reef, *Halimeda tuna*, displayed a negative calcification response when exposed to a pH drop of 0.5 units (8 to 7.5) (Borowitzka & Larkum 1986).

Cold Water Corals (Azooxanthellate)

Cold water corals and the ecologically rich bioherms they form are widely distributed throughout the world oceans (see Fig. 1). A great number of these highly productive ecosystems have been discovered only in the last decade, and it is thought that the area covered by these organisms may surpass the total area of tropical zooxanthellate reef systems (Mortensen *et al.* 2001; Freiwald *et al.* 2004; Freiwald & Roberts 2005; Guinotte *et al.* 2006; Turley *et al.* 2007). Cold water corals are azooxanthellate, which means they do not contain photosynthetic algae, and thus are not limited to the photic zone. The majority of cold water corals are found in depths of 200–1000 m or more, and some solitary colonies have been found at depths of several thousand meters (Freiwald 2002; Freiwald *et al.* 2004). There

are six species of azooxanthellate, bioherm-forming, scleractinian corals (*Lophelia pertusa*, *Madrepora oculata*, *Goniocorella dumosa*, *Oculina varicosa*, *Enallopsammia profunda*, and *Solenosmilia variabilis*), all of which produce calcium carbonate skeletons of aragonite. Cold water corals bioherms have extremely high biodiversity and provide habitat and nursery areas for many deep-sea organisms, including several commercially important fish species (Rogers 1999; Fossa *et al.* 2002; Husebo *et al.* 2002). Scleractinian cold water corals are not the only azooxanthellate habitat formers.

The “coral gardens” of the North Pacific are biodiversity hotspots dominated by octocorals (soft corals, stoloniferans, sea fans, gorgonians, and sea pens) and stylasterids, the majority of which produce calcite spicules and holdfasts (Cairns & Macintyre 1992; Guinotte *et al.* 2006; Stone 2006). Stone (2006) reported that 85% of the economically important fish species observed on submersible transects in waters off the Aleutian Islands were associated with corals and other emergent epifauna. The waters off the Aleutian Islands have the highest abundance and diversity of cold-water corals found to date in high-latitude ecosystems (Heifetz *et al.* 2005; Stone 2006), but well-developed scleractinian bioherms are curiously absent from this region even though scleractinian bioherm-forming species are found in North Pacific waters (Guinotte *et al.* 2006).

The reason scleractinian bioherms are not present in North Pacific waters could be a function of the shallow depth of the aragonite saturation horizon and high dissolution rates throughout the region (Guinotte *et al.* 2006). If this hypothesis is true, then decreasing carbonate saturation state will probably impact scleractinian cold-water corals earlier than shallow-water reef builders. Cold-water corals are bathed in cold, deep waters that have naturally high levels of CO_2 (global average $\Omega_{\text{arag}} = 2$). The low carbonate saturation state environment in which they live probably contributes to their slow growth/calcification rates, which are an order of magnitude slower

than tropical zooxanthellate corals (global average $\Omega_{\text{arag}} = 4$). Indeed, some deeper cold-water coral bioherms could already be experiencing corrosive conditions with respect to aragonite saturation state ($\Omega_{\text{arag}} < 1$), though no evidence of this has been documented.

Greater than 95% of the present day distribution of bioherm-forming scleractinian species occur in waters that are supersaturated with aragonite (Guinotte *et al.* 2006). Future aragonite saturation state projections from Orr and co-authors (2005) indicate that 70% of scleractinian cold-water coral bioherms could be in undersaturated water with respect to aragonite by the end of the century (Guinotte *et al.* 2006; Turley *et al.* 2007) (see Fig. 1). Laboratory experiments are currently being conducted to test whether cold water corals scleractinians (*Lophelia pertusa*) are sensitive to decreasing aragonite saturation state (Riebesell pers. comm.), but no lab experiments have been conducted to test the sensitivity of cold-water octocorals and stylasterids to decreasing carbonate saturation states. Manipulative CO_2 experiments to determine cold-water coral sensitivity and calcification response to decreasing carbonate saturation states are a top priority for future research (Guinotte *et al.* 2006; Kleypas *et al.* 2006; Roberts *et al.* 2006; Turley *et al.* 2007).

Benthic Mollusks, Bryozoans, and Echinoderms

The physiological and ecological impacts of increasing pCO_2 on benthic mollusks, bryozoans, and echinoderms are not well known, and few manipulative experiments have been carried out to determine sensitivity to elevated pCO_2 (Kleypas *et al.* 2006). The negative effects of acidic waters on bivalves have been investigated in a small number of studies (Kuwatani & Nishii 1969; Bamber 1987, 1990; Michaelidis *et al.* 2005; Berge *et al.* 2006), and only one investigated the negative calcification response to pCO_2 levels within the range predicted by the IPCC (Gazeau *et al.* 2007). Gazeau and colleagues (2007) found

that calcification rates of the mussel (*Mytilus edulis*) and Pacific oyster (*Crassostrea gigas*) can be expected to decline linearly with increasing pCO_2 , 25% and 10% respectively, by the end of the century (ca. 740 ppmv, IPCC IS92a scenario). Both species are important coastal ecosystem engineers and represent a significant portion of global aquaculture production (Gazeau *et al.* 2007). Bivalves that settle in coastal estuarine areas may be particularly vulnerable to anthropogenic ocean acidification. These organisms naturally experience extremely high mortality rates (>98%) in their transition from larvae to benthic juveniles (reviewed by Green *et al.* 2004), and any increase in juvenile mortality due to ocean acidification could have serious effects on estuarine bivalve populations.

Kurihara and colleagues (2007) demonstrated that increased pCO_2 of seawater projected to occur by the year 2300 (pH 7.4) will severely impact the early development of the oyster *Crassostrea gigas* and highlighted the importance of acidification effects on larval development stages of marine calcifiers. Because early life stages appear to be more sensitive to environmental disturbance than adults and most benthic calcifiers possess planktonic larval stages, fluctuations in larval stages due to high mortality rates may exert a strong influence on the population size of adults (Green *et al.* 2004). Kurihara and co-authors (2004) investigated the effects of increased pCO_2 on the fertilization rate and larval morphology of two species of sea urchin embryos (*Hemicentrotus pulcherrimus* and *Echinometra mathaei*) and found the fertilization rate of both species declined with increasing CO_2 concentration. In addition, the size of pluteus larvae decreased with increasing CO_2 concentration and malformed skeletogenesis was observed in larval stages of both species. Kurihara and Shirayama (2004) concluded that both decreasing pH and altered carbonate chemistry affect early development and life history of many marine organisms, which will result in serious consequences for marine ecosystems.

Experiments focusing on the direct effects of increasing ocean acidification on marine calcifiers have been the dominant activity to date, but numerous and ecologically significant indirect effects are probable. Bibby and colleagues (2007) documented interesting behavioral, metabolic, and morphological responses of the intertidal gastropod *Littorina littorea* to acidified seawater (pH = 6.6). This marine snail produced thicker shells when exposed to predation (crab) cues in control experiments, but this defensive response was disrupted when pH was decreased. The snails also displayed reduced metabolic rates and an increase in avoidance behavior, both of which could have significant ecosystem implications via organism interactions, energy requirements, and predator–prey relationships. This study investigated only one species of mollusk, but other marine organisms will probably have indirect responses to ocean acidification (Bibby *et al.* 2007).

Coccolithophores, Foraminifera, and Pteropods

The major planktonic producers of CaCO_3 are coccolithophores (single-celled algae), foraminifera (protists), and euthecosomatous pteropods (planktonic snails). Coccolithophores and foraminifera secrete CaCO_3 in the form of calcite, whereas pteropods secrete shells made of aragonite, which is about 50% more soluble in seawater than calcite (Mucci 1983). These planktonic groups differ with respect to their size, trophic level, generation time, and other ecological attributes. High quality, quantitative data on the latitudinal and vertical distributions and abundances of these calcareous taxa are lacking, and estimates of their contributions to global calcification rates are poorly constrained.

The calcification response of coccolithophores, foraminifera, and pteropods to ocean acidification has been investigated to date in very few species. Most studies have involved bloom-forming coccolithophores, and these species (*Emiliania huxleyi* and *Geophyro-*

capsa oceanica) show decreased calcification rates ranging from 25 to 66% when pCO_2 is increased to 560–840 ppmv, respectively (TABLE 2) in lab and mesocosm experiments. In lab experiments with the coccolithophore *Coccolithus pelagicus*, however, Langer *et al.* (2006) found that calcification did not change with increased CO_2 . Moreover, there is evidence suggesting that at least one coccolithophore species may have the capacity to adapt to changing pCO_2 over long periods. Experimental manipulations show that *Calcidiscus leptoporus* exhibits highest calcification rates at present-day CO_2 levels, with malformed coccoliths and coccospheres at both lower and higher pCO_2 (Langer *et al.* 2006). Because no malformed coccoliths were observed in sediments from the Last Glacial Maximum (when pCO_2 levels were about 200 ppmv), the authors concluded that *C. leptoporus* has adapted to present-day CO_2 levels.

In lab experiments with two species of planktonic foraminifera, shell mass decreased as the carbonate ion concentration of seawater decreased (Spero *et al.* 1997; Bijma *et al.* 1999, 2002). When grown in lab experiments in seawater chemistry equivalent to pCO_2 values of 560 and 740 ppmv, shell mass of the foraminifera *Orbulina universa* and *Globigerinoides sacculifer* declined by 4–8% and 6–14%, respectively, compared to the shell mass secreted at the preindustrial pCO_2 value.

Data for a single species of shelled pteropods suggest that net shell dissolution occurs in live pteropods when the aragonite saturation is forced to <1.0 (Orr *et al.* 2005; Fabry *et al.* 2008). When live pteropods (*Clio pyramidata*) were collected in the subarctic Pacific and exposed to a level of aragonite undersaturation similar to that projected for Southern Ocean surface waters by the year 2100 under the IS92a emissions scenario, shell dissolution occurred within 48 hours, even though animals were actively swimming.

The response of planktonic calcifying organisms to elevated pCO_2 may not be uniform among species or over time. To date,

published research indicates that most calcareous plankton show reduced calcification in response to decreased carbonate ion concentrations; however, the limited number of species investigated precludes identification of widespread or general trends. All studies thus far on the impacts of ocean acidification on calcareous plankton have been short-term experiments, ranging from hours to weeks. Nothing is known about the long-term impacts of elevated $p\text{CO}_2$ on the reproduction, growth, and survivorship of planktonic calcifying organisms or their ability to adapt to changing seawater chemistry. Chronic exposure to increased $p\text{CO}_2$ may have complex effects on the growth and reproductive success of calcareous plankton or may induce adaptations that are absent in short-term experiments. No studies have investigated the possibility of differential impacts with life stage or age of the organism. Additional experimental evidence from planktonic calcifiers is urgently needed if we are to develop a predictive understanding of the impacts of ocean acidification on planktonic communities.

Physiological Responses

Fishes

Elevated CO_2 partial pressures (hypercapnia) will affect the physiology of water-breathing animals by inducing acidosis in the tissues and body fluids of marine organisms, including fishes (Roos & Boron 1981; Portner *et al.* 2004). pH, bicarbonate, and CO_2 levels within the organism are altered with long-term effects on metabolic functions, growth, and reproduction, all of which could be harmful at population and species levels (Portner *et al.* 2004). Short-term effects of elevated CO_2 on fishes include alteration of the acid–base status, respiration, blood circulation, and nervous system functions, while long-term effects include reduced growth rate and reproduction (Ishimatsu & Kita 1999; Ishimatsu *et al.*

2004, 2005). Most experiments undertaken to date involved altering pH to levels consistent with conditions that would be present if CO_2 were to be directly injected to the seafloor (pH ca. 5.8–6.2). These experiments have shown adverse negative effects of acidified seawater on fish throughout their entire life cycle (eggs, larvae, juveniles, and adults) (Kikkawa *et al.* 2003, 2004; Ishimatsu *et al.* 2004; Portner *et al.* 2004).

Fish in early developmental stages are more sensitive to environmental change than adults and a limited number of studies have shown this to be true when fish eggs, larvae, and juveniles were exposed to elevated CO_2 (McKim 1977; Kikkawa *et al.* 2003, 2004; Ishimatsu *et al.* 2004). Ishimatsu and co-authors (2004) state, “Even if the severity of environmental hypercapnia due to CO_2 sequestration is made tolerable to adults, a gradual reduction in population size and changes in marine ecosystem structures are unavoidable consequences when young individuals cannot survive” (p. 732). The long-term effects and adaptation potential of fishes experiencing future $p\text{CO}_2$ levels consistent with IPCC scenarios are not known.

Photosynthetic Organisms

Phytoplankton and Cyanobacteria

Most species of marine phytoplankton have carbon-concentrating mechanisms that accumulate inorganic carbon either as CO_2 or HCO_3^- or both (Giordano *et al.* 2005). Owing in large part to their carbon-acquisition mechanisms and efficiencies, most marine phytoplankton tested to date in single-species lab experiments or natural community-perturbation experiments show either no change or small increases (generally $\leq 10\%$) in photosynthetic rates when grown under high $p\text{CO}_2$ conditions equivalent to ca. 760 micro atmosphere (μatm) (Tortell *et al.* 1997; Hein & Sand-Jensen 1997; Burkhardt *et al.* 2001; Tortell and Morel 2002; Rost *et al.* 2003; Beardall & Raven 2004;

Schippers *et al.* 2004; Giordano *et al.* 2005; Martin & Tortell 2006). Unlike other major phytoplankton groups investigated thus far, the coccolithophorid *Emiliania huxleyi* has low affinity for inorganic carbon and could be carbon-limited in today's ocean (Rost & Riebesell 2004). Whether *E. huxleyi* will show increased rates of photosynthesis with progressive oceanic uptake of atmospheric CO₂, however, may depend on nutrient availability and light conditions (Zondervan 2007). In a recent mesocosm CO₂ manipulation, study, Riebesell and colleagues (2007) reported that CO₂ uptake by a phytoplankton community (primarily diatoms and coccolithophores) in experimental pCO₂ treatments of 700 and 1050 μatm was 27% and 39% higher, respectively, relative to the pCO₂ treatment of 350 μatm.

Ocean acidification will be accompanied by climate warming in large expanses of the oceans. Higher sea-surface temperatures increase thermal stratification of the upper ocean, thereby reducing the vertical mixing of nutrients to surface waters, and have been linked to observed decreases in phytoplankton biomass and productivity, particularly at low and mid-latitudes (Behrenfeld *et al.* 2006). In warm, nutrient-poor tropical and subtropical regions, however, continued ocean absorption of anthropogenic CO₂ may enhance fixation of atmospheric nitrogen and could lead to increased total primary productivity. Nitrogen-fixing cyanobacteria in the genus *Trichodesmium*, which support a large portion of primary productivity in such low-nutrient areas of the world's oceans, show increased rates of nitrogen and carbon fixation under elevated pCO₂ (Hutchins *et al.* 2007; Barcelos e Ramos *et al.* 2007). At CO₂ levels of 750 ppmv, *Trichodesmium* increased N₂ fixation rates by 35–100% and CO₂ fixation rates by 15–128%, relative to present-day CO₂ conditions (Hutchins *et al.* 2007).

In a review of coastal marine phytoplankton, Hinga (2002) found that while some species grow well at a wide range of pH, others have growth rates that vary greatly over a 0.5 to

1.0 pH unit change. He concluded that small changes in ambient seawater pH could affect species growth rates, abundances, and succession in coastal phytoplankton communities. Eutrophication and ocean acidification may act in concert to amplify the pH range found in coastal habitats, which in turn could lead to increased frequency of blooms of those species with tolerance to extreme pH (cf. Hinga 2002). In both coastal and open ocean environments, ocean acidification could also affect primary productivity through pH-dependent speciation of nutrients and metals (Zeebe & Wolf-Gladrow 2001; Huesemann *et al.* 2002).

Seagrasses

Seagrasses represent one of the most biologically rich and productive marine ecosystems in the ocean. They create critical nursery grounds for juvenile fishes and important habitat for adult fishes, invertebrates, and mollusks. Several higher order and endangered species rely on seagrasses for a significant portion of their diet (e.g., dugongs, manatees, and green sea turtles). Seagrass ecosystems are a critical component to maintaining the biological diversity of the oceans and could be one of the few ecosystems that stand to benefit from increasing levels of CO₂ in seawater. Seagrasses are capable of dehydrating HCO₃⁻, but many appear to use CO₂ (aq) for at least 50% of their carbon requirements used for photosynthesis (Palacios & Zimmerman 2007). Zimmerman and colleagues (1997) found that short-term (ca. 45 days) CO₂ (aq) enrichment increased photosynthetic rates and reduced light requirements for eelgrass (*Zostera marina* L) shoots in laboratory experiments.

Longer-term (1 year) experiments exposing *Zostera marina* L to CO₂ (aq) concentrations of 36–1123 μM (pH 7.75–6.2) conducted by Palacios and Zimmerman (2007) resulted in higher reproductive output, an increase in below-ground biomass, and vegetative proliferation of new shoots when light was in abundant supply. These findings suggest that as the CO₂

content of the surface ocean rises, so too will the productivity of seagrass meadows, which in turn may positively influence invertebrate and fish populations. This increase in productivity will probably be true for other seagrass species as most appear to be photosynthetically limited by the present-day availability of CO₂ (Durako 1993; Invers *et al.* 2001; Palacios and Zimmerman 2007). Palacios and Zimmerman (2007) noted that a significant indirect effect of increased eelgrass density could be an increase in sediment retention, which could lead to increased water clarity and an expansion in the depth distribution of eelgrasses to deeper waters.

Community 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 (Pollard 1984; Parrish 1989; Beck *et al.* 2001; Sheridan & Hays 2003; Mumby *et al.* 2004; Dorenbosch *et al.* 2005). The net effect of increasing CO₂ on seagrass ecosystems will probably be increased seagrass biomass and productivity, assuming water quality and clarity (low suspended sediment) are sufficient for photosynthesis to occur. Under these conditions, 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 reef-building marine calcifiers 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 (Guinotte *et al.* 2003; Buddemeier *et al.* 2004). The magnitude of both ecosystem responses to ocean acidification and other environmental changes working in synergy is difficult to predict as are

the net effects on fish abundance and diversity. Predicting the net effects on fish populations is further complicated by the plethora of unknowns surrounding the long-term effects of increasing CO₂ on fish physiology, metabolism, and probable range shifts due to 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 shallow-water coral-reef systems, which is due in large part to logistical challenges and the expense of operating vessels and submersibles in the deep sea. However, cold-water coral ecosystems are thought to provide important habitat, feeding grounds, and recruitment/nursery functions for many deep-water species, including several commercially important fish species (Mortensen 2000; Fossa *et al.* 2002; Husebo *et al.* 2002; Roberts *et al.* 2006). Many of the species relationships are thought to be facultative, but nonetheless, high fish densities have been reported for these structure-forming ecosystems (Husebo *et al.* 2002; Costello *et al.* 2005; Stone 2006). Populations of grouper, snapper, and amberjack use the *Oculina varicosa* reefs off the Florida coast as feeding and spawning areas (Reed 2002), even though their numbers have been dramatically reduced by commercial and recreational fishing in recent decades (Koenig *et al.* 2000). Large aggregations of redfish (*Sebastes* spp.), ling (*Molva molva*), and tusk (*Brosme brosme* Ascanius) have been documented in the *Lophelia pertusa* reefs of the North Atlantic (Husebo *et al.* 2002), and strong fish–coral associations exist in the cold-water coral ecosystems of the North Pacific (Stone 2006).

Ocean acidification could have significant indirect effects on fishes and other deep-sea organisms that rely on cold-water coral ecosystems for protection and nutritional requirements. Roberts and Gage (2003) documented over 1300 species living on the *Lophelia*

pertusa reefs in the NE Atlantic. Future depth projections for the aragonite saturation horizons indicate 70% of cold-water scleractinians will be in undersaturated waters by the end of the century, and significant decreases in calcification rate could occur well before corals experience undersaturated conditions as aragonite saturation state decreases progressively over time (Guinotte *et al.* 2006). Quantifying the indirect impacts of ocean acidification on coral-associated fishes is not possible due to uncertainties surrounding facultative and obligate species relationships, but the net effects are likely to be negative as cold-water coral growth, distribution, and area decrease.

Plankton

If reduced calcification decreases a calcifying organism's fitness or survivorship, then some planktonic calcareous species may undergo shifts in their distributions as the inorganic carbon chemistry of seawater changes. Calcifying species that are CO_2^- sensitive could potentially be replaced by noncalcifying species and/or those species not sensitive to elevated pCO_2 .

By 2100, surface waters of polar and sub-polar regions are projected to become undersaturated with respect to aragonite (Orr *et al.* 2005). Pteropods are important components of the plankton in high-latitude systems, with densities reaching thousands of individuals m^{-3} (e.g., Bathmann *et al.* 1991; Pane *et al.* 2004). If pteropods require seawater that is supersaturated with respect to aragonite, then their habitat would become increasingly limited, first vertically in the water column and then latitudinally, by the shoaling of the aragonite saturation horizon over the next century (Feely *et al.* 2004; Orr *et al.* 2005). If high-latitude surface waters do become undersaturated with respect to aragonite, pteropods could eventually be eliminated from such 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 (*Oncorhynchus gobuscha*), as well as chum and sockeye salmon, pollock, and other commercially important fishes (Aydin pers. comm.). Armstrong and co-authors (2005) reported interannual variability in the diet of juvenile pink salmon, with a single species of pteropod (*Limacina helicina*) comprising 15 to 63% by weight of pink salmon diets during a 3-year study. Because Pacific pink salmon have a short, 2-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).

Jellyfish blooms (scyphomedusae, hydromedusae, and cubomedusae) have increased over the last several decades (Purcell *et al.* 2007), but it is too soon to determine whether such recent jellyfish increases will persist or the populations will fluctuate with climatic regime shifts, particularly those at decadal scales, as has been observed previously (Purcell 2005). Attrill and colleagues (2007) reported a significant correlation of jellyfish frequency in the North Sea from 1971 to 1995 with decreased pH (from 8.3 to 8.1) of surface waters. Although the causative mechanism is not known, Attrill and colleagues (2007) suggest that projected climate change and declining ocean pH will increase the frequency of jellyfish in the North Sea over the next century. Jellyfish are both predators and potential competitors of fish and may substantially affect pelagic and coastal ecosystems (Purcell & Arai 2001; Purcell 2005). It is important to resolve possible linkages between jellyfish blooms and ocean acidification and determine whether continued changes in the seawater inorganic carbon system will exacerbate problematic increases in jellyfish that have been associated with climate change, overfishing, eutrophication, and other factors (Purcell *et al.* 2007).

Planktonic ecosystems are complex nonlinear systems, and the consequences of ocean acidification on such ecosystems are largely unknown. Substantial changes to species diversity

and abundances, food-web dynamics, and other fundamental ecological processes could occur; however, the interactions and feedbacks among the effects of chronic, progressively increasing ocean acidification and other environmental variables are difficult to predict. Ecosystem responses will also depend on the ability of biota to adapt to seawater chemistry changes that are occurring at rates they have not encountered in their recent evolutionary history (Siegenthaler *et al.* 2005). Future progress will likely require integrated approaches involving manipulative experiments, field observations, and models, particularly at regional scales.

Summary and 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 shallow-water scleractinian corals. Some data sets allow the identification of “tipping points” or “thresholds” of seawater carbonate chemistry when ocean acidification will cause net calcification rates to be less than net dissolution rates in coral reef systems (Yates & Halley 2006; Hoegh-Guldberg *et al.* 2007). In contrast, the potential effects ocean acidification may have for the vast majority of marine species are not known. Research into the synergistic 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 ecosystem health.

Future ocean acidification research needs include increased resources and efforts devoted to lab, mesocosm, and *in situ* experiments, all of which will aid in determining the biological responses of marine taxa to increased pCO₂. Mesocosm and *in situ* experiments may simulate and/or provide more natural conditions than single-species lab experiments, but they have thus far used abrupt changes in seawater chemistry which do not allow for potential acclimation or adaptation by marine organisms. There is an additional need for experiments on taxa with no commercial value but which provide critical habitat and occupy important trophic levels within marine food webs. Direct CO₂ experiments on commercially important species are clearly necessary, but non-commercial species play crucial roles in marine ecosystems and the life history of most commercial species. The effects of ocean acidification on less charismatic species and/or species with no economic value should not be overlooked. The biological response of marine organisms (both commercial and noncommercial) to ocean acidification will be key to making informed policy decisions that conform to sound ecosystem-based management principles.

There is a critical need for well-developed spatial and temporal models that give accurate present day and future estimates of aragonite and calcite saturation states in the coastal zones. The shallow continental shelves are some of the most biologically productive areas in the sea and are home to the majority of the world's fisheries, but accurate carbonate saturation state data do not currently exist for most coastal regions. Ocean acidification information should also be integrated into existing ecosystem models, which attempt to predict the effects of environmental changes on marine populations and ecosystem structure (e.g., Ecopath and Ecosim). Development of these tools is essential to making credible predictions of future ocean acidification effects on marine ecosystems and will aid in guiding management decisions.

The overwhelming volume of scientific evidence collated by the IPCC documenting the dangers of human-induced climate change, of which ocean acidification is only one, should end the lingering CO₂ emissions reduction debate. The global CO₂ experiment which has been under way since the Industrial Revolution and the potentially dire consequences this uncontrolled experiment poses for marine organisms and indeed, all life on Earth, leave no doubt that human dependence on fossil fuels must end as soon as possible. International collaboration, political will, and large-scale investment in clean energy technologies are essential to avoiding the most damaging effects of human-induced climate change.

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Conflict of Interest

The authors declare no conflicts of interest.

References

- Agegian, C.R. 1985. The Biogeochemical Ecology of *Porolithon gardineri* (Foslie). Ph.D. thesis, University of Hawaii, Honolulu.
- Armstrong, J.L. *et al.* 2005. Distribution, size, and interannual, seasonal and diel food habits of northern Gulf of Alaska juvenile pink salmon, *Oncorhynchus gorbuscha*. *Deep-Sea Res. II* **52**: 247–265.
- Attrill, M., J. Wright & M. Edwards. 2007. Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnol. Oceanogr.* **52**: 480–485.
- Augustin, L. *et al.* 2004. Eight glacial cycles from an Antarctic ice core. *Nature* **429**: 623–628.
- Aydin, K.Y. *et al.* Linking oceanic foodwebs to coastal production and growth rates to Pacific salmon (*Oncorhynchus* spp.), using models on three scales. *Deep Sea Res. II* **52**: 757–780.
- Bamber, R.N. 1990. The effects of acidic seawater on 3 species of lamellibranch mollusk. *J. Exp. Mar. Biol. Ecol.* **143**: 181–191.
- Bamber, R.N. 1987. The effects of acidic sea water on young carpet-shell clams *Venerupis decussata* (L.) (Mollusca: Veneracea). *J. Exp. Mar. Biol. Ecol.* **108**: 241–260.
- Barcelos e Ramos, J. *et al.* 2007. Effect of rising atmospheric carbon dioxide on the marine nitrogen fixer *Trichodesmium*. *Global Biogeochem. Cycles* **21**: np.
- Bathmann, U. *et al.* 1991. Short-term variations in particulate matter sedimentation off Kapp Norvegia, Weddell Sea, Antarctica: relation to water mass advection, ice cover, plankton biomass and feeding activity. *Polar Biol.* **11**: 185–195.
- Beardall, J. & J.A. Raven. 2004. The potential effects of global climate change in microalgal photosynthesis, growth and ecology. *Phycologia* **43**: 31–45.
- Beck, M.W. *et al.* 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* **51**: 633–641.
- Beck, M.W. *et al.* 2003. The role of nearshore ecosystems as fish and shellfish nurseries. *Issues Ecol.* **11**: 1–12.
- Beerling, D.J. & R.A. Berner. 2002. Biogeochemical constraints on the Triassic-Jurassic boundary carbon cycle event. *Global Biogeochem. Cycles* **16**: 101–113.
- Behrenfeld, M.J. *et al.* 2006. Climate-driven trends in contemporary ocean productivity. *Nature* **444**: 752–755.
- Berge, J.A. *et al.* 2006. Effects of increased sea water concentrations of CO₂ on growth of the bivalve *Mytilus edulis* L. *Chemosphere* **62**: 681–687.
- Bibby, R. *et al.* 2007. Ocean acidification disrupts induced defences in the intertidal gastropod *Littorina littorea*. *Biol. Lett.* **3**: 699–701.
- Bijma, J., H.J. Spero, & D.W. Lea. 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*. G. Fischer & G. Wefer, Eds.: 489–512. Springer-Verlag, New York.
- Bijma, J., B. Honisch, & R.E. Zeebe. 2002. The impact of the ocean carbonate chemistry on living foraminiferal shell weight: Comment on “Carbonate ion concentration in glacial-age deep waters of the Caribbean Sea” by W.S. Broecker & E. Clark. *Geochem. Geophys. Geosyst.* **3**: 1064.
- Borowitzka, L.J. & A.W.D. Larkum 1986. Reef algae. *Oceanus* **29**: 49–54.

- Broecker, W.S. 2003. *The Ocean CaCO₃ Cycle*. In *The Oceans and Marine Geochemistry*. H. Elderfield, Ed.: 1–21. Treatise on Geochemistry, Elsevier Pergamon, Oxford.
- Broecker, W.S. *et al.* 1979. Fate of fossil fuel carbon dioxide and the global carbon budget. *Science* **206**: 409–418.
- Broecker, W.S. & T. Takahashi. 1966. Calcium carbonate precipitation on the Bahama Banks. *J. Geophys. Res.* **71**: 1575–1602.
- Broecker, W.S. & T. Takahashi. 1977. Neutralization of fossil fuel CO₂ by marine calcium carbonate. In *The Fate of Fossil Fuel in the Oceans*. N.R. Andersen & A. Malahoff, Eds.: 213–241. Plenum Press, New York.
- Buddemeier, R.W., J.A. Kleypas & R. Aronson. 2004. Coral Reefs and Global Climate Change. Potential Contributions of Climate Change to Stresses on Coral Reef Ecosystems. *Pew Center for Global Climate Change*. Arlington, VA. 42 pp.
- Buddemeier, R.W. 2007. *The future of tropical reefs and coastlines*. Presented at the American Association for the Advancement of Science Annual Meeting. San Francisco, CA, Feb 16.
- Burkhardt, S. *et al.* 2001. CO₂ and HCO₃ uptake in marine diatoms acclimated to different CO₂ concentrations. *Limnol. Oceanogr.* **46**: 1378–1391.
- Cairns, S.D. & I.G. Macintyre. 1992. Phylogenetic implications of calcium carbonate mineralogy in the Stylasteridae (Cnidaria:Hydrozoa). *Palaeos* **7**: 96–107.
- Caldeira, K. & M.R. Rampino. 1993. Aftermath of the end-Cretaceous mass extinction: possible biogeochemical stabilization of the carbon cycle and climate. *Paleoceanography* **8**: 515–525.
- Caldeira, K. & M.E. Wickett. 2003. Anthropogenic carbon and ocean pH. *Nature* **425**: 365.
- Caldeira, K. & M.E. Wickett. 2005. Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *J. Geophys. Res.* **110**: np.
- Caldeira, K. *et al.* 2007. Comment on “Modern-age buildup of CO₂ and its effects on seawater acidity and salinity” by Hugo A. Loaiciga. *Geophysical Research Letters* **34**: L18608. doi: 10.1029/2006GL027288.
- Chisholm, J.R.M. 2000. Calcification by crustose coralline algae on the northern Great Barrier Reef, Australia. *Limnol. Oceanogr.* **45**: 1476–1484.
- Costello, M. *et al.* 2005. Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In *Cold-water Corals and Ecosystems*. A. Freiwald & J.M. Roberts, Eds.: 771–805. Springer-Verlag, Berlin, Heidelberg.
- Davies, P.J. & J.F. Marshall. 1985. *Halimeda* bioherms – low energy reefs, northern Great Barrier Reef. *Proceedings of the Fifth International Coral Reef Congress* **1**: 1–7.
- Delille, B. *et al.* 2005. Response of primary production and calcification to changes of pCO₂ during experimental blooms of the coccolithophorid *Emiliania huxleyi*. *Global Biogeochem. Cycles* **19**: np.
- Diaz-Pulido, G. *et al.* 2007. Vulnerability of macroalgae of the Great Barrier Reef to climate change. In *Climate Change and the Great Barrier Reef*. J.E. Johnson & P.A. Marshall, Eds.: 154–192. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Australia.
- Dickson, A.G. & F.J. Millero. 1987. A comparison of the equilibrium constants for the dissociation of carbonic acid in seawater media. *Deep-Sea Res. A* **34**: 1733–1743.
- Doney, S.C. *et al.* 2007. The impacts of anthropogenic nitrogen and sulfur deposition on ocean acidification and the inorganic carbon system. *Proc. Natl. Acad. Sci.* **104**: 14580–14585.
- Dorenbosch, M. *et al.* 2005. Indo-Pacific seagrass beds and mangroves contribute to fish density and diversity on adjacent coral reefs. *Mar. Ecol. Prog. Ser.* **302**: 63–76.
- Drew, E.A., & K.M. Abel. 1988. Studies on *Halimeda* I. The distribution and species composition of *Halimeda* meadows throughout the Great Barrier Reef Province. *Coral Reefs* **6**: 195–205.
- Durako, M.J. 1993. Photosynthetic utilization of CO₂ (aq) and HCO₃ in *Thalassia testudinum* (Hydrocharitaceae). *Mar. Biol.* **115**: 373–380.
- Edmunds, P.J. 2007. Evidence for a decadal-scale decline in the growth rates of juvenile scleractinian corals. *Mar. Ecol. Prog. Ser.* **341**: 1–13.
- Fabry, V.J. *et al.* 2008. Impacts of ocean acidification on marine fauna and ecosystems processes. *J. Mar. Sci.* In Press.
- Feely, R.A. *et al.* 1988. Winter-summer variations of calcite and aragonite saturation in the northeast Pacific. *Mar. Chem.* **25**: 227–241.
- Feely, R.A., & C.T.A. Chen. 1982. The effect of excess CO₂ on the calculated calcite and aragonite saturation horizons in the Northeast Pacific. *Geophys. Res. Lett.* **9**: 1294–1297.
- Feely, R.A. *et al.* 2008. Present and future changes in seawater chemistry due to ocean acidification. AGU Monograph, *The Science and Technology of CO₂ Sequestration*. In Press.
- Feely, R.A. *et al.* 2004. Impact of anthropogenic CO₂ on the CaCO₃ system in the oceans. *Science* **305**: 362–366.
- Feely, R.A. *et al.* 1984. Factors influencing the degree of saturation of the surface and intermediate waters of the North Pacific Ocean with respect to aragonite. *J. Geophys. Res.* **89**: 631–640.
- Fine, M. & D. Tchernov. 2007a. Scleractinian coral species survive and recover from decalcification. *Science* **315**: 1811.

- Fine, M. & D. Tchernov. 2007b. Response to "Ocean acidification and scleractinian corals". *Science* **317**: 1032–1033.
- Fossa, J.H., P.B. Mortensen, & D.M. Furevik. 2002. The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia* **13**: 1–12.
- Freiwald, A. 2002. Reef-forming cold-water corals. In *Ocean Margin Systems*. G. Wefer, D. Billett, D.B.B. Hebbeln Jorgensen, et al., Eds.: 365–385. Springer. Heidelberg.
- Freiwald, A. et al. 2004. *Coldwater Coral Reefs*. UNEP-WCMC, Cambridge, UK.
- Freiwald, A. & J.M. Roberts. 2005. *Cold-Water Corals and Ecosystems*. Springer. Heidelberg.
- Gattuso, J.-P. et al. 1998. Effect of calcium carbonate saturation of seawater on coral calcification. *Global Planet. Change* **18**: 37–46.
- Gazeau, F. et al. 2007. Impact of elevated CO₂ on shellfish calcification. *Geophys. Res. Lett.* L07603, doi:10.1029/2006GL028554.
- Giordano, M., J. Beardall & J.A. Raven. 2005. CO₂ concentrating mechanisms in algae: mechanisms, environmental modulation, and evolution. *Annu. Rev. Plant Biol.* **56**: 99–131.
- Green, M.A. et al. 2004. Dissolution mortality of juvenile bivalves in coastal marine deposits. *Limnol. Oceanogr.* **49**: 727–734.
- Guinotte, J.M., R.W. Buddemeier, & J.A. Kleypas. 2003. Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. *Coral Reefs* **22**: 551–58.
- Guinotte, J.M. et al. 2006. Will human induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? *Front. Ecol. Environ.* **4**: 141–146.
- Harrington, L. et al. 2005. Synergistic effects of diuron and sedimentation on photosynthesis and survival of crustose coralline algae. *Mar. Pollut. Bull.* **51**: 415–427.
- Heifetz, J. et al. 2005. Corals of the Aleutian Islands. *Fisheries Oceanogr.* **14**: 131–138.
- Hein, M. & K. Sand-Jensen. 1997. CO₂ increases oceanic primary production. *Nature* **388**: 526.
- Heyward, A.J. & A.P. Negri. 1999. Natural inducers of coral larval metamorphosis. *Coral Reefs* **18**: 273–279.
- Hillis-Colinvaux, L. 1980. Ecology and taxonomy of *Halimeda*: primary producers of coral reefs. *Adv. Mar. Biol.* **17**: 1–327.
- Hoegh-Guldberg, O. et al. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* **318**: 1737–1742.
- Hinga, K.R. 2002. Effects of pH on coastal marine phytoplankton. *Mar.Ecol.Prog.Ser.* **238**: 281–300.
- Hossain, M.M.M. & S. Ohde. 2006. Calcification of cultured *Porites* and *Fungia* under different aragonite saturation states of seawater. Proc. 10th Int.Coral Reef Sym. *Jpn. Coral Reef Soc.* 597–606.
- Houghton, J.T. et al. 2001. *Climate Change 2001: The Scientific Basis*. Cambridge University Press. Cambridge, UK.
- Huesemann, M.H., A.D. Skillman, & E.A. Crecelius. 2002. The inhibition of marine nitrification by ocean disposal of carbon dioxide. *Mar. Pollut. Bull.* **44**: 142–148.
- Husebo, A. et al. 2002. Distribution and abundance of fish in deep-sea coral habitats. *Hydrobiologia* **471**: 91–99.
- Hutchins, D.A. et al. 2007. CO₂ control of *Trichodesmium* N₂ fixation, photosynthesis, growth rates, and elemental ratios: implications for past, present, and future ocean biogeochemistry. *Limnol. Oceanogr.* **52**: 1293–1304.
- Invers, O. et al. 2001. Inorganic carbon sources for sea-grass photosynthesis: an experimental evaluation of bicarbonate use in species inhabiting temperate waters. *J. Exp. Mar. Biol. Ecol.* **265**: 203–217.
- Ishimatsu, A. et al. 2005. Physiological effects on fishes in a high-CO₂ world. *J. Geophys. Res.* **110**: np.
- Ishimatsu, A. et al. 2004. Effects of CO₂ on marine fish: larvae and adults. *J. Oceanogr.* **60**: 731–741.
- Ishimatsu, A. & J. Kita. 1999. Effects of environmental hypercapnia on fish, Jpn. *J. Ichthyol.* **46**: 1–13.
- Kikkawa, T., A. Ishimatsu & J. Kita. 2003. Acute CO₂ tolerance during the early developmental stages of four marine teleosts. *Environ. Toxicol.* **18**: 375–382.
- Kikkawa, T., J. Kita, & A. Ishimatsu. 2004. Comparison of the lethal effect of CO₂ and acidification on red sea bream (*Pagrus major*) during the early developmental stages. *Mar. Pollut. Bull.* **48**: 108–110.
- Kleypas, J.A. et al. 1999a. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* **284**: 118–120.
- Kleypas, J.A. et al. 1999b. Environmental limits to coral reef development: where do we draw the line? *Am Zool* **39**: 146–159.
- Kleypas, J.A. et al. 2006. Impacts of Ocean Acidification on Coral Reefs and Other Marine Calcifiers: A Guide for Future Research, report of a workshop held 18–20 April 2005, St. Petersburg, FL, sponsored by NSF, NOAA, and the U.S. Geological Survey, 88 pp.
- Kleypas, J.A. & C. Langdon. 2002. Overview of CO₂-induced changes in seawater chemistry. World Coral Reefs in the New Millennium: Bridging Research and Management for Sustainable Development. In Proceedings of the 9th International Coral Reef Symposium, 2. M.K. Moosa, S. Soemodihardjo, A. Soegiarto, et al., Eds.: 1085–1089. Ministry of Environment, Indonesian Institute of Sciences, International Society for Reef Studies, Bali, Indonesia.

- Koenig, C. *et al.* 2000. Protection of fish spawning habitat for the conservation of warm- temperate reef-fish fisheries of shelf-edge reefs of Florida. *Bull. Mar. Sci.* **66**: 593–616.
- Kuffner, I.B. *et al.* 2008. Decreased abundance of crustose coralline algae due to ocean acidification. *Nature Geoscience* In Press.
- Kurihara, H., S. Kato, & A. Ishimatsu. 2007. Effects of increased seawater pCO₂ on early development of the oyster *Crassostrea gigas*. *Aquat. Biol.* **1**: 91–98.
- Kurihara, H., S. Shimode, & Y. Shirayama. 2004. Sublethal effects of elevated concentration of CO₂ on planktonic copepods and sea urchins. *J. Oceanogr.* **60**: 743–750.
- Kurihara, H. & Y. Shirayama. 2004. Effects of increased atmospheric CO₂ on sea urchin early development. *Mar. Ecol. Prog. Ser.* **274**: 161–169.
- Kuwatani, Y. & T. Nishii. 1969. Effects of decreased pH of culture water on the growth of the Japanese pearl oyster. *Bull. Jap. Soc. Sci. Fish.* **35**: 342–350.
- Langdon, C. *et al.* 2000. Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochem. Cy.* **14**: 639–654.
- Langdon, C. *et al.* 2003. Effect of elevated CO₂ on the community metabolism of an experimental coral reef. *Global Biogeochem. Cy.* **17**: 1011, doi: 10.1029/2002GB001941.
- Langdon, C. & M.J. Atkinson. 2005. Effect of elevated pCO₂ on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *J. Geophys. Res.* **110**: np.
- Langer, M.R. *et al.* 2006. Species-specific responses of calcifying algae to changing seawater carbonate chemistry. *Geochem. Geophys. Geosyst.* **7**: np.
- Leclercq, N., J.-P. Gattuso, & J. Jaubert. 2000. CO₂ partial pressure controls the calcification rate of a coral community. *Global Change Biol.* **6**: 329–334.
- Leclercq, N. *et al.* 2002. Primary production, respiration, and calcification of a coral reef mesocosm under increased CO₂ partial pressure. *Limnol. Oceanogr.* **47**: 558–564.
- Littler, M.M. & D.S. Littler. 1984. Models of tropical reef biogenesis: the contribution of algae. *Prog. Phycol. Res.* **3**: 323–364.
- Lueker, T.J., A.G. Dickson, & C.D. Keeling. 2000. Ocean pCO₂ calculated from dissolved inorganic carbon, alkalinity, and equations for K₁ and K₂: validation based on laboratory measurements of CO₂ in gas and seawater at equilibrium. *Mar. Chem.* **70**: 105–119.
- Marshall, A.T. & P.L. Clode. 2002. Effect of increased calcium concentration in sea water on calcification and photosynthesis in the scleractinian coral *Galaxea fascicularis*. *J. Exp. Biol.* **205**: 2107–2113.
- Martin, C.L. & P.D. Tortell. 2006. Bicarbonate transport and extracellular carbonic anhydrase activity in Bering Sea phytoplankton assemblages: Results from isotope disequilibrium experiments. *Limnol. Oceanogr.* **51**: 2111–2121.
- Marubini, F., C. Ferrier-Pagès & J.P. Cuif. 2003. Suppression of skeletal growth in scleractinian corals by decreasing ambient carbonate-ion concentration: a crossfamily comparison. *Proc. Roy. Soc. Lond. B* **270**: 179–184.
- Marubini, F., H. Barnett, C. Langdon & M.J. Atkinson. 2001. Dependence of calcification on light and carbonate ion concentration for the hermatypic coral *Porites compressa*. *Mar. Ecol.-Prog. Ser.* **220**: 153–162.
- Marubini, F. & B. Thake. 1999. Bicarbonate addition promotes coral growth. *Limnol. Oceanogr.* **44**: 716–720.
- McKim, J.M. 1977. Evaluation of tests with early life stages of fish for predicting long- term toxicity. *J. Fish. Res. Board Can.* **34**: 1148–1154.
- Medina, M.A. *et al.* 2006. Naked corals: skeleton loss in Scleractinia. *Proc. Natl. Acad. Sci. USA* **103**: 9096–9100.
- Meehl, G.A. *et al.* 2007. Global Climate Projections. In *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. S. Solomon, D. Qin, M. Manning, *et al.*, Eds.: Cambridge University Press. Cambridge, UK, and New York, NY.
- Mehrbach, C. *et al.* 1973. Measurement of apparent dissociation constants of carbonic acid in seawater at atmospheric pressure. *Limnol. Oceanogr.* **18**: 897–907.
- Michaelidis, B.C. *et al.* 2005. Effects of long-term moderate hypercapnia on acid-base balance and growth rate in marine mussels *Mytilus galloprovincialis*. *Mar. Ecol. Prog. Ser.* **293**: 109–118.
- Milliman, J.D. & A.W. Droxler. 1996. Neritic and pelagic carbonate sedimentation in the marine environment: Ignorance is not bliss. *Geol. Rundsch.* **85**: 496–504.
- Mortensen, P.B. *et al.* 2001. Distribution, abundance and size of *Lophelia pertusa* coral reefs in mid-Norway in relation to seabed characteristics. *J. Mar. Biol. Assoc. UK* **81**: 581–597.
- Mortensen, P.B. 2000. *Lophelia pertusa* (Scleractinia) in Norwegian waters; distribution, growth, and associated fauna. Ph.D. thesis, University of Bergen, Bergen, Norway.
- Mucci, A. 1983. The solubility of calcite and aragonite in seawater at various salinities, temperatures, and one atmosphere total pressure. *Am. J. Sci.* **283**: 780–799.
- Mumby, P.J. *et al.* 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* **427**: 533–536.

- Ohde, S. & M.M.M. Hossain. 2004. Effect of CaCO₃ (aragonite) saturation state of seawater on calcification of Porites coral. *Geochem. J.* **38**: 613–621.
- Ohde, S. & R. Van Woesik. 1999. Carbon dioxide flux and metabolic processes of a coral reef. *Bull. Mar. Sci.* **65**: 559–576.
- Orr, J.C. *et al.* 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* **437**: 681–686.
- Palacios, S. & R.C. Zimmerman. 2007. Response of eelgrass *Zostera marina* to CO₂ enrichment: possible impacts of climate change and potential for remediation of coastal habitats. *Mar. Ecol. Prog. Ser.* **344**: 1–13.
- Pane, L. *et al.* 2004. Summer coastal zooplankton biomass and copepod community structure near the Italian Terra Nova Base (Terra Nova Bay, Ross Sea, Antarctica). *J. Plank. Res.* **26**: 1479–1488.
- Parrish, J.D. 1989. Fish communities of interacting shallow-water habitats in tropical oceanic regions. *Mar. Ecol. Prog. Ser.* **58**: 143–160.
- Petit, J.R. *et al.* 1999. Climate and atmospheric history of the past 420000 years from the Vostok ice core, Antarctica. *Nature* **399**: 429–436.
- Pollard, D.A. 1984. A review of ecological studies on seagrass fish communities, with particularly reference to recent studies in Australia. *Aquat. Bot.* **18**: 3–42.
- Portner, H.O., M. Langenbuch & A. Reipschlagel. 2004. Biological impacts of elevated ocean CO₂ concentrations: lessons from animal physiology and earth history. *J. Oceanogr.* **60**: 705–718.
- Purcell, J.E. 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. *J. Mar. Biol. Ass. UK* **85**: 461–476.
- Purcell, J.E. & M.N. Arai. 2001. Interactions of pelagic cnidarians and ctenophores with fishes: a review. *Hydrobiologia* **451**: 27–44.
- Purcell, J.E., S. Uye & W.-T. Lo. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Mar. Ecol. Prog. Ser.* **350**: 153–174.
- Reed, J.K. 2002. Deep-water *Oculina* coral reefs of Florida: biology, impacts and management. *Hydrobiologia* **471**: 43–55.
- Renegar, D.A. & B.M. Riegl. 2005. Effect of nutrient enrichment and elevated CO₂ partial pressure on growth rate of Atlantic scleractinian coral *Acropora cervicornis*. *Mar. Ecol.-Prog. Ser.* **293**: 69–76.
- Reynaud, S. *et al.* 2003. Interacting effects of CO₂ partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. *Global Change Biol.* **9**: 1660–1668.
- Riebesell, U. *et al.* 2000. Reduced calcification of marine plankton in response to increased atmospheric CO₂. *Nature* **407**: 364–367.
- Riebesell, U. *et al.* 2007. Enhanced biological carbon consumption in a high CO₂ ocean. *Nature* **450**: 545–548.
- Roberts, J.M., J.D. Gage & the ACES party. 2003. Assessing biodiversity associated with cold-water coral reefs: Pleasures and pitfalls. *Erlanger Geol. Abh.* **4**: 73.
- Roberts, J.M., A.J. Wheeler, & A. Freiwald. 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science* **312**: 543–547.
- Rogers, A.D. 1999. The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep- water reef-forming corals and impacts from human activities. *Int. Rev. Hydrobiol.* **84**: 315–406.
- Roos, A. & W.F. Boron. 1981. Intracellular pH. *Physiol. Rev.* **61**: 296–434.
- Rost, B., U. Riebesell & S. Burkhardt. 2003. Carbon acquisition of bloom-forming marine phytoplankton. *Limnol. Oceanogr.* **48**: 55–67.
- Rost, B. & U. Riebesell. 2004. Coccolithophores and the biological pump: responses to environmental changes. In *Coccolithophores—From Molecular Processes to Global Impact*. H.R. Thierstein & J.R. Young, Eds.: 76–99. Springer, Berlin Heidelberg.
- Royal Society. 2005. *Ocean Acidification Due to Increasing Atmospheric Carbon Dioxide. Policy Document 12/05*. The Royal Society, London, UK.
- Sabine, C.L. *et al.* 2004. The oceanic sink for anthropogenic CO₂. *Science* **305**: 367–371.
- Schippers, P., M. Lurling & M. Scheffer. 2004. Increase of atmospheric CO₂ promotes phytoplankton productivity. *Ecol. Lett.* **7**: 446–451.
- Schneider, K. & J. Erez. 2006. The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystroma*. *Limnol. Oceanogr.* **51**: 1284–1293.
- Sciandra, A. *et al.* 2003. Response of coccolithophorid *Emiliana huxleyi* to elevated partial pressure of CO₂ under nitrogen limitation. *Mar. Ecol.-Prog. Ser.* **261**: 111–122.
- Sheridan, P. & C. Hays. 2003. Are mangroves nursery habitat for transient fishes and decapods? *Wetlands* **23**: 449–458.
- Siegenthaler, U. *et al.* 2005. Stable carbon cycle-climate relationship during the late Pleistocene. *Science* **310**: 1313–1317.
- Silverman, J., B. Lazar & J. Erez. 2007. Effect of aragonite saturation, temperature, and nutrients on the community calcification rate of a coral reef. *J. Geophys. Res.* **112**: C05004, doi:10.1029/2006JC003770.
- Skirrow, G. & M. Whitfield. 1975. The effect of increases in the atmospheric carbon dioxide content on the carbonate ion concentration of surface water at 25°C. *Limnol. Oceanogr.* **20**: 103–108.
- Spero, H.J. *et al.* 1997. Effect of seawater carbonate concentration on foraminiferal carbon and oxygen isotopes. *Nature* **390**: 497–500.

- Stanley, G.D., Jr. 2006. Photosymbiosis and the evolution of modern coral reefs. *Science* **312**: 857–858.
- Stanley, G.D., Jr. 2007. Ocean acidification and scleractinian corals. *Science* **317**: 1032–1033.
- Stanley, G.D., Jr. & D.G. Fautin. 2001. The Origin of Modern Corals. *Science* **291**: 1913–1914.
- Stone, R.P. 2006. Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. *Coral Reefs* **25**: 229–238.
- Tortell, P.D. & F.M.M. Morel. 2002. Sources of inorganic carbon for phytoplankton in the eastern Subtropical and Equatorial Pacific Ocean. *Limnol. Oceanogr.* **47**: 1012–1022.
- Tortell, P.D., J.R. Reinfeldler, & F.M.M. Morel. 1997. Active uptake of bicarbonate by diatoms. *Nature* **390**: 243–244.
- Turley, C.M., J.M. Roberts, & J.M. Guinotte. 2007. Corals in deep-water: will the unseen hand of ocean acidification destroy cold-water ecosystems? *Coral Reefs* **26**: 445–448.
- Veron, J.E. 2008. *A Reef in Time: The Great Barrier Reef from Beginning to End*. Harvard University Press. Cambridge, MA.
- Whitfield, M. 1975. Future impact of fossil CO₂ on sea-Reply. *Nature* **254**: 274–275.
- Yates, K.K. & R.B. Halley. 2006. CO₃ concentration and pCO₂ thresholds for calcification and dissolution on the Molokai reef flat, Hawaii. *Biogeosciences* **3**: 357–369.
- Zachos, J.C. *et al.* 2005. Rapid acidification of the ocean during the Paleocene-Eocene Thermal Maximum. *Science* **308**: 1611–1615.
- Zeebe, R.E. & D. Wold-Gladrow. 2001. CO₂ in Seawater: Equilibrium, Kinetics, Isotopes. *Elsevier Oceanography Series 65*. Amsterdam. pp. 346.
- Zimmerman, R.C. *et al.* 1997. Impacts of CO₂-enrichment on productivity and light requirements of eelgrass. *Plant Physiol.* **115**: 599–607.
- Zondervan, I. 2007. The effects of light, macronutrients, trace metals and CO₂ on the production of calcium carbonate and organic carbon in coccolithophores – A review. *Deep Sea Res. II* **54**: 521–537.
- Zondervan, I. *et al.* 2001. Decreasing marine biogenic calcification: A negative feedback on rising atmospheric pCO₂. *Global Biogeochem. Cy.* **15**: 507–516.