SPECIAL ISSUE FEATURE

Ocean Acidification's Potential to Alter Global Marine Ecosystem Services

BY SARAH R. COOLEY, HAUKE L. KITE-POWELL, AND SCOTT C. DONEY

ABSTRACT. Ocean acidification lowers the oceanic saturation states of carbonate minerals and decreases the calcification rates of some marine organisms that provide a range of ecosystem services such as wild fishery and aquaculture harvests, coastal protection, tourism, cultural identity, and ecosystem support. Damage to marine ecosystem services by ocean acidification is likely to disproportionately affect developing nations and coastal regions, which often rely more heavily on a variety of marine-related economic and cultural activities. Losses of calcifying organisms or changes in marine food webs could significantly alter global marine harvests, which provided 110 million metric tons of food for humans and were valued at US$160 billion in 2006. Some of the countries most dependent on seafood for dietary protein include developing island nations with few agricultural alternatives. Aquaculture, especially of mollusks, may meet some of the future protein demand of economically developing, growing populations, but ocean acidification may complicate aquaculture of some species. By 2050, both population increases and changes in carbonate mineral saturation state will be greatest in low-latitude regions, multiplying the stresses on tropical marine ecosystems and societies. Identifying cost-effective adaptive strategies to mitigate the costs associated with ocean acidification requires development of transferable management strategies that can be tailored to meet the specific needs of regional human and marine communities.

INTRODUCTION

Human fossil fuel use and land-use changes associated with global industrialization and population growth have increased atmospheric CO_2 concentrations by about 38% from pre-industrial conditions to approximately 385 ppm today. At the same time, oceanic uptake of anthropogenic CO_2 has caused a wholesale shift in the seawater chemistry of the upper water column worldwide, increasing aqueous CO_2 [$CO_2(aq)$] and decreasing pH, carbonate ion (CO_3^{2-}) concentrations, and the saturation states (Ω) of calcium carbonate minerals such as calcite (Ω_{ca}) and aragonite (Ω_{ar}) (Feely et al., 2004; Orr et al., 2005). By 2050, atmospheric CO_2 likely will reach a range of 467–555 ppm (IPCC, 2007), which would cause further declines in surface ocean pH from, on average, 8.1 today to approximately 7.8 and decrease global mean surface Ω_{ca} and Ω_{ar} by about 25% relative to today (Cooley and Doney, 2009). The present rate of CO_2 emissions is near the upper limit or exceeds the high end of Intergovernmental Panel on Climate Change (IPCC) scenarios developed in the 1990s (Canadell et al., 2007; Raupach et al., 2007), and thus the changes in surface seawater chemistry by mid century could be even larger.

Both laboratory and in situ studies show that seawater chemistry changes due to ocean acidification (higher CO_2(aq) and lower pH, CO_3^{2-}, and Ω) can substantially alter the physiology of some marine organisms. In particular, the calcification rates of mollusks, corals, and echinoderms decline with decreasing CO_3^{2-} ion concentrations in seawater (reviewed in Kleypas et al., 2006; Fabry et al., 2008; Doney et al., 2009a). Crustacean calcification also changes (Ries et al., 2008), and the mass and calcification of planktonic lobster larvae carapaces decline (Arnold et al., 2009). Reproduction of some mollusks and echinoderms also suffers from increased seawater CO_2 concentrations (Doney et al., 2009a). In contrast, photosynthesis and nitrogen fixation of some coccolithophores, prokaryotes, and cyanobacteria either stay the same or rise in higher-CO_2 water (Doney et al., 2009a). Developing taxonomy-based conclusions about the biological consequences of ocean acidification is complicated, though, because even closely related species (e.g., *Crassostrea virginica* and *Crassostrea ariakensis*; Miller et al., 2009) or strains (e.g., coccolithophores) appear to respond differently (Iglesias-Rodriguez et al., 2008; Riebesell et al., 2000).

Species-specific studies are beginning to identify some common ecosystem-level consequences of ocean acidification associated with life histories, trophic relationships, or biological guilds. Ocean acidification does not necessarily kill the planktonic larvae of mollusks and corals, but it often delays or stunts their development of calcified structures, thus delaying settlement from the water column (Albright et al., 2008; Dupont et al., 2008; Green et al., 2009; Miller et al., 2009; Anne Cohen, Woods Hole Oceanographic Institution, *pers. comm.*, 2009). Young, slow-growing calcifiers thus may experience greater mortality either from predation or from depleting their energy for growth, metamorphosis, and reproduction (Arnold et al., 2009; Green et al., 2009). Ocean acidification seems likely to affect trophic relationships also; for example, lower pH decreases survival and development of at least one keystone predator, the calcified Atlantic Ocean brittlestar *Ophiothrix fragilis* (Dupont et al., 2008). And, ocean acidification may promote biogeographic shifts in calcifying prey such as coccolithophores, pteropods, or mollusk and coral larvae (Orr et al., 2005).

Some ecosystem-level changes caused by decreasing pH or increasing dissolved CO_2 have already been observed. In a coastal lagoon, a 0.4-unit pH decline over eight years was associated with a 10–40% decrease in calcifying organism populations (Wootton et al., 2008). Near natural CO_2 vents, no calcifying organisms were present where Ω_{ar} dipped near 1 (Hall-Spencer et al., 2008). In both studies, fleshy macroalgae and seagrasses became dominant. These results support earlier predictions that calcifiers (particularly corals and crustose coralline algae) harmed by ocean acidification and environmental damage (e.g., Anthony et al., 2008) may give way to more aquatic vegetation and herbivores (Hoegh-Guldberg et al., 2007), creating future marine ecosystems that are significantly different from today's. But, as ocean CO_2 levels rise, many people will be unaware of this profound shift in global chemistry until ocean acidification significantly affects the marine ecosystems from which people harvest food and earn income.

ECOSYSTEM SERVICES VULNERABLE TO OCEAN ACIDIFICATION

Humans' relationships with marine environments can be described by the ecosystem services and benefits to society that marine resources provide. Ecosystem services are typically divided into four categories: provisioning, regulation, culture, and support (UNEP, 2006; Millennium Ecosystem Assessment Board, 2005). These services can generate direct income, as do natural resource harvests, or they can provide benefits that are more difficult to constrain, such as cultural identity. By altering marine ecosystem function, ocean acidification is likely to affect each of these service categories.

Ocean acidification may directly affect some marine species that supply provisioning services. Mollusks and crustaceans support valuable commercial and recreational fisheries (Cooley and Doney, 2009), and coral reef ecosystems support a variety of subsistence, recreational, and commercial fisheries worldwide (Bryant et al., 1998). Calcifiers also provide pearls, shells, and coral pieces for jewelry. Declines in populations of small calcifiers, like planktonic pteropods and larval mollusks and corals, may increase competition among predatory finfish and may decrease abundance of some commercial finfish or species diversity. Provisioning services for present-day conditions are in principle straightforward to quantify, although data availability and quality are uneven. Here, we estimate marine harvests using global data from the Food and Agriculture Organization (FAO) of the United Nations, but we must interpret the data cautiously because harvest data are known to contain errors due to reporting and interannual variability in species harvests (Watson and Pauly, 2001). Improved methodologies are being developed for estimating ex-vessel landings (the price received by the fisher at the point of landing) by species and country, which can be combined with geographic catch data in the future to give spatial maps of economic revenue (Sumaila et al., 2007). Current estimates suggest that worldwide marine capture fisheries and aquaculture provided 143.7 million metric tons of marine products in 2006 (FAO, 2009). If Chinese production estimates are excluded because of the uncertainties surrounding China's data, total worldwide production adjusts to 74.5 million metric tons (FAO, 2009). Of the global total, 110 million metric tons were used directly as food for humans (FAO, 2009). The first-sale values of global marine capture fisheries and aquaculture were about US$91.2 billion and US$78.8 billion, respectively, in 2006 (FAO, 2009). Global fisheries associated with coral reefs alone are valued at US$5.7 billion annually (Conservation International, 2008). Decreases in marine harvests due to ocean acidification thus could result in significant economic losses.

Regulating ecosystem services such as coastline protection and shoreline stabilization could also be compromised by ocean acidification. Coral reefs physically buffer coastal zones from storm waves and tsunamis. Without them, losses would be greater, and coastal development would be more expensive (e.g., requiring seawalls or other fortification). The global economic value of shoreline protection by coral reefs is estimated at US$9.0 billion per year (Cesar et al., 2003). Values depend on local real estate values, storm patterns, and protected area sizes (see examples in Table 1). In many reef ecosystems, mangroves provide additional protection, but whether ocean acidification will affect mangroves is currently unknown. The full economic value of these reefs has not been estimated in detail, and unit values are likely to vary significantly with local potential for tourism and the nature and exposure of the shoreline protected by the reef. If we assume that coral reefs generate economic value on the order of \$100,000 km^{-2} yr^{-1} (the lower bound of

Sarah R. Cooley (*scooley@whoi.edu*) *is Postdoctoral Investigator, Marine Chemistry and Geochemistry, Woods Hole Oceanographic Institution, Woods Hole, MA, USA.* **Hauke L. Kite-Powell** *is Research Specialist, Marine Policy Center, Woods Hole Oceanographic Institution, Woods Hole, MA, USA.* **Scott C. Doney** *is Senior Scientist, Marine Chemistry and Geochemistry, Woods Hole Oceanographic Institution, Woods Hole, MA, USA.*

Table 1. Examples of some published ecosystem services values

Nation	Year	Value (US $)	Source
Shoreline protection by reefs			
St. Lucia	2006	$28–50 million	Burke et al., 2008
Tobago	2006	$18–33 million	Burke et al., 2008
Belize	2007	$120–180 million	Cooper et al., 2008
Shoreline protection by mangroves			
Belize	2007	$120–180 million	Cooper et al., 2008
Direct economic impacts of coral reef tourism			
Tobago	2006	$43.5 million (15% of GDP)	Burke et al., 2008
St. Lucia	2006	$91.6 million (11% of GDP)	Burke et al., 2008
Indirect economic impacts of coral reef tourism			
Trinidad & Tobago	2006	$58–86 million	Burke et al., 2008
St. Lucia	2006	$68–102 million	Burke et al., 2008
Belize	Annually	$26–69 million	Cooper et al., 2008
Reef tourism direct and indirect impacts			
Belize	2007	$150–196 million	Cooper et al., 2008

a range suggested by Burke and Maidens [2004]), the global economic value generated by the world's reefs is on the order of $30 billion per year.

Cultural ecosystem services include recreation, tourism, and spiritual and aesthetic benefits, which provide direct and indirect income for coastal communities and contribute to many communities' overall sense of identity. Especially in many developing and island nations, marine resources often generate significant values through their roles in tourism (see examples in Table 1). Recreational fishing also generates significant direct and indirect benefits for nations. In the United States, recreational saltwater fishing accounted for US$43 billion in expenditures in 2000, including all indirect expenditures on services, equipment, and travel (Steinback et al., 2004). Globally, it is likely that the economic value generated by recreational fishing is of a magnitude similar to that generated by commercial fishing. After including potential effects on nonfishing marine tourism and recreation, degradation of coastal and coral ecosystems due to ocean acidification could significantly alter the economic benefits provided by these cultural ecosystem services.

Supporting ecosystem services, such as nutrient recycling through coastal food webs or the availability of coral reef habitats, are difficult to value. Carbon sequestration, a supporting service provided by the wetlands associated with coral reef-mangrove ecosystems, has been valued at US$4.0 billion in Jamaica's Portland Bight Protected Area (Conservation International, 2008). In a synthesis of prior studies, Costanza et al. (1997)[1] estimated the biogeochemical ecosystem value of marine estuaries at the equivalent of $12,695 acre^{-1} yr^{-1} for estuaries and $10,759 acre^{-1} yr^{-1} for seagrass/algae beds, in 2007 US dollars. The role of acidification-vulnerable species in such supporting ecosystem services has not been fully resolved, and estimating the value of ocean acidification-vulnerable supporting ecosystem services remains a challenge.

If marine ecosystem services change in response to ocean acidification in ways that impose costs on economic activities, human users are likely to seek ways to mitigate these effects. Extractive users such as fishermen, aquaculturists, and seafood consumers may face additional costs if harvests of commercially or recreationally valuable marine species decrease, or their culture becomes more costly as a result of ocean acidification. Adaptation could include shifting consumption to newly prevalent wild species, shifting aquaculture production to species less strongly affected by acidification, moving centers of aquaculture to areas less affected by acidification, or moving aquaculture production to controlled environments, among others. All of these scenarios are likely to result in higher production costs, with indirect effects on supporting businesses and local and regional economies.

POTENTIAL EFFECTS ON GLOBAL SEAFOOD HARVESTS

Examining current global marine harvest patterns may shed light on the primary and secondary consequences of future ocean acidification. To illustrate the biological linkages that could change in the future, marine organisms can be grouped according to their relationships with calcifying organisms: calcifiers, their predators, top predators, and organisms that rely on calcified structures (e.g., coral, oyster beds) for habitat. Global production of all marine products in 2006, including capture and aquaculture fisheries, totaled 143.7 million metric tons and was valued at about US$170 billion (FAO, 2009; Figure 1). Of the catches that are classified, Pacific harvests are most evenly divided among the biological groups used here. The Atlantic harvests are dominated slightly by predators, while the Indian Ocean harvests and those from outside the Antarctic region ("other" in Figure 1) rely mostly on predatory finfish. Southern Ocean harvests are almost entirely krill. The heavy reliance of Atlantic and Pacific fisheries on acidification-vulnerable groups (red tones in Figure 1) and on crustaceans (yellow tones in Figure 1) suggests that if ocean acidification decreases calcifier harvests, as hypothesized by Cooley and Doney (2009), harvests in those basins could decline by millions of metric tons and billions of dollars in revenue. (Note that while crustaceans are also calcifiers, they may respond differently to ocean acidification than mollusks [Ries et al., 2008].) Moreover, changes in calcifiers' abundance or the structures they create could also affect predators or reef dwellers, further altering global harvests.

The effects of ocean acidification on calcifying organisms will have different consequences for nations, depending on their location, wealth, and reliance

[1] These estimates are for marginal values of ecosystem services. There has been considerable criticism of the Costanza et al. (1997) approach to scaling from marginal values to global values. It is appropriate to apply these marginal value estimates only to local or regional changes in habitat.

on seafood for protein (Figure 1b–d). Developing nations in the Pacific depend heavily on calcifying species, relying on mollusks, sponges, and corals for about 20% of their catches and crustaceans for another 7%. The 82 nations in this category include many small island nations that have limited agricultural alternatives. Many of these nations depend heavily on coral reefs to support subsistence or artisanal fisheries that provide both income and protein (Burke and Maidens, 2004). In contrast, industrial nations generally harvest or import mollusks and crustaceans as a relatively minor component (and often a luxury item) within a broader range of protein sources for human consumption. Adaptive strategies for addressing ocean acidification that industrial nations are already considering include enhanced aquaculture or selective breeding (e.g., Miller et al., 2009; Welch, 2009). These efforts can benefit both developed and developing nations if strategies are designed to be low cost and easy to use so that they can be applied to multiple fisheries worldwide.

The harvest breakdowns in Figure 1 underscore the need for specific additional data. Better reporting of the categories harvested, especially by developing nations, will allow better monitoring of ocean acidification impacts and development of ecosystem-specific management measures. A stronger

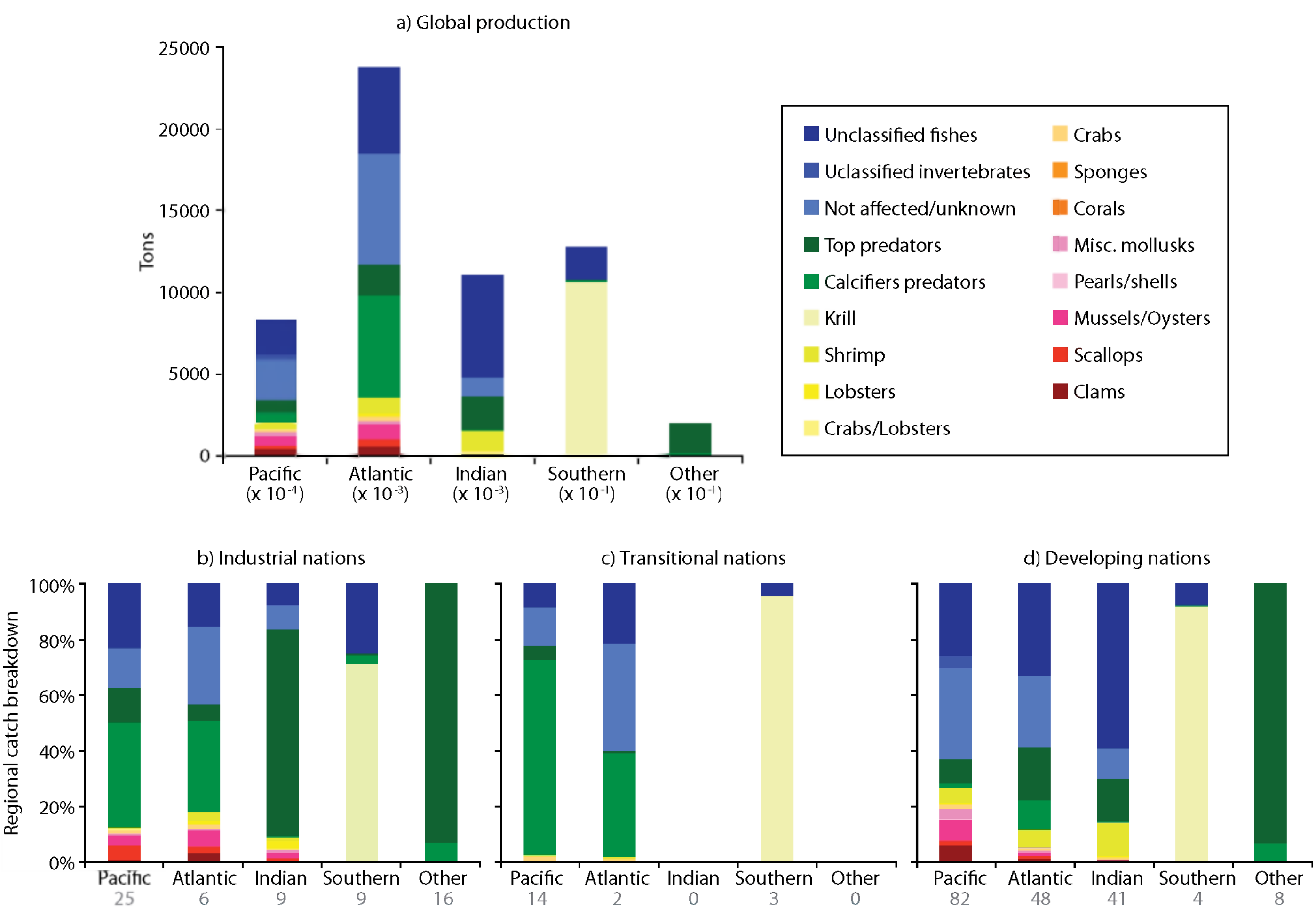

Figure 1. Summary diagrams of FAO global marine fish and fishery production (capture plus aquaculture) statistics for 2006 (FAOStat, *http://faostat.fao.org/*), grouped by biological taxonomic groups. Color families indicate biological groups that may be differently susceptible to ocean acidification: reds and oranges include mollusks, corals, and sponges; yellows indicate crustaceans; greens indicate predators that may be indirectly affected by food-web effects; and blues indicate species whose responses to acidification are unknown. (a) Global fish and fishery production, in metric tons. Note the different scaling factors (below the horizontal axis labels) applied to harvests from different regions. Proportional catches of different taxonomic groups in percent, broken down by ocean region, for (b) industrial nations, (c) transitional nations, and (d) developing nations. Numbers below the horizontal axis labels in b–d reflect the number of nations reporting catches in a particular region.

understanding of predators' trophic behavior and the role of calcifiers in the ecosystem is needed to predict the probable worldwide secondary consequences of ocean acidification on finfish stocks. Understanding prey switching and interspecies competition within ecosystems will improve our understanding of higher trophic interactions and will allow policymakers to develop appropriate management strategies.

SEAFOOD'S CONTRIBUTION TO WORLD NUTRITION

Analyzing the current global consumption of seafood and mollusks provides a starting point for understanding the possible implications of ocean acidification on global food supply. Marine capture fisheries and aquaculture provided an average of 13.6 kg per capita seafood in 2006 (FAO, 2009). The consumption of protein from seafood is unevenly distributed worldwide; in countries such as Bangladesh, Cambodia, Equatorial Guinea, French Guiana, Gambia, Ghana, Indonesia, and Sierra Leone, citizens get more than 50% of their protein from seafood (FAO, 2009). Furthermore, seafood provides at least 15% of the total daily protein for a number of countries in Southeast Asia, western coastal Africa, and western and northern Europe (Figure 2a), and it remains a significant source of dietary protein in most other developed nations and many coastal developing nations. Countries that consume the largest proportions of mollusks (Figure 2b) are developed nations in Europe and North America, as well as China and Japan, but also include the developing island nation of Fiji. Some of the high rates of seafood consumption reflect high overall protein consumption patterns, such as for the United States and European countries (Figure 2c). Developing nations, including much of Africa, India, and Southeast Asia, consume the least protein per person daily, and seafood consumption rates are mixed and reflect cultural or geographic differences.

Making the conservative assumption that protein consumption per capita will remain roughly the same by country until 2050, we can project the minimum increased protein demand in 2050 (Figure 2d) by multiplying per capita consumption by the projected population increase from 2005–2050. Population projections used in this paper are based on past and current populations from the International Data Base Division of the US Census Bureau (http://www.census.gov/ipc/www/idb/ranks.html) and use the standard exponential geometric growth models of the United Nations Statistics Division. This calculation suggests that increases in

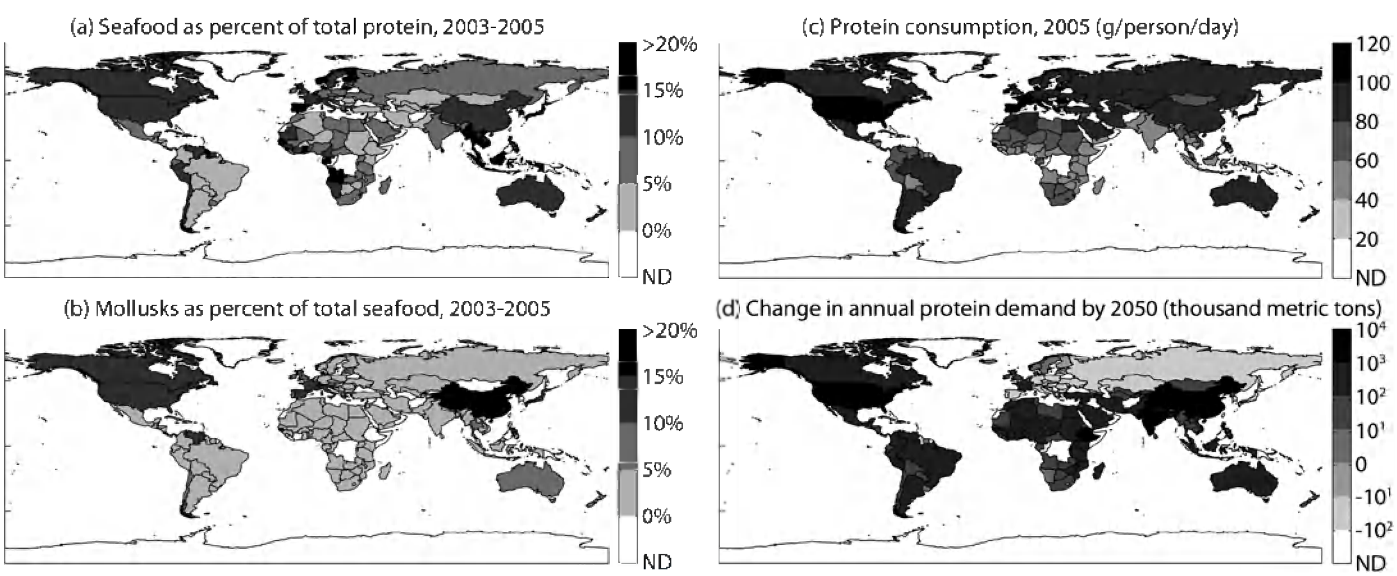

Figure 2. Global maps displaying seafood and protein consumption by country. (a) Seafood consumed as a percent of total protein consumed by weight, 2003–2005. (b) As in (a), but for mollusks as a percent of seafood. (c) Daily protein consumption per capita in 2005. (d) Estimated change in annual protein demand from 2005–2050 in thousand metric tons (see text for details). ND indicates no data. *Consumption data are from the FAOStat-Consumption database (http://faostat.fao.org)*

countries' annual protein demand by 2050 will be on the same order of magnitude in nations that are both developed (e.g., North America, Australia) and developing (e.g., South America, Africa, Asia), partly owing to the large quantities of protein consumed by developed nations and partly to the greater population growth expected in developing nations. In fact, the developing world estimates may be low because increasing wealth usually leads to increased protein consumption (Millennium Ecosystem Assessment Board, 2005).

Aquaculture has allowed global seafood production to keep pace with increasing protein demand. Global capture harvests plus aquaculture have provided about 13 kg per capita seafood annually for the past 40 years (FAO, 2009); as capture harvests declined slightly since the mid 1980s from about 12.5 kg per capita to 10 kg per capita in 2006, aquaculture harvests made up the gap (Figure 44 in FAO, 2009). Aquaculture production grew by an average of 4% per year in the developed world and by 8% per year in developing countries since 1970. Over the same period, global mollusk aquaculture grew at 7.7% per year and today exceeds 14 million metric tons and US$10 billion in annual value.

It is unclear by what mix of sources the world's protein needs will be met in 2050, but given constraints on water and other inputs to land-based agriculture, it seems likely that significant additional aquaculture production will provide a portion (Liu and Sumaila, 2007). Mollusk aquaculture is arguably the most ecologically benign form of marine seafood farming; it requires no input of feed, and filter-feeding shellfish perform valuable ecosystem services as they grow. Shellfish aquaculture today is concentrated in a few regions, but there is significant potential for expansion. Even if mollusk aquaculture grows until 2050 at only 5% per year, significantly less than its growth rate over the past four decades, it would account for over 120 million metric tons and close to US$100 billion in annual production (at today's prices) by 2050.

INTENSIFYING ENVIRONMENTAL PRESSURES ON MARINE ECOSYSTEMS

The countries expected to have the greatest proportional population growth from 2005–2050 are in the low latitudes, where the change in aragonite saturation state Ω_{ar} will be greatest (Figure 3). Here, Ω_{ar} is calculated using the Lueker et al. (2000) refit dissociation constants and dissolved inorganic carbon, alkalinity, and salinity fields generated by the Community Climate System Model (CCSM3.1) T31-gx3v5, case B31.161n (Doney et al., 2009b; Thornton et al., 2009), interpolated to a regular 2° x 2° grid for analysis. Because future surface ocean aragonite saturation state (e.g., Feely et al., 2009) in the low latitudes is estimated to remain oversaturated ($\Omega_{ar} \geq \sim 3$ by mid century and $\geq \sim 2$ by the end of the century), it is tempting to speculate that tropical ecosystems are "safer" from ocean acidification than high-latitude environments. However, the more rapid decline in Ω_{ar} by 2050 in low latitudes could be more deleterious to tropical marine ecosystems than the actual numerical value of Ω_{ar}, which is a geochemical index that does not necessarily have as direct biological relevance. Just as terrestrial insects live close to their optimal temperature ranges and future temperature increases may exceed the range over which tropical insects can adapt (Deutsch et al., 2008), marine calcifiers may be living close to their optimal chemical environment and may be strongly impacted by the coming ocean acidification-related shifts.

The combined effect of simultaneous large changes in carbonate saturation state and fast population growth in low latitudes may multiply pressures on marine ecosystems. Comparing the rate of change of Ω_{ar} with the natural variability in the ocean carbonate system places the magnitude of ocean acidification in context with ecosystems' exposure to variability (Figure 4) (Boyd et al., 2008). Ecosystems with weaker natural variability may be less resilient to anthropogenic perturbations. Figure 4 displays a map of the change in Ω_{ar} from the present to mid century ($\Omega_{ar,\,2005}-\Omega_{ar,\,2050}$), computed from the CCSM model, divided by the root mean square (RMS) of the anomaly from the mean annual cycle of Ω_{ar}, calculated after removing the long-term secular trend, for the same simulation and time period. The analysis suggests that anthropogenically driven change in Ω_{ar} over this 45-year period exceeds the natural variability of the system everywhere, but especially in the southwestern North Atlantic Ocean and in much of the western Indian and South Atlantic oceans. Compounding this chronic chemical stress, these bodies of water will experience heavy acute anthropogenic pressures as the populations surrounding them grow.

Estimating the severity of the anthropogenically driven change in Ω_{ar} by comparing it to natural variability using model data provides a conservative overview of regions under stress. Because CCSM's skill in coastal regions is limited by its resolution and its lack of realistic mesoscale physical processes, such as coastal upwelling (Collins et al., 2006), our ability to quantify ocean-acidification-associated coastal variability in carbonate chemistry with this model is very limited. In addition, seawater carbonate chemistry in nearshore regions can be altered significantly by variations in hydrology, atmospheric deposition, and nutrient runoff from land that are independent of rising atmospheric CO_2 (e.g., Doney et al., 2007; Salisbury et al., 2008; Miller et al., 2009). Making predictions about specific regions requires fine-scale coastal models (e.g., Fennel et al., 2008; Hauri et al., 2009) that include realistic circulation, river chemistry, and biogeochemical cycling. In many regions whose ecosystems are likely to be most stressed by chemical changes and population growth, much of the data needed to parameterize and evaluate such models has not yet been collected.

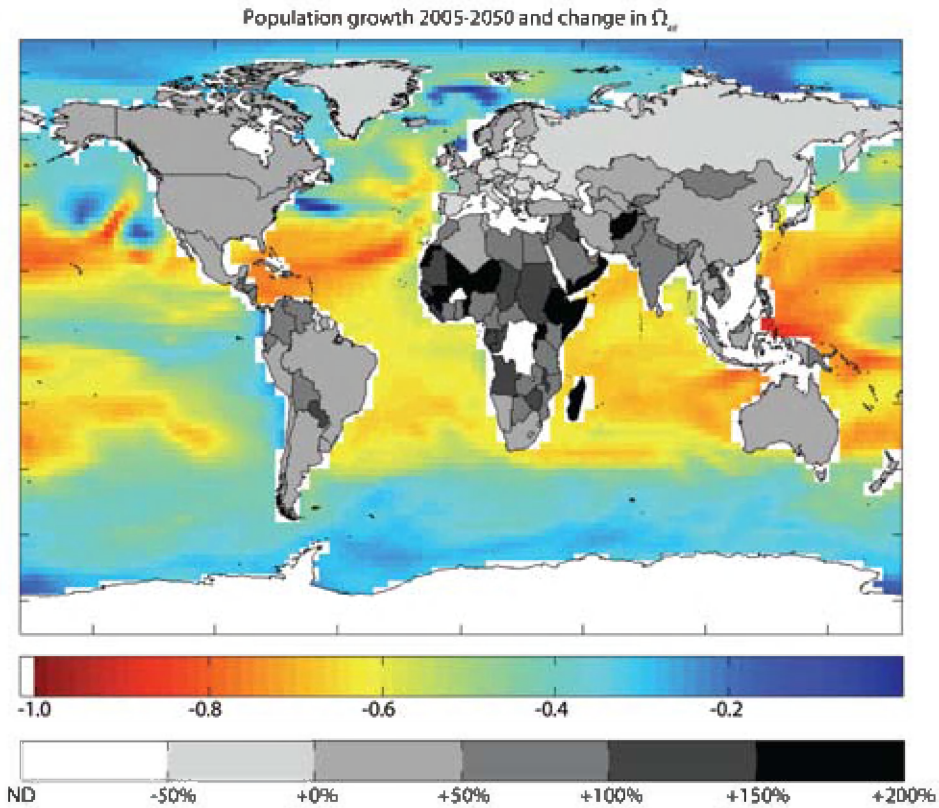

Figure 3. Global map of the percent change in each country's population growth from 2005–2050 (grayscale) and change in mean modeled surface ocean aragonite saturation state Ω_{ar} from 2005–2050. ND indicates no data. Note that both the greatest increases in population (darker shaded countries) and the greatest changes in ocean carbonate chemistry (warmer colors in ocean areas) will occur in low-latitude regions, suggesting that the greatest combined stresses in the near future may occur in tropical ecosystems.

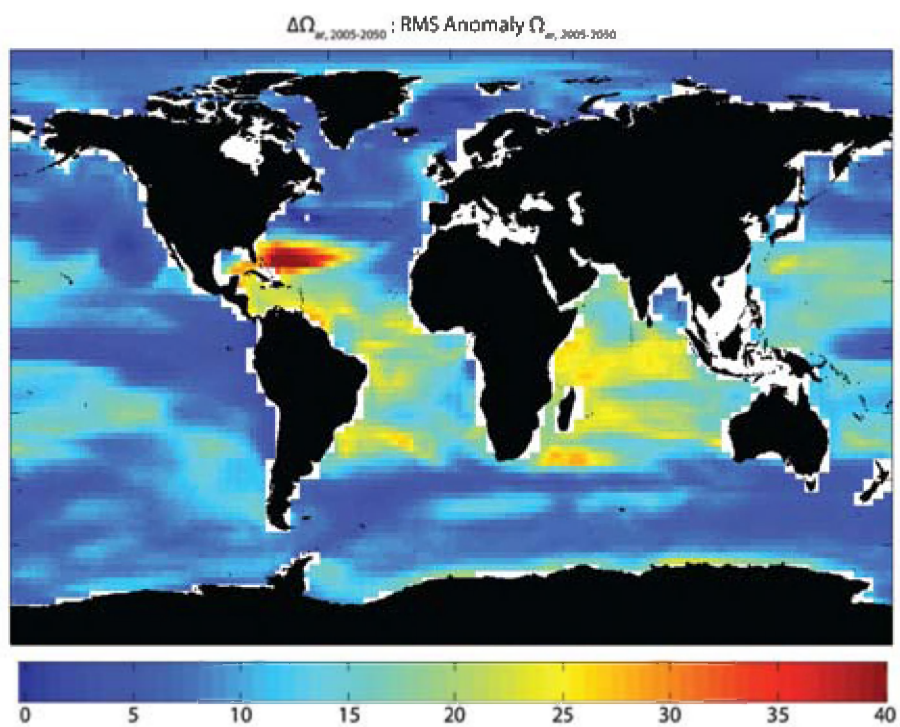

Figure 4. Global map comparing the magnitude of anthropogenic ocean acidification to natural variability. The colors display the ratio of the change in mean annual surface ocean aragonite saturation state Ω_{ar} (2005–2050) to the root mean square (RMS) anomaly of Ω_{ar} from the mean annual cycle for 2005–2050. The color bar (unitless) shows how many times greater ocean acidification is than natural variability. In other words, areas with warmer colors will have undergone shifts in ocean carbonate chemistry by 2050 that far exceed natural variability. Not only will low-latitude areas exhibit the greatest changes in ocean carbonate chemistry (Figure 3), but these changes will also far exceed natural variability in the system.

FUTURE COSTS OF OCEAN ACIDIFICATION

The future cost of ocean acidification depends on the response of the marine ecosystem and on changes in human uses of marine resources. Instead of eliminating entire swaths of marine life, ocean acidification will likely stress particular marine species, each of which will adapt to, flee from, or succumb to the new conditions. New trophic or biogeographic relationships will arise and alter marine ecosystems from their present states, also changing the beneficial services they currently provide to human communities. At present, our understanding of the roles of calcifiers in marine ecosystem services and our ability to predict adaptation in human uses are not yet sufficient to allow us to calculate the total dollar value of ocean-acidification-related changes (see, e.g., the discussion of Hoagland et al. [2002] about the complexities of estimating economic losses associated with harmful algal blooms). Nevertheless, considering the potential economic cost of acidification helps identify the missing information needed to assess adaptive strategies. Coupled ecosystem and socioeconomic models are needed to compare outcomes of different management choices and to quantify economic losses due to stressors like ocean acidification, climate change, overfishing, and pollution. Adaptations are likely to be region-specific, so these models will have to take into account local differences in resources and uses.

Because considerable uncertainties about future effects are probable, adaptive management strategies are likely to be most useful. In general, it is likely that reducing anthropogenic pressures on ocean ecosystems (e.g., mitigation of CO_2 emissions, limiting marine pollution, curtailing overfishing) will have a positive effect on the ability of marine environments to adapt to acidifying conditions, and will increase the likelihood that these ecosystems will continue to provide the services that we depend on. Ecosystem-based management and approaches that focus on collaboration among users, regulators, and policymakers are required to engage stakeholders in adjusting traditional uses of ecosystem services, if that should become necessary. Collaboration between developed and developing nations may also ease some of the burdens from the responses to ocean acidification that may be warranted. As with the effects of climate change resulting from greenhouse gas emissions, the most costly effects of ocean acidification lie mainly in the future (over time scales of decades and centuries), and their magnitudes are potentially large but uncertain. Near-term investments to mitigate these effects must compete with other pressing human needs for scarce resources, and the investments should be based on their expected contributions to reduced future losses. Sound choices about those investments will require much additional information (and many models) on the magnitude and timing of the bio-economic consequences of ocean acidification and associated uncertainties. This information will improve over time, and management strategies should adapt with it.

ACKNOWLEDGEMENTS

S. Doney and S. Cooley were supported in part by a grant from the National Science Foundation (NSF ATM-0628582). H. Kite-Powell's participation in this work was supported in part by the WHOI Marine Policy Center. We are grateful for the thoughtful suggestions of two anonymous reviewers.

REFERENCES

Albright, R., B. Mason, and C. Langdon. 2008. Effect of aragonite saturation state on settlement and post-settlement growth of *Porites astreoides* larvae. *Coral Reefs* 27(3):485–490.

Anthony, K.R.N., D.I. Kline, G. Diaz-Pulido, S. Dove, and O. Hoegh-Guldberg. 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences of the United States of America* 105(45):17,442–17,446.

Arnold, K.E., H.S. Findlay, J.I. Spicer, C.L. Daniels, and D. Boothroyd. 2009. Effect of CO_2-related acidification on aspects of the larval development of the European lobster, *Homarus gammarus* (L.). *Biogeosciences* 6:1,747–1,754.

Boyd, P.W., S.C. Doney, R. Strzepek, J. Dusenberry, K. Lindsay, and I. Fung. 2008. Climate-mediated changes to mixed-layer properties in the Southern Ocean: Assessing the phytoplankton response. *Biogeosciences* 5:847–864.

Bryant, D., L. Burke, J. McManus, and M. Spalding. 1998. *Reefs at Risk: A Map-Based Indicator of Threats to the World's Coral Reefs.* World Resources Institute, Washington DC, 60 pp.

Burke, L., S. Greenhalgh, D. Prager, and E. Cooper. 2008. *Coastal Capital–Economic Valuation of Coral Reefs in Tobago and St. Lucia.* World Resources Institute, Washington, DC, 76 pp.

Burke, L., and J. Maidens. 2004. *Reefs at Risk in the Caribbean.* World Resources Institute, Washington, DC, 80 pp.

Canadell, J.G., C. Le Quere, M.R. Raupach, C.B. Field, E.T. Buitenhuis, P. Ciais, T.J. Conway, N.P. Gillett, R.A. Houghton, and G. Marland. 2007. Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences of the United States of America* 104(47):18,866–18,870.

Cesar, H.J.S., L. Burke, and L. Pet-Soede. 2003. *The Economics of Worldwide Coral Reef Degradation.* Cesar Environmental Economics Consulting, Arnhem, and WWF-Netherlands, Zeist, The Netherlands, 23pp. Available online at: http://assets.panda.org/downloads/cesardegradationreport100203.pdf (accessed June 28, 2009).

Collins, W.D., M.L. Blackmon, G.B. Bonan, J.J. Hack, T.B. Henderson, J.T. Kiehl, W.G. Large, D.S. McKenna, C.M. Bitz, C.S. Bretherton, and others. 2006. The Community Climate System Model Version 3 (CCSM3). *Journal of Climate* 19(11):2,122–2,143.

Conservation International. 2008. *Economic Values of Coral Reefs, Mangroves, and Seagrasses: A Global Compilation.* Conservation International, Arlington, VA, USA, 23 pp.

Cooley, S.R., and S.C. Doney. 2009. Anticipating ocean acidification's economic consequences for commercial fisheries. *Environmental Research Letters* 4, 024007, doi:10.1088/1748-9326/4/2/024007.

Cooper, E., L. Burke, and N. Bood. 2008. *Coastal Capital: Economic Contribution of Coral Reefs and Mangroves to Belize.* World Resources Institute, Washington, DC, 6 pp.

Costanza, R., R. d'Arge, R. deGroot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neill, J. Paruelo, and others. 1997. The value of the world's ecosystem services and natural capital. *Nature*. 387(6630):253–260.

Deutsch, C.A., J.J. Tewksbury, R.B. Huey, K.S. Sheldon, C.K. Ghalambor, D.C. Haak, and P.R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* 105(18):6,668–6,672.

Doney, S.C., V.J. Fabry, R.A. Feely, and J.A. Kleypas. 2009a. Ocean acidification: The other CO_2 problem. *Annual Reviews in Marine Science* 1:169–192.

Doney, S.C., I. Lima, J.K. Moore, K. Lindsay, M.J. Behrenfeld, T.K. Westberry, N. Mahowald, D.M. Glover, and T. Takahashi. 2009b. Skill metrics for confronting global upper ocean ecosystem-biogeochemistry models against field and remote sensing data. *Journal of Marine Systems* 76:95–112.

Doney, S.C., N. Mahowald, I. Lima, R.A. Feely, F.T. Mackenzie, J.-F. Lamarque, and P.J. Rasch. 2007. The impact of anthropogenic atmospheric nitrogen and sulfur deposition on ocean acidification and the inorganic carbon system. *Proceedings of the National Academy of Sciences of the United States of America* 104:14,580–14,585, doi:10.1073/pnas.0702218104.

Dupont, S., J. Havenhand, W. Thorndyke, L. Peck, and M. Thorndyke. 2008. Near-future level of CO_2-driven ocean acidification radically affects larval survival and development in the brittlestar *Ophiothrix fragilis*. *Marine Ecology Progress Series* 373:285–294.

Fabry, V.J. 2008. Ocean Science: Marine calcifiers in a high-CO_2 ocean. *Science* 320:1,020–1,022, doi:10.1126/science.1157130.

FAO. 2009. *The State of Fisheries and Aquaculture 2008*. Food and Agriculture Organization of the United Nations, Rome, Italy, 196 pp.

Feely, R.A., C.L. Sabine, L. Kitack, W. Berelson, J. Kleypas, V.J. Fabry, and F.J. Millero. 2004. Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science* 305:362–366, doi:10.1126/science.1097329.

Feeley, R.A., S.C. Doney, and S.R. Cooley. 2009. Ocean acidification: Present conditions and future changes in a high-CO_2 world. *Oceanography* 22(4):36–47.

Fennel K., J. Wilkin, M. Previdi, and R. Najjar. 2008. Denitrification effects on air-sea CO_2 flux in the coastal ocean: Simulations for the northwest North Atlantic. *Geophysical Research Letters* 35, L24608, doi:10.1029/2008GL036147.

Green, M.A., G.G. Waldbusser, S.L. Reilly, K. Emerson, and S. O'Donnell. 2009. Death by dissolution: Sediment saturation state as a mortality factor for juvenile bivalves. *Limnology and Oceanography* 54(4):1,037–1,047.

Hall-Spencer, J.M., R. Rodolfo-Metalpa, S. Martin, E. Ransome, M. Fine, S.M. Turner, S.J. Rowley, D. Tedesco, and M.-C. Buia. 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* 454:96–99.

Hauri, C., N. Gruber, G.-K. Plattner, S. Alin, R.A. Feely, B. Hales, and P.A. Wheeler. 2009. Ocean acidification in the California Current System. *Oceanography* 22(4):60–71.

Hoagland, P., D.M. Anderson, Y. Kaoru, A.W. White. 2002. The economic effects of harmful algal blooms in the United States: Estimates, assessment issues, and information needs. *Estuaries* 25:819–837.

Hoegh-Guldberg, O., P.J. Mumby, A.J. Hooten, R.S. Steneck, P. Greenfield, E. Gomez, C.D. Harvell, P.F. Sale, A.J. Edwards, K. Caldeira, and others. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318(5857):1,737–1,742.

Iglesias-Rodriguez, M.D., P.R. Halloran, R.E.M. Rickaby, I.R. Hall, E. Colmenero-Hidalgo, J.R. Gittins, D.R.H. Green, T. Tyrrell, S.J. Gibbs, P. von Dassow, and others. 2008. Phytoplankton calcification in a high-CO_2 world. *Science* 320:336–339.

IPCC. 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Intergovernmental Panel on Climate Change, Geneva, Switzerland, 1,009 pp. Available online at: http://www.ipcc.ch/ipccreports/ar4-wg1.htm (accessed November 17, 2009).

Kleypas, J.A., R.A. Feely, V.J. Fabry, C. Langdon, C.L. Sabine, L.L. Robbins. 2006. *Impacts of Ocean Acidification on Coral Reefs and Other Marine Calcifiers: A Guide for Future Research.* NSF, NOAA, US Geological Survey, St Petersburg, FL, workshop report, April 18–20, 2006, 96 pp.

Liu, Y., and U.R. Sumaila. 2007. Can farmed salmon production keep growing? *Marine Policy* 3:497–501.

Lueker, T.J., A.G. Dickson, and C.D. Keeling. 2000. Ocean pCO_2 calculated from dissolved inorganic carbon, alkalinity, and equations for K-1 and K-2: Validation based on laboratory measurements of CO_2 in gas and seawater at equilibrium. *Marine Chemistry* 70(1–3):105–119.

Millennium Ecosystem Assessment Board. 2005. Ecosystems and human well-being: Current state and trends, volume 2. Millennium Ecosystem Assessment Board, 47 pp.

Miller, A.W., A.C. Reynolds, C. Sobrino, and G.F. Riedel. 2009. Shellfish face uncertain future in high-CO_2 world: Influence of acidification on oyster larvae calcification and growth in estuaries. *PLoS One* 4(5):e5661, doi:10.1371/journal.pone.0005661.

Orr, J.C., V.J. Fabry, O. Aumont, L. Bopp, S.C. Doney, R.A. Feely, A. Gnanadesikan, N. Gruber, A. Ishida, F. Joos, and others. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681–686.

Raupach, M.R., G. Marland, P. Ciais, C. Le Quere, J.G. Canadell, G. Klepper, and C.B. Field. 2007. Global and regional drivers of accelerating CO_2 emissions. *Proceedings of the National Academy of Sciences of the United States of America* 104:10,288–10,293.

Riebesell, U., I. Zondervan, B. Rost, P.D. Tortell, R.E. Zeebe, and F.M.M. Morel. 2000. Reduced calcification of marine plankton in response to increased atmospheric CO_2. *Nature* 407:364–367.

Ries, J.B., A.L. Cohen, and D.C. McCorkle. 2008. The mineralogical responses of marine calcifiers to CO_2-induced ocean acidification. *Eos, Transactions, American Geophysical Union*, Fall Meeting Supplement, Abstract 89 os33e-04.

Salisbury, J., M. Green, C. Hunt, and J. Campbell. 2008. Coastal acidification by rivers: A threat to shellfish? *Eos, Transactions, American Geophysical Union* 89(50):513–514.

Steinback, S., B. Gentner, and J. Castle. 2004. *The Economic Importance of Marine Angler Expenditures in the United States.* National Marine Fisheries Service, National Oceanic and Atmospheric Administration. NOAA Professional Paper 2. Available online at: http://aquacomm.fcla.edu/2491/ (accessed November 4, 2009).

Sumaila, U.R., A.D. Marsden, R. Watson, and D. Pauly. 2008. A global ex-vessel fish price database: Construction and applications. *Journal of Bioeconomics* 9:39–51.

Thornton, P.E., S.C. Doney, K. Lindsay, J.K. Moore, N. Mahowald, J.T. Randerson, I. Fung, J.-F. Lamarque, J.J. Feddema, and Y.-H. Lee. 2009. Carbon-nitrogen interactions regulate climate-carbon cycle feedbacks: Results from an atmosphere-ocean general circulation model. *Biogeosciences* 6:2,099-2,120.

UNEP. 2006. *Marine and Coastal Ecosystems and Human Wellbeing: A Synthesis Report Based on the Findings of the Millennium Ecosystem Assessment.* United Nations Environment Programme, 76 pp.

Watson, R., and D. Pauly. 2001. Systematic distortions in world fisheries catch trends. *Nature* 414:534–546.

Welch, C. 2009. Oysters in deep trouble: Is Pacific Ocean's chemistry killing sea life? *The Seattle Times.* June 14, 2009. Available online at: http://seattletimes.nwsource.com/html/localnews/2009336458_oysters14m.html (accessed November 4, 2009).

Wootton, J.T., C.A. Pfister, and J.D. Forester. 2008. Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. *Proceedings of the National Academy of Sciences of the United States of America.* 105(48):18,848–18,853.