8

Aquatic Life

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Introduction

According to the Intergovernmental Panel on Climate Change (IPCC), CO_2-induced global warming is increasing the temperatures of Earth's oceans and seas and lowering their pH values, a process called acidification. Both processes, according to the IPCC, are likely to harm aquatic life. "Many studies incontrovertibly link coral bleaching to warmer sea surface temperature … and mass bleaching and coral mortality often results beyond key temperature thresholds" (IPCC 2007-II, p. 235). "Modelling," the IPCC goes on to say, "predicts a phase switch to algal dominance on the Great Barrier Reef and Caribbean reefs in 2030 to 2050." The IPCC further claims that "coral reefs will also be affected by rising atmospheric CO_2 concentrations … resulting in declining calcification" (ibid.).

The Nongovernmental Panel on Climate Change (NIPCC) disagreed with the IPCC in 2009, presenting a review of the extensive literature on coral reefs showing, inter alia, that there was no simple linkage between high temperatures and coral bleaching, that coral reefs have persisted through geologic time when temperatures were as much as $10° – 15°C$ warmer than at present and when CO_2 concentrations were two to seven times higher than they are currently, and that coral readily adapts to rising sea levels (Idso and Singer, 2009).

In the following pages we review new scientific research on coral reefs, finding new support for Idso and Singer's positions, and expand the analysis to include research on the effects of rising temperature and acidification on other marine plants, marine animals, and marine ecosystems.

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8.1. Temperature-Induced Stress

8.1.1. Effects on Corals

Coral bleaching is the process whereby the corals in Earth's seas expel the algal symbionts, or *zooxanthellae*, living within their tissues, upon which they depend for their sustenance, when subjected to various environmental stresses, one of the most discussed of which is rising water temperatures. Calls for reductions in anthropogenic CO_2 emissions are often justified as necessary in order to prevent species of corals from being driven to extinction. But the science underlying this popular trope points in quite different directions.

Carricart-Ganivet and Gonzalez-Diaz (2009) measured yearly coral extension rates and densities of the dominant Caribbean reef-building coral *Montastraea annularis* for the period 1991 to 2003 at two reef sites on the northwest coast of Cuba—one in the Guanahacabibes Gulf just off the Pinar del Rio Province and the other north of Havana Bay, from which data they calculated annual coral calcification rates. Plotting the calcification data against mean annual sea surface temperature (SST, obtained from the U.K.'s Hadley Centre), Carricart-Ganivet and Gonzalez-Diaz compared their results with those of Carricart-Ganivet (2004), who had identified a similar relationship between coral calcification rate and annual average SST based on data collected from colonies of the same coral species at several localities in the Gulf of Mexico and the Caribbean Sea.

The results of the two investigations are presented in Figure 8.1.1. Coral calcification, or growth, increases linearly with temperature at a rate of approximately 0.5 g cm^{-2} year^{-1} for each 1°C increase in annual average SST. Thus the dominant reef-building corals of the tropical Atlantic Ocean seem not only to do fine, but actually to do better, when the waters within which they grow periodically warm. In addition, it is noteworthy that when Carricart-Ganivet (2004) had earlier pooled his calcification data with those of *M. annularis* and *M. faveolata* growing at Carrie Bow Cay, Belize, those from reefs at St. Croix

in the U.S. Virgin Islands, and those of *M. faveolata* at Curacao, Antilles, he also obtained a mean increase in calcification rate of ~0.5 g cm^{-2} year^{-1} for each 1°C increase in annual average SST, which finding is similar to other studies from distant locations around the world, as reported by Idso and Singer (2009).
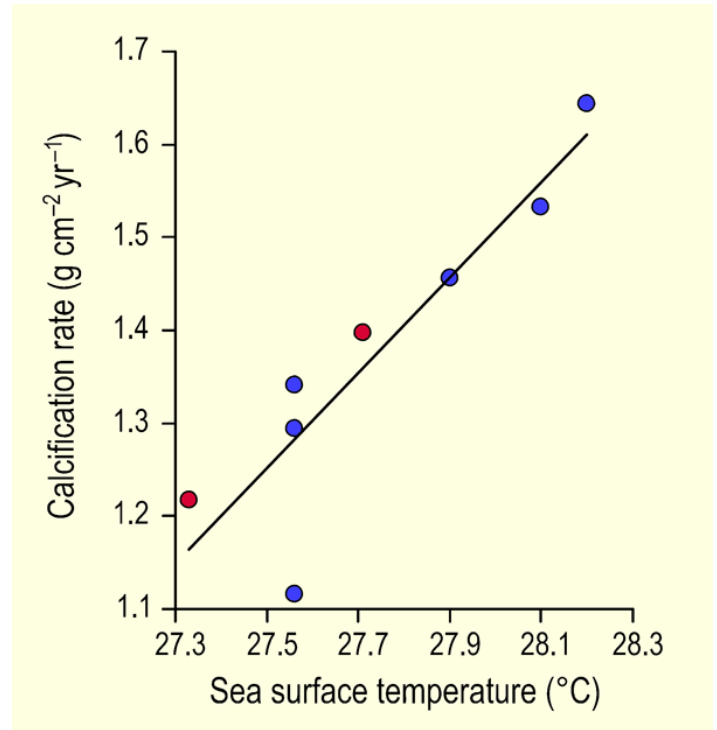
Figure 8.1.1. Mean yearly calcification rate of *Montastraea annularis* vs. mean annual sea surface temperature for the several sites studied by Carricart-Ganivet (2004) (blue circles) and the two sites studied by Carricart-Ganivet and Gonzalez-Diaz (2009) (red circles). The line that has been fit to the data is described by: Calcification Rate = 0.51 SST - 12.85 (r^2 = 0.82, p < 0.002). Adapted from Carricart-Ganivet and Gonzalez-Diaz (2009).

So why do some corals exhibit a propensity to bleach and die as temperatures rise, when the data of Carricart-Ganivet and Gonzalez-Diaz and others suggest their growth should increase? To answer this question, we turn to an article published in the journal *Coral Reefs*, where Maynard et al. (2008a) questioned the wisdom of "popularizing predictions based on essentially untested assumptions," among which they list the commonly heard claims that (1) "all corals

live close to their thermal limits" and (2) "corals cannot adapt/acclimatize to rapid rates of change."

In discussing the first of these "untested assumptions," the three Australian researchers note "predictions that reefs will disappear as a result of global warming are based, at least in part, on the assumption that corals are living close to their maximum thermal limits." However, they observe "the severity of bleaching responses varies dramatically within and among taxa," citing McClanahan et al. (2009a), and "such variable bleaching susceptibility implies that there is a considerable variation in the extent to which coral species are adapted to local environmental conditions."

The three scientists further report little is known about the sensitivity of coral population response to climate-induced changes in vital rates, but they note a large body of evidence "supports temperature tolerance varying among species, populations, communities, and reef regions (Marshall and Baird, 2000; Coles and Brown, 2003)." They conclude, "even in the absence of an adaptive response, a change in the relative abundance of species is a far more likely outcome of climate change than the disappearance of reef corals," citing Loya et al. (2001), McClanahan et al. (2002), and Hughes et al. (2003).

As to whether there is indeed "an adaptive response" in contradiction of the second untested assumption Maynard et al. (2008a) discuss, the three researchers clearly believe there is. They state, "a number of studies suggest that bleaching mortality rates have declined and thermal tolerance has increased in some regions." As one example, they report "mortality rates in the Eastern Pacific were significantly lower in 1998 when compared with 1982 and 1983 (Glynn et al., 2001)," and as another example they note "Maynard et al. (2008b) found thermal tolerance of three common coral genera on the Great Barrier Reef to be greater in 2002 than that expected from the relationship between temperature stress and bleaching severity observed in 1998."

As to how this adaptation is accomplished, the Australian scientists state there is "circumstantial evidence for ongoing evolution of temperature tolerance between both species and reefs," citing the review of Coles and Brown (2003). In addition, they suggest "symbiont shuffling from less to more stress-resistant clades is another mechanism by which corals may increase the thermal tolerance of the holobiont."

And they observe "there is growing evidence that such shuffling can increase thermal tolerance, at least in the short term," citing Berkelmans and van Oppen (2006). Maynard et al. (2008a) conclude "it is premature to suggest that widespread reef collapse is a certain consequence of ongoing bleaching, or that this will inevitably lead to fisheries collapses."

Other studies further demonstrate the resilience and adaptive nature of corals to warmer ocean temperatures. Grimsditch et al. (2010) write, "it has been shown that it is possible for [coral] colonies to acclimatize to increased temperatures and high irradiance levels so that they are able to resist bleaching events when they occur." They note, in this regard, "threshold temperatures that induce coral bleaching-related mortality vary worldwide—from 27°C in Easter Island (Wellington et al., 2001) to 36°C in the Arabian Gulf (Riegl, 1999)—according to the maximum water temperatures that are normal in the area, implying a capacity of corals and/or zooxanthellae to acclimatize to high temperatures depending on their environment."

In further exploration of this phenomenon, Grimsditch et al. examined "bleaching responses of corals at four sites (Nyali, Mombasa Marine Park, Kanamai and Vipingo) representing two distinct lagoon habitats on the Kenyan coast (deeper and shallower lagoons)." This was done for the coral community as a whole, while zooxanthellae densities and chlorophyll levels were monitored for three target species (*Pocillopora damicornis*, *Porites lutea,* and *Porites cylindrica*) during a non-bleaching year (2006) and a mild bleaching year (2007).

According to the four researchers, results indicated "during the 2007 bleaching season, corals in the shallow lagoons of Kanamai and Vipingo were more resistant to bleaching stress than corals in the deeper lagoons of Mombasa Marine Park and Nyali," which suggests, in their words, "corals in the shallower lagoons have acclimatized and/or adapted to the fluctuating environmental conditions they endure on a daily basis and have become more resistant to bleaching stress." Such results suggest corals have the ability to evolve in such a way as to successfully adjust to changing environmental conditions that when first encountered may prove deadly to a significant percentage of their populations. Those individuals genetically blessed to better withstand various stresses weather the storm, so to speak, to grow and widely proliferate another day.

In another study, Stuart-Smith et al. (2010) write, "despite increasing scientific and public concerns [about] the potential impacts of global ocean warming on marine biodiversity, very few empirical data on community-level responses to rising water temperatures are available." To help fill this important data void, they undertook, as they describe it, "a study of sub-tidal reef communities over a decadal time scale, comparing data on fishes, macroinvertebrates and macroalgae collected at 136 sites, spanning hundreds of kilometers around the island of Tasmania (southeastern Australia) in the early to mid 1990s, with data from the same sites in 2006/2007." This region, in their words, "has experienced relatively rapid warming during the last century as a consequence of a strengthening of the warm East Australian Current (Ridgway, 2007)," such that there has been "an increase in sea surface temperature of 2.28 ± 0.35°C per century for the period 1944–2002 (Ridgway, 2007), which is considerably more rapid than the global mean of 0.6 ± 0.2°C per century estimated by Smith and Reynolds (2003), and a mean increase in surface air temperature of 0.6–0.8°C (Salinger, 2005; Hansen et al., 2006)." The warming around this part of Tasmania has been more than three times greater than that of the global mean.

Contrary to what they had expected to find, the four researchers discovered "Tasmanian shallow rocky reef communities have been relatively stable over the past decade," in spite of the "substantial rise in sea surface temperature over this period" and the "continuation of a considerable warming trend in oceanographic conditions over the last 50 years." They report "the northeast and southeast bioregions, which are most influenced by the East Australian Current and hence have experienced the greatest warming over the past century, appeared to have changed very little." In addition, "not only were Tasmanian reef communities remarkably similar between 1994 and 2006 in a multivariate sense, but univariate community characteristics such as species richness and total fish abundance were also consistent." Thus, contrary to many people's expectations and the researchers' own initial thoughts on the subject, the Australian scientists found very little evidence to support the "doomsday" scenarios of the IPCC, who foresee continued global warming decimating Earth's costal marine ecosystems.

In another study, Mydlarz et al. (2008) set out to learn what resources corals may possess that could help them cope with possible future global warming and various diseases that may accompany and/or be facilitated by rising temperatures. Specifically, they documented the responses of Caribbean sea fan corals (Anthozoa, Alcyonacea; Gorgoniidae) and their cell-based immune defenses (granular acidophilic amoebocytes, which are known to be involved in wound repair and histocompatibility) to both (1) naturally occurring infections and (2) experimental inoculations with the fungal pathogen *Aspergillus sydowii*, as well as to (3) experimentally induced increases in water temperature under laboratory conditions and (4) warming associated with the 2005 Caribbean Bleaching Event, which they describe as a "once-in-hundred-year climate event."

Their results indicated "an increase of amoebocytes was observed in sea fan corals naturally temperature stressed during the 2005 Caribbean-wide bleaching event, as well as experimentally temperature stressed sea fans in the lab," and "with both naturally occurring infections and experimental inoculations with the fungal pathogen *Aspergillus sydowii*, an inflammatory response, characterized by a massive increase of amoebocytes, was evident near infections." In addition, they note "the sea fan has been shown to produce lipid-based anti-fungal metabolites which can halt growth of *A. sydowii* in culture (Kim et al., 2000)," and they note Ward et al. (2007) observed "higher anti-fungal activity of sea fans during experimental heat stress and detected a dramatic (176%) increase in potency of anti-fungal metabolites extracted from the sea fans kept at 31.5°C (2.5°C above summer ambient) and exposed to fungus, relative to controls."

What all of this reveals about the likely future of these corals, according to Mydlarz et al., is this: "taken together, these studies suggest an unexpected degree of resilience under adverse environmental conditions." Indeed, they state, "it is clear from the data presented in this paper that the sea fan aggressively combats infection in the gorgonian-*Aspergillus* pathosystem and exhibits the capability for resilience against multiple challenges," including warming of the surrounding waters.

In another study of corals, Meyer et al. (2009) write, "whether corals can adapt to increasing temperatures over the course of generations will depend in part on heritable variation in thermal physiology and dispersal potential, which may serve as the raw material for natural selection." In an effort to determine such potential, Meyer et al. "performed

controlled crosses between three genetically distinct colonies of the branching coral *Acropora millepora*," after which they "compared the families of larvae (which in this species naturally lack symbionts) for several physiological traits." This work was conducted at the standard culturing temperature of 28°C, an elevated temperature of 32°C, and an even higher temperature of 34°C that was maintained for two days.

The U.S., Canadian, and Australian researchers confirmed the existence of phenotypic variance for several pertinent thermal and dispersive factors among the families of coral they studied. This finding, in their words, "suggests the existence of considerable heritable variation in natural coral populations," which in turn supports "the possibility of effective adaptive responses to climate change." In addition, they report other analyses of the species they studied have found "high levels of genetic diversity both within and between reefs (Smith-Keune and van Oppen, 2006)," and "studies in other coral species have also uncovered substantial genetic diversity within populations (Ayre and Hughes, 2000; Underwood, 2009; Wang et al., 2009)."

Based on these findings, Myer et al. conclude, "additive genetic variance exists within coral populations for several traits that might reasonably be expected to have fitness consequences during global climate change," which "supports the possibility of effective adaptive responses to climate change."

Such effective adaptive responses might well be illustrated in another 2009 study by Scopelitis et al. (2009), who constructed a history of changes in a coral community on Saint-Leu Reef on la Reunion (a mountainous volcanic island of the Mascarene Archipelago in the South West Indian Ocean) over a period of 35 years (1973–2007). During this time the reef was subjected to a series of major devastating events, including a category 5 cyclone (Firinga, of 29 January 1989) that "caused 99% coral cover loss (Naim et al., 1997)," a severe coral bleaching event in March 2002 that followed on the heels of cyclone Dina of January 2002, plus other bleaching episodes in 1983, March–April 1987, and February 2003. Yet "despite the multiple disturbance events," in the words of the six scientists, "the coral community distribution and composition in 2006 on Saint-Leu Reef did not display major differences compared to 1973." This pattern of recurrent recovery is truly remarkable in light of the fact that "in the wake of cyclone Firinga, Saint-Leu Reef phase-shifted and

became algae-dominated for a period of five years." Remarkably, following an unnamed cyclone of 27 January 1948, *no* corals survived.

In light of these findings, the Australian and French researchers state their results suggest "a high degree of coral resilience at the site, led by rapid recovery of compact branching corals," which demonstrates the ability of corals to cope with bleaching and other devastating effects.

These studies suggest this may be the way all corals behave when not burdened by a host of local assaults on their environment through impacts of mankind. Destructive cyclones and high temperature excursions always have been a part of the coral reef environment, but the intensive activities of modern human societies have not. It is these newer activities that likely constitute the greatest threat to the health of Earth's corals. Mitigate them significantly, and coral reefs likely would cope successfully with the vagaries of nature.

In illustrating this latter point, it has been hypothesized that any increases in coral bleaching that may have occurred in response to periods of elevated water temperature over the past two decades have occurred because of a long-term weakening of coral resistance to thermal stress caused by the gradual intensification of a multitude of local anthropogenic assaults upon the environments in which corals live (Idso et al., 2000). These include, among a large number of other things, chemical insults to reef environments, such as the rising levels of nutrients and toxins in coastal waters caused by runoff from agricultural activities on land and associated increases in sediment delivery. Nearly a decade later, scientists are providing significant evidence for the validity of that contention.

Carilli et al. (2009) collected 92 cores from *Montastraea faveolata* corals growing at four different sites on the Mesoamerican Reef off the coast of Belize in the Caribbean Sea that had been exposed to either relatively high (Sapodilla Cayes, Utila) or low (Turneffe Atoll, Cayos Cochinos) chronic local stress levels induced by "(1) sedimentation, (2) nutrient input, (3) local human population size adjacent to [the] sites, and (4) a relative measure of fishing pressure based on fish abundance surveys." Then, based on measurements made on these cores, they determined yearly coral extension rates from 1955 to 2006, from which they assessed the degree of rapidity with which the corals at each site recovered

from the huge growth-retarding bleaching event of 1998.

Following the 1998 bleaching event, the researchers found, "coral growth rates at sites with higher local anthropogenic stressors remained suppressed for at least eight years, while coral growth rates at sites with lower stress recovered in two to three years." Thus the authors state "it is clear that coral colonies experiencing higher local stress before 1998 were more severely affected by bleaching and recovered more slowly than those exposed to lower chronic stress," and "local stressors such as increased sedimentation may depress a coral's energy reserves (Rogers, 1990), making it less likely to survive or recover from a bleaching event (Rodrigues and Grottoli, 2007)." Therefore, they confidently conclude "local conservation efforts that reduce stress, such as reducing runoff by replanting mangroves at the coast or protecting an area from overfishing, could have significant impacts on the ability of corals to withstand the effects of climate change," or as they state more succinctly in the final sentence of their abstract, "reducing chronic stress through local coral reef management efforts may increase coral resilience to global climate change."

In another paper illustrating the significance of local threats to coral health, authors Hoeksema and Koh (2009) note Singapore "is one of the busiest ports of the world and land area is very limited," so "space needed for industrial activities depending on maritime resources [has been] created at the coast or in the sea, which has caused suspended matter to decrease light penetration in coastal waters." In addition, they note, "besides the creation of landfills and dredging activities for port extensions, the seawater may also become sediment-enriched by logging and subsequent terrigenous run-off along the nearby coastline." And they state "all these activities may cause damage to coral growth and survival," citing the work of Dodge et al. (1974), Dodge and Vaisnys (1977), Rogers (1990), and McClanahan and Obura (1997).

Against this backdrop, Hoeksema and Koh studied the characteristics of mushroom corals (Scleractinia: Fungiidae) that had been collected from the coastal waters of Singapore or photographed in place, based on historical records and specimen collections maintained at Singapore's Raffles Museum of Biodiversity Research, which were provided by researchers in the 1860s, 1890s, 1970, 1986–1991, and 2006, with the goal of identifying all the species present at each of the times of observation.

All of the records together yielded a total of 19 species, but "four species represented in collections made before 2006 were not observed during the 2006 survey." In addition, the researchers state, three of the four species "are usually absent on reefs close to river outlets and most abundant on offshore reefs (Hoeksema and Moka, 1989; Hoeksema, 1990,1993)." This suggests, in their words, that these species "are less capable to withstand sedimentation" and, therefore, that the "increase in sediment load at Singapore is a likely cause for their disappearance."

Focusing more on the topic at hand, Hoeksema and Koh state, "although Singapore's reefs suffered severe coral bleaching in 1998, some species (including *Fungia* spp.) were also known to have recovered quite soon," citing Chou (2001). Likewise, they state, "coral populations in the offshore Thousand Islands off Jakarta showed recovery after the 1983 bleaching event (Brown and Suharsono, 1990; Hoeksema, 1991)," and "during a coral reef survey in 2005 species richness of mushroom corals in the same area showed no visible decrease in species numbers." Therefore, they continue, "coral bleaching is not a likely cause for a decrease in fungiid species richness in Singapore."

Hoeksema and Koh concluded: "The observed loss in mushroom coral species in Singapore is most likely linked to an increased sediment load of the water and the reefs as a result of land reclamation projects in the harbor of Singapore (Hilton and Chou, 1999) and deforestation of Singapore's hinterland (Brook et al., 2003)."

In examining local threats from another angle, Mumby and Harborne (2010) note that while the efficacy of no-take marine reserves in promoting biodiversity and fish biomass by reducing local-scale stressors, such as fishing, has been widely documented, there remains a need to determine "whether reserves can also build coral resilience and offset the effects of global climate change that elevate coral mortality and constrain coral calcification."

To explore this question, Mumby and Harborne "studied coral population dynamics at 10 sites throughout the Exuma Cays (Bahamas) over a 2.5-year period (2004–2007) in order to contrast the trajectories of coral populations both inside and outside reserves [that were] severely disturbed by the 1998 coral bleaching event, and later by hurricane Frances in the summer of 2004." This approach was

taken based on the oft-observed fact that "protecting large herbivorous fishes from fishing can generate a trophic cascade that reduces the cover of macroalgae," which are major competitors of corals.

The two researchers determined "the proportional increase in coral cover after 2.5 years was fairly high at reserve sites (mean of 19% per site) and significantly greater than that in non-reserve sites which, on average, exhibited no net recovery." This differential response was attributed by them to the reduced density of competing macroalgae in the marine reserves that were "depleted by more abundant communities of grazers that benefit[ed] from reduced fishing pressure." Mumby and Harborne conclude marine reserves can indeed "build coral resilience and offset the effects of global climate change." They also suggest that were it not for the site-specific deleterious effects of humanity on reef environments, this resilience likely would be the case nearly everywhere. This, in turn, suggests the local environmental impacts of human activities are what are harming Earth's corals, not the more speculative global impacts the IPCC typically blames on anthropogenic CO_2 emissions.

In a contemporaneous study, Sandin et al. (2010) note "ecological baselines of the structure and functioning of ecosystems in the absence of human impacts can provide fundamental insights for conservation and restoration," which is especially important in understanding likely responses of coral reefs to possible future global warming. Thus, Sandin et al. "surveyed coral reefs on uninhabited atolls in the northern Line Islands to provide a baseline of reef community structure, and on increasingly populated atolls to document changes associated with human activities."

On the uninhabited atolls, the 19 researchers observed fish biomass and the proportion of apex predators "greater than previously described from any coral reef ecosystem," and "high cover of reef-building corals and crustose coralline algae, abundant coral recruits, and low levels of coral disease." They also note "uninhabited reefs appear to retain greater capacity to survive or recover from major episodes of coral disease or bleaching," whereas reefs with highly altered food webs "do not." Consequently, they state the uninhabited atolls of the Line Islands "have remained remarkably intact in comparison to the global norm."

In light of their results, Sandin et al. conclude "protection from overfishing and pollution appears to increase the resilience of reef ecosystems to the effects of global warming," which is essentially the aforementioned position espoused by Idso et al. (2000), who concluded more than ten years ago that "increases in coral bleaching that may have occurred in response to periods of elevated water temperature over the past two decades have only occurred because of a long-term weakening of coral resistance to thermal stress caused by the gradual intensification of a multitude of local anthropogenic assaults upon the watery environments in which corals live."

In another view of the subject, McClanahan et al. (2009b) note many people are so convinced about the postulated negative impact of global warming on coral reefs that they automatically assume "climate overrides and undermines local resource use and management" and there is thus a "need for management of the atmosphere at the global scale."

In a study designed to evaluate that assumption, McClanahan et al. conducted surveys of coral reefs in northern Tanzania "in 2004/5 with the aim of comparing them over an ~8-year period during a time of increased efforts at fisheries management and the 1998 El Niño Southern Oscillation (ENSO) and Indian Ocean Dipole coral mortality event that caused 45% mortality in northern Tanzania and much of the Indian Ocean."

According to the Kenyan, Swedish, Tanzanian, and U.S. researchers, their repeated surveys "indicate general stability of these reefs over time," and "in the context of the high bleaching and mortality of western Indian Ocean reefs after 1998 (Goreau et al., 2000; McClanahan et al., 2007), the general stability and improvement of these reefs six to seven years after the largest ENSO in recent history (McPhaden, 1999) indicates reefs with considerable resilience to climate change."

Given that "all reefs exhibited some resilience and ecological stability and even improvements during this time of climate and management change," as they describe it, McClanahan et al. concluded this observation "creates considerably more optimism for poor countries, such as Tanzania, to effectively manage their reefs in an environment of climate change." Consequently, they state, "Tanzanian and possibly many other reefs that exhibit similar environmental conditions have the ability to recover from large-scale climatic and human disturbances."

Finally, we highlight the work of Woodroffe et al. (2010), who noted "coral reefs track sea level and are particularly sensitive to changes in climate" and

wondered whether "warmer sea surface temperatures might enable reef expansion into mid latitudes." To explore this possibility, Woodroffe et al. employed sonar mapping of the seabed topography around Lord Howe Island (31°30'S)—which is fringed by the southernmost reef in the Pacific Ocean—supplemented with single-beam echosounder and Laser Airborne Depth Sounder (LADS) data, while bottom sediments were examined using an acoustic sub-bottom profiler and a grab sampler aided by radiocarbon and uranium-series dating. This work enabled the nine researchers to discover an extensive relict coral reef around Lord Howe Island in water depths of 25–50 meters, which flourished in early Holocene times, about 9,000 to 7,000 years ago. They describe this reef as "immense," as it was "more than twenty times the area" of the modern reef at that site.

Woodroffe et al. state this finding "demonstrates that reefs were much more extensive 9000 years ago than they are at present at this latitudinal limit to reef growth," and they conclude the "relict reef, with localized re-establishment of corals in the past three millennia, could become a substrate for reef expansion in response to warmer temperatures, anticipated later this century and beyond." Indicating this situation is not unique, they report "shelf-edge reefs are common throughout the Caribbean (Hubbard et al., 2008), and backstepped to modern reef locations 7000–6500 years ago," while noting "complex early Holocene shelf reefs flourished 9000–7000 years ago in southeast Florida, at the northern latitudinal limit to reef growth, ceasing growth before 6000 calendar years before present (Toscano and Lundberg, 1998; Banks et al., 2008)." They opine that these and similar sites "may represent important refugia from increases in sea surface temperature," citing additionally in this regard the work of Riegl and Piller (2003).

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8.1.2. Effects on Other Marine Plants and Animals

Since the 2009 NIPCC report (Idso and Singer, 2009), several new studies have investigated the effects of rising temperatures on aquatic species other than corals. In this section we highlight several of them, beginning with a study examining marine phytoplankton.

Renaudie et al. (2010) conducted a quantitative micropalaeontological analysis of siliceous phytoplankton remains found in a sediment core extracted from the seabed at an ocean depth of 2,549 meters at ODP Site 1260 (~9.2°N, 54.65°W) on the Demerara Rise, which is a continental shelf located off the coast of Surinam, focusing on a 200,000-year period of warmth during the Eocene between approximately 40.0 and 40.2 million years ago. According to the five French scientists, their results indicated "the pre-warming flora, dominated by cosmopolitan species of the diatom genus *Triceratium*, was replaced during the warming interval by a new and more diverse assemblage,

dominated by *Paralia sulcata* (an indicator of high productivity) and two endemic tropical species of the genus *Hemiaulus*." In addition, they state "the critical warming interval was characterized by a steady increase in tropical species of the genus *Hemiaulus*." They also state "the microflora preserved above the critical interval was once again of low diversity and dominated by various species of the diatom genus *Hemiaulus*."

Renaudie et al.'s findings establish that warmer is better, a maxim exemplified in the current case by (1) the greater productivity of the tropical ocean during the warmer period and (2) the ocean's continuous upward trend in the diversity of phytoplanktonic species throughout the period of warming.

Simultaneously, while noting "temperature is a dominant environmental factor that mediates the behavior, physiology, growth, survival, distribution, and recruitment of ectothermic animals living in temperate and high latitudes," Stoner et al. (2010) explored how the growth and survival of the red king crab (RKC: *Paralithodes camtschaticus*) "may be affected by warming trends expected in Alaska," since the RKC was once that state's "most economically valuable crustacean fishery." Specifically, Stoner et al. reared RKC "using four temperature treatments ranging from 1.5 to 12°C for a period of 60 days, both individually and in low-density populations," and at the end of that period they measured various physiological processes and properties of the RKC.

Among other things, the three researchers report finding "temperature had no significant effect on survival of RKC," while noting "there was no consistent difference in survival between individually cultured crabs and those in populations." As for growth, they found it "was very slow at 1.5°C, and increased rapidly with temperature with both a contracted inter-molt period and small increase in growth increment." In addition, they state "20% of the crabs held at 1.5°C never molted, while more than 90% of the crabs in 12°C reached juvenile state 4 or higher." Overall, therefore, "growth increased as an exponential function of temperature, with slightly higher growth rates observed in populations than for isolated individuals." Also of great importance, they found "no evidence that culturing RKC juveniles at elevated temperatures led to a decrease in condition or nutritional status."

In addition to the benefits listed above, which bode well for the RKC in a possibly warmer future world, Stoner et al. conclude the "accelerated growth" they observed in the RKC raised at the highest temperature might yet have a "positive, indirect effect on survival," in that "larger size associated with high temperature could provide for earlier refuge in size from the typical fish and invertebrate predators on RKC."

In a study that investigated a freshwater fish species, Rypel (2009) applied tree-ring techniques to incremental growth patterns in largemouth bass (*Micropterus salmoides* Lacepede) otoliths—the aragonite ($CaCO_3$) structures in fish that are used for acoustic perception and balance—in order to explore potential relationships between annual bass growth and various climate metrics in the southeastern United States, as manifest in six rivers and seven reservoirs distributed across Alabama, Georgia, and Mississippi sampled during the summers and autumns of 2005–2008, and from which 397 largemouth bass were collected and analyzed.

Rypel reports, "results from multiple regressions suggested that on average roughly 50% of the annual variability in largemouth bass growth was attributable to climatic variations," with annual growth indices typically being found to be "above-average during the warmest, driest years, and below-average during the coldest, wettest years," because "annual bass growth was significantly negatively correlated with annual precipitation metrics, and significantly positively correlated with annual temperature metrics."

Considering these findings, the warming the IPCC contends will occur in many places would appear to be good news for largemouth bass and the people who love to catch them—and for many other types of fish as well, because an increase in temperature generally "stimulates metabolism, and enhances growth rates of fishes," according to Rypel, citing the studies of Beitinger and Fitzpatrick (1979) and Brander (1995).

In one final study with a different twist on ocean warming, Peck et al. (2010) note the loss of glaciers and ice shelves is often thought of as something that "will predominantly increase warming of the earth because of changes in albedo and heat uptake by newly uncovered ground and ocean." However, they state an important opposing effect of this phenomenon "is the opening up of new areas for biological productivity."

Working with the database of Cook et al. (2005) that contains a detailed centennial history of changes in all coastal ice fronts associated with the Antarctic

Peninsula—compiled from historical accounts, aerial photographs, and satellite imagery—Peck et al. developed a time series of changes in the surface ice/water boundary surrounding the Antarctic Peninsula since the early twentieth century. Complementing this information with a ten-year time series of chlorophyll depth profiles (1997–2007) obtained from a near-shore site in northern Marguerite Bay developed by Clarke et al. (2008), they reconstructed the magnitude of new oceanic production that developed around the Antarctic Peninsula as sea ice progressively gave way to ever-more open water.

The five researchers with the British Antarctic Survey report that as the ice cover along the Antarctic Peninsula has retreated over the past 50 years, "more than 0.5 Mtonnes of carbon has been incorporated into biological standing stock that was not there previously, 3.5 Mtonnes is fixed by phytoplankton blooms and 0.7 Mtonnes deposited to the seabed." Regarding likely future trends, they state that if only 15 percent of the remaining ice-covered areas act in the same way, "over 50 Mtonnes of new carbon would be fixed annually and around 10 Mtonnes of this deposited to the seabed in coastal or adjacent areas," while "over 9 Mtonnes of carbon would be locked up in biological communities in the water column or on the sea bed." And they suggest that over a period of tens, hundreds, or thousands of years, "this process may act as a climate control mechanism."

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8.1.3. Effects on Biodiversity

Closely tied to the prior two sections, but deserving its own treatment, is the potential effect of CO_2-induced global warming on aquatic biodiversity. Some experts claim rising temperatures will suppress or reduce ecosystem species richness. We examine this hypothesis as it pertains to both freshwater and saltwater ecosystems.

Working in Switzerland along an elevation gradient stretching from 210 to 2,760 meters above sea level, Rosset et al. (2010) identified 55 colline ponds with an overlying mean annual air temperature of more than 8°C, 27 montane ponds with mean annual air temperatures of 5–8°C, 15 subalpine ponds in the 2.5–5°C temperature range, and 16 alpine ponds with temperatures less than 2.5°C. For all of these ponds, they evaluated species richness in five taxonomic groups: aquatic vascular plants, aquatic gastropoda, aquatic coleoptera (larvae and adults), odonata adults, and amphibia. Then, utilizing 15 environmental variables—including mean annual air temperature, which they found to be "the best climatic variable to characterize pond thermal conditions"—they developed generalized additive models of species richness and used them to predict richness for the end of the next century (2090–2100) based on the temperature increase predicted to occur in conjunction with the A2 emission scenario of the IPCC.

The paper's authors found "temperature rise could significantly increase pond species richness," while noting "for the five taxonomic groups pooled, species richness would potentially increase from 41 to 75 (+83%) in lowland ponds," and "in presently species-poor high altitude ponds, the potential increase would be particularly marked, with a proportional increase (+150%; from 14–35 species) almost double that in lowland areas."

Prior to the Rosset et al. study, the effects of global warming on the biodiversity of small ecosystems had been given little attention. At the regional scale, species richness had "been shown to increase under the influence of climate warming in Europe and North America (e.g. Iverson and Prasad, 2001; Daufresne and Boet, 2007; Buisson et al., 2008)." And Rosset et al. write "it is also well-known and well-described in almost every ecology textbook, that terrestrial and freshwater species richness tends to be lower in colder areas, i.e., at higher altitude or latitude (e.g. Gaston and Spicer, 2004; Nagy and Grabherr, 2009)." They note "this trend has also been well-described at the local scale for plants, invertebrates, and vertebrates (reviewed in Rahbek, 1995)," while noting still further "among the few existing studies, Henderson (2007) and Hiddink and ter Hofstede (2008), using time series, report an increase in fish species richness in marine ecosystems in response to climate warming," and "long-term monitoring of vegetation plots in terrestrial environments indicates an increase in local species richness (Pauli et al., 2007; Vittoz et al., 2009)." Clearly, the findings of Rosset et al. harmonize well with a vast body of other research conducted at many scales and across many different environments, all of which demonstrate warming tends to increase ecosystem species richness.

Investigating another way in which temperatures have been hypothesized to harm aquatic ecosystem biodiversity, D'Odorico et al. (2008) write, "recent climate change predictions indicate that, in addition to trends in the mean values of climate variables, an increase in interannual variability is expected to occur in the near future." Adding that "environmental fluctuations are usually believed to play a 'destructive role' in ecosystem dynamics," they go on to explore the validity of this assumption within the context of current climate model predictions, asking the question, "Can environmental variability have only 'negative' effects on ecosystem dynamics?"

After lengthy mathematical analysis, D'Odorico et al. ultimately determined "opportunities for species existence/coexistence are found to increase with 'moderate' values of the variance of environmental fluctuations, while they decrease when these fluctuations are relatively strong." This outcome constitutes the "intermediate disturbance hypothesis," which grew out of the work of Connell (1978)—who in the words of D'Odorico et al. suggested "coral reefs and rain forests maintain high levels of diversity only in a non-equilibrium state"—and Huston (1979), who noted "most communities have relatively high levels of diversity because environmental variability maintains them in a non-equilibrium state." Furthermore, citing a number (Chapin et al., 1997; Steneck et al., 2002; Bengtsson et al., 2003; Elmqvist et al., 2003; Bellwood et al., 2004; Folke et al., 2004)of real-world indications that "biodiversity may enhance ecosystem resilience," the four researchers provide a theoretical basis for this phenomenon. As noted in Chapter 6, CO_2-enriched conditions that the IPCC assumes to be unfavorable may actually be just what is needed to increase the diversity and resilience of terrestrial and aquatic ecosystems.

Exploring this from another angle, Brown et al. (2010) state "climate change is altering the rate and distribution of primary production in the world's oceans," which in turn "plays a fundamental role in structuring marine food webs (Hunt and McKinnell, 2006; Shurin et al., 2006)," which are "critical to maintaining biodiversity and supporting fishery catches." They examine what the future might hold in this regard, noting "effects of climate-driven production change on marine ecosystems and fisheries can be explored using food web models that incorporate ecological interactions such as predation and competition," citing the work of Cury et al. (2008), which is what they set out to do.

Specifically, Brown et al. first used the output of an ocean general circulation model driven by a "plausible" greenhouse gas emissions scenario (IPCC 2007 scenario A2) to calculate changes in climate over a 50-year time horizon. The results were then fed into a suite of models for calculating primary production of lower trophic levels (phytoplankton, macroalgae, seagrass, and benthic microalgae), after which the results of the latter set of calculations were used as input to "twelve existing Ecopath with Ecosim (EwE) dynamic marine food web models to describe different Australian marine ecosystems." This protocol ultimately predicted "changes in fishery

catch, fishery value, biomass of animals of conservation interest, and indicators of community composition."

The 17 scientists state that under the IPCC's "plausible climate change scenario, primary production will increase around Australia" with "overall positive linear responses of functional groups to primary production change," and "generally this benefits fisheries catch and value and leads to increased biomass of threatened marine animals such as turtles and sharks." In addition, the calculated responses "are robust to the ecosystem type and the complexity of the model used." Given these findings, Brown et al. state the primary production increases suggested by their work to result from future IPCC-envisioned greenhouse gas emissions and their calculated impacts on climate "will provide opportunities to recover overfished fisheries, increase profitability of fisheries and conserve threatened biodiversity." That set of consequences is obviously different from the unmitigated catastrophe the IPCC forecasts.

Returning to real-world observations, working in lagoons on the north shore of Moorea (French Polynesia) throughout 2002–2003, Holbrook et al. (2008) used a combination of reef surveys and field experimentation to (1) estimate the functional forms of the local relationships between variation in coral cover and three attributes of the associated fish assemblage (species richness, total abundance, and species composition), and (2) isolate the influence of variation in the cover of living coral tissue from that due merely to the physical presence of the coral, be it living or dead. The latter objective was achieved through the use of 25 experimental patch reefs, which they constructed on a sand plain in the Maharepa lagoon by transplanting different proportions of live and dead colonies of the branching coral *Pocillopora eydouxi*, while the first objective was achieved by scuba divers who identified and counted all reef-associated fish and mapped the corals in each of 19 50x10-m survey plots located midway between the shore and barrier reef in the Vaipahu and Maharepa lagoons.

The results indicated "all measured attributes of the fish community were insensitive to changes in live coral cover over a wide range before falling sharply as live coral cover approached zero," and the researchers determined "there was qualitative agreement in the pattern of abundance response of fish with variation in cover of live coral between the experiment and field surveys." Holbrook et al. state "the apparent tipping point for these attributes of the fish community occurred when cover of live coral fell below 5%."

In discussing their findings, Holbrook et al. state their results suggest "that local fish assemblages could be resistant to variation in abundance of live coral, changing significantly only as coral becomes rare, while recovery may occur with only modest increases in live coral." Put another way, the three researchers state that after a major disturbance such as a temperature-induced coral bleaching episode, "the observed functional relationships in [their] study suggest that biodiversity, trophic structure, and overall abundance of fishes could essentially recover to their pre-disturbance states after only a modest return in the cover of living coral."

Similar findings have been reported by Cheal et al. (2008), who examined several responses of reef fish communities to varied levels of coral decline—caused by a combination of crown-of-thorns starfish outbreaks, coral bleaching, and cyclones—derived from annual surveys conducted over the 11-year period 1995–2005 of 22 individual reefs located between 14 and 24°S latitude that comprised parts of Australia's Great Barrier Reef system.

Based on seven different measures of species diversity, Cheal et al. found "fish diversity rarely decreased due to coral declines, even on seven reefs that suffered massive coral losses," where living coral cover declined by more than 75 percent in these "worst-case scenarios." What generally did happen was that there were often "increases in abundance of large herbivores and decreases in abundance of both coral-dependent fishes and species with no obvious dependence on coral."

The five researchers write their findings are "encouraging," in that "maintenance of fish diversity should assist recovery of fish species whose abundances declined with coral cover," and "maintenance of a wide taxonomic range of species should also confer greater stability on a community during major perturbations through functional redundancy." They speculate, however, that "widespread abundance decreases might lead to loss of ecosystem function," yet they add "the significance of the functional roles of many fish taxa to coral reef resilience is not known, nor is it clear what abundances of fishes are necessary to retain ecosystem services." Consequently, their "compelling" finding that "reef fish diversity was

maintained despite large coral declines" must indeed be considered to be "encouraging," as they described it.

In another coral reef-related study, Stuart-Smith et al. (2010) write, "despite increasing scientific and public concerns [about] the potential impacts of global ocean warming on marine biodiversity, very few empirical data on community-level responses to rising water temperatures are available." In an effort designed to help fill this important data void, the authors undertook what they describe as "a study of sub-tidal reef communities over a decadal time scale, comparing data on fishes, macroinvertebrates and macroalgae collected at 136 sites, spanning hundreds of kilometers around the island of Tasmania (southeastern Australia) in the early to mid 1990s, with data from the same sites in 2006/2007." This region, in their words, "has experienced relatively rapid warming during the last century as a consequence of a strengthening of the warm East Australian Current (Ridgway, 2007)," such that there has been "an increase in sea surface temperature of 2.28 ± 0.35°C per century for the period 1944–2002 (Ridgway, 2007), which is considerably more rapid than the global mean of 0.6 ± 0.2°C per century estimated by Smith and Reynolds (2003), and a mean increase in surface air temperature of 0.6–0.8°C (Salinger, 2005; Hansen et al., 2006)." In fact, the warming around this part of Tasmania has been more than three times greater than that of the global mean.

Contrary to what they had expected to find, the four researchers discovered "Tasmanian shallow rocky reef communities have been relative stable over the past decade," in spite of the "substantial rise in sea surface temperature over this period" and the "continuation of a considerable warming trend in oceanographic conditions over the last 50 years." Indeed, they report "the northeast and southeast bioregions, which are most influenced by the East Australian Current and hence have experienced the greatest warming over the last century, appeared to have actually changed very little," adding "not only were Tasmanian reef communities remarkably similar between 1994 and 2006 in a multivariate sense, but univariate community characteristics such as species richness and total fish abundance were also consistent." Thus, contrary to many people's expectations as well as their own initial thoughts on the subject, the Australian scientists found very little evidence to support the IPCC's doomsday scenarios in which continued global warming decimates Earth's highly productive costal marine ecosystems.

In one final study based on real-world observations, Rombouts et al. (2009) developed the first global description of geographical variation in the diversity of marine copepods, which are small crustaceans that are found throughout the world's oceans and form a key trophic link between phytoplankton and fish, some of which are planktonic and drift in sea water, and some of which are benthic and live on the ocean floor. The results of their work indicated "ocean temperature was the most important explanatory factor among all environmental variables tested, accounting for 54 percent of the variation in diversity." Hence it was not surprising that "diversity peaked at subtropical latitudes in the Northern Hemisphere and showed a plateau in the Southern Hemisphere where diversity remained high from the equator to the beginning of the temperate regions." This pattern, in their words, "is consistent with latitudinal variations found for some other marine taxa, e.g. foraminifera (Rutherford et al., 1999), tintinnids (Dolan et al., 2006) and fish (Worm et al., 2005; Boyce et al., 2008), and also in the terrestrial environment, e.g. aphids, sawflies and birds (Gaston and Blackburn, 2000)."

"Given the strong positive correlation between diversity and temperature," the six scientists write, "local copepod diversity, especially in extra-tropical regions, is likely to increase with climate change as their large-scale distributions respond to climate warming." This state of affairs is much the same as what has typically been found on land for birds, butterflies, and several other terrestrial life-forms as their ranges expand and overlap in response to global warming. And with more territory available to them, their "foothold" on the planet becomes ever stronger, fortifying them against forces (many of them human-induced) that might otherwise lead to their extinction.

In considering all of the results presented above, it is difficult not to conclude that global warming—be it natural or anthropogenic—will likely enhance the biodiversity of aquatic ecosystems.

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8.2. Marine and Freshwater Acidification

The global increase in the atmosphere's CO_2 content has been hypothesized to possess the potential to harm corals and other aquatic life by inducing changes in water chemistry that can lead to reductions in the calcium carbonate saturation state of the water in which the organisms live, producing negative responses in various growth and developmental parameters, and in some cases even death.

Concerns about the viability of Earth's corals and other calcifying organisms were brought to light in the debate over rising anthropogenic CO_2 emissions with the publication of the papers of Kleypas et al. (1999) and Langdon et al. (2000), which claimed the ongoing rise in the air's CO_2 content was slowly but surely lowering oceanic pH, making it increasingly difficult for calcifying organisms to produce their calcium carbonate skeletons and possibly leading to their extinction. In summarizing the anxiety expressed by the IPCC on this issue, Feely et al. (2009) reviewed what is supposedly known about the current pH status of the world's oceans, as well as what they state it is likely to be by the end of the century.

The three researchers write in the abstract of their paper, "estimates based on the Intergovernmental Panel on Climate Change business-as-usual emission scenarios suggest that atmospheric CO_2 levels could approach 800 ppm near the end of the century," and "corresponding biogeochemical models for the ocean indicate that surface water pH will drop from a pre-industrial value of about 8.2 to about 7.8 in the IPCC A2 scenario by the end of this century." As a result, they state, "skeletal growth rates of calcium-secreting organisms will be reduced," ending with the warning that "if anthropogenic CO_2 emissions are not dramatically reduced in the coming decades, there is the potential for direct and profound impacts on our living marine ecosystems."

Expressing similar sentiments on the subject of ocean acidification, Pelejero et al. (2010) write, "the surface waters of the oceans have already acidified by an average of 0.1 pH unit from pre-industrial levels," and "by the end of the twenty-first century, projections based on different scenarios indicate that ocean pH will have decreased by 0.3 to 0.4 pH unit." This "steady acidification of the oceans (nicknamed the 'evil twin' of global warming)," as they describe it, is said by them to be yet another "insidious consequence of rising levels of atmospheric CO_2," and "evidence gathered over the last years suggests that ocean acidification could represent an equal (or perhaps even greater) threat to the biology of our planet."

In assessing these claims, we should first consider the absolute pH values pertinent to them. The preindustrial-to-present 0.1-pH-unit drop reported to have occurred by Pelejero et al. represents a decline from a mean value of about 8.16 to a value of 8.06, as best as can be discerned from their graphical representation of the decline. However, another of their graphs depicts interannual pH variations in the North Atlantic Ocean near Bermuda ranging from a high of approximately 8.18 to a low of about 8.03 at

various times over the period 1984 to 2007 (Bates, 2007), which demonstrates that even larger pH variations are occurring in some ocean basins as a result of seasonal seawater pH variability.

Even greater natural pH variability is evident on both shorter and longer time scales in still other of Pelejero et al.'s graphs. Over a mere two days in July 2001 on a Molokai (Hawaii) Reef flat, for example, seawater pH ranged from a high of 8.29 to a low of 7.79 (Yates and Halley, 2006); and over a period of about a decade in the mid-twentieth century, the pH at Arlington Reef in Australia's Great Barrier Reef system ranged from a high of approximately 8.25 to a low of about 7.71 (Wei et al., 2009). Both of these natural and recurring pH declines (0.50 and 0.54) are greater than the 0.3 to 0.4 projected decline that Pelejero et al. expect to occur between now and the end of the century. What is more, the calcifying organisms in these regions have fared just fine, as they have faced and successfully adapted to each of these worse-than-"evil" pH declines.

Moving more closely to the substance of the analysis of Pelejero et al., Tans (2009) found the pH decline expected by Pelejero et al. between now and the end of the century is fully twice as great as what is likely to occur in reality, and that by AD 2500 the spatial and vertical pH distributions within the world's oceans will likely have returned to almost the same sets of values that are characteristic of today.

Tans begins his analysis by indicating the effect of CO_2 on climate—and on its own concentration in the atmosphere—"depends primarily on the total amount emitted, not on the rate of emissions," and that "unfortunately, the IPCC reports have not helped public understanding of this fact by choosing, somewhat arbitrarily, a rather short time horizon (100 years is most commonly used) for climate forcing by CO_2." Thus, "instead of adopting the common economic point of view, which, through its emphasis on perpetual growth, implicitly assumes infinite earth resources," Tans notes the cumulative extraction of fossil-fuel carbon currently stands at about 345 GtC, and that there appears to be another 640 or so GtC of proven reserves, yielding a total original reserve of about 1,000 GtC, from which he proceeds with his analysis.

Figure 8.2.1 shows much of the past and projected history of fossil-fuel carbon utilization, together with historical and projected atmospheric CO_2 concentrations out to the year 2500, as calculated by Tans. As can be seen there, his analysis indicates the air's CO_2 concentration peaks well before 2100 and at only 500 ppm, as compared to the 800 ppm projected by the IPCC. In addition, by the year 2500 the air's CO_2 concentration will have fallen to about what it is today.

Based on his more modest projections of future atmospheric CO_2 concentrations, Tans also finds the projected pH reduction of ocean waters in the year 2100 (as compared to preindustrial times) to be only one-half of the 0.4 value calculated by Feely et al. (2009) and Pelejero et al. (2010), with a recovery to a
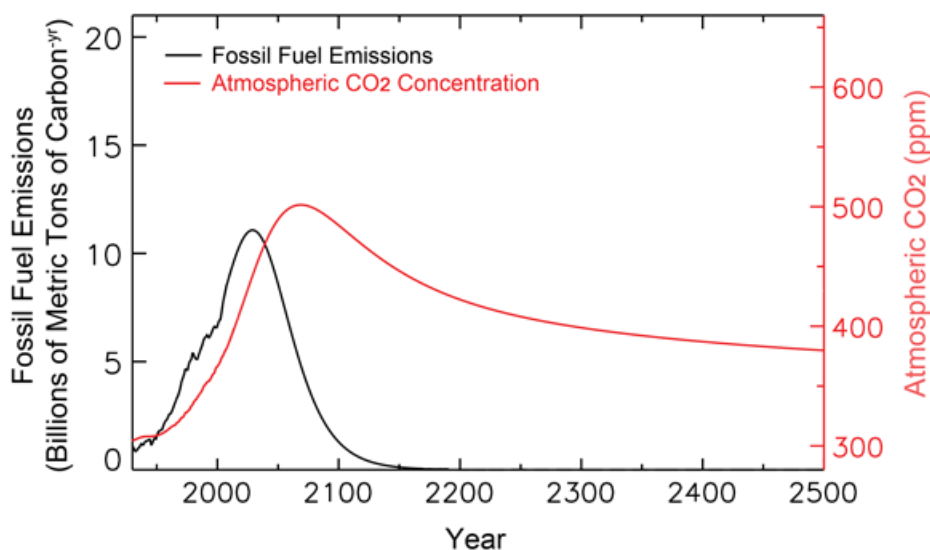
Figure 8.2.1. Past and projected trends of fossil-fuel carbon utilization and atmosphereic CO_2 concentration. Adapted from Tans (2009).

reduction of just over 0.1 pH unit by 2500, which is less than the range of pH values typical of today's oceans (8.231 in the Arctic Ocean minus 8.068 in the North Indian Ocean equals 0.163, according to Feely et al.).

Another reason to doubt Pelejero et al.'s forecast of falling pH levels is that high rates of aquatic photosynthesis by marine micro- and macro-algae, which have been shown to be stimulated and maintained by high levels of atmospheric CO_2—see, for example, Wu et al. (2008), Fu et al. (2008), and Egge et al. (2009)—can dramatically increase the pH of marine bays, lagoons, and tidal pools (Gnaiger et al., 1978; Santhanam et al., 1994; Macedo et al., 2001; Hansen, 2002; Middelboe and Hansen, 2007) and significantly increase the surface-water pH of areas as large as the North Sea (Brussaard et al., 1996). Thus it is logical to presume anything else that enhances marine photosynthesis, such as nutrient delivery to the waters of the world's coastal zones (i.e., eutrophication), may increase pH as well.

Thinking along these lines, Borges and Gypens (2010) employed an idealized biogeochemical model of a river system (Billen et al., 2001) and a complex biogeochemical model describing carbon and nutrient cycles in the marine domain (Gypens et al., 2004) "to investigate the decadal changes of seawater carbonate chemistry variables related to the increase of atmospheric CO_2 and of nutrient delivery in the highly eutrophied Belgian coastal zone over the period 1951–1998."

The findings of the two researchers indicate, as they describe it, that "the increase of primary production due to eutrophication could counter the effects of ocean acidification on surface water carbonate chemistry in coastal environments," and "changes in river nutrient delivery due to management regulation policies can lead to stronger changes in carbonate chemistry than ocean acidification," as well as changes that are "faster than those related solely to ocean acidification." And to make these facts perfectly clear, they add, "the response of carbonate chemistry to changes of nutrient delivery to the coastal zone is stronger than ocean acidification."

As more and more pertinent studies have been conducted, the extreme view of ocean acidification has been greatly tempered. In a review of the subject by Doney et al. (2008), for example, it was reported many calcifying species "exhibit reduced calcification and growth rates in laboratory experiments under high-CO_2 conditions," but they also report "some photosynthetic organisms (both calcifying and non-calcifying) have higher carbon fixation rates under high CO_2." And as Idso et al. (2000) have noted in the case of corals, the "photosynthetic activity of zooxanthellae is the chief source of energy for the energetically-expensive process of calcification," and much evidence suggests, in their words, that "long-term reef calcification rates generally rise in direct proportion to increases in rates of reef primary production."

In light of these divergent observations, plus the fact that most of what we know about the topic "stems largely from short-term laboratory and mesocosm experiments," as Doney et al. describe them, the latter conclude the ultimate long-term response of "individual organisms, populations, and communities to more realistic gradual changes [in atmospheric CO_2 concentration] is largely unknown." Additionally acknowledging, therefore, that "the broader implications for ocean ecosystems are not well known," they state "the impact of rising CO_2 on marine biota will be more varied than previously thought." Instead of one grand catastrophe for Earth's calcifying marine life, there may well be both "winners and losers," as they put it, with the vast bulk of species likely sandwiched somewhere in between these two extremes. In fact, when real-world evidence for rapid adaptation and evolution is considered, the future actually looks quite bright for Earth's aquatic (and terrestrial) life (Idso, 2009; Idso and Idso, 2009).

In the ensuing subsections we review the results of numerous ocean acidification experiments that have been performed on various types of marine organisms, results that further demonstrate ocean acidification is not as bad as the IPCC makes it out to be.

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8.2.1. Effects on Marine Plants

8.2.1.1. Phytoplankton

Writing in the Journal Club section of *Nature*, Stoll (2009) restates the IPCC's mantra that "ocean acidification in response to excess carbon dioxide in the atmosphere could become a problem for marine organisms, especially those that make skeletons or shells out of calcium carbonate," including "the coccolithophorids—microscopic algae that are, by volume, the most important shell producers." She has a much more optimistic view of the subject, however, thanks in large part to the research of Langer et al. (2009).

The latter scientists—hailing from France, Germany, Spain, and the Netherlands—grew four different strains of the coccolithophore *Emiliania*

huxleyi in dilute batch cultures of seawater with carbonate chemistries characteristic of those expected to prevail beneath an atmosphere of four different CO_2 concentrations ranging from approximately 200 to 1200 ppm, while they measured particulate organic carbon content, particulate inorganic carbon content, and organic and inorganic carbon production. In doing so, they found the four strains "did not show a uniform response to carbonate chemistry changes in any of the analyzed parameters and none of the four strains displayed a response pattern previously described for this species."

In light of these findings—plus other aspects of their earlier studies (Langer et al., 2006, 2007) and the diverse findings of others who had studied still other strains of the species—the five scientists concluded "the sensitivity of different strains of *E. huxleyi* to acidification differs substantially and that this likely has a genetic basis." Stoll agrees with this assessment, stating that Langer et al. "argue convincingly" in this regard, and she adds that the work of those who foresee disastrous consequences typically "precludes the kind of natural selection and adaptation that might occur over decades and centuries in the ocean."

In further discussing the subject, Langer et al. (2009) write, "shifts in dominance between species and/or between clones within a species might therefore be expected," as the air's CO_2 content continues to rise; but they state that too often "the possibility of adaptation is not taken into account." This should not be assumed away, for the great genetic diversity that exists both among and within species, in the words of Stoll, "is good insurance in a changing ocean." Indeed, this could be interpreted as evidence that Earth's coccolithophorids are well prepared for whatever the future may thrust at them in this regard, for as Langer et al. (2006) have more boldly and explicitly stated, "genetic diversity, both between and within species, may allow calcifying organisms to prevail in a high CO_2 ocean."

Support for that notion was, in fact, provided one year earlier. Based on data obtained from a sediment core extracted from the subpolar North Atlantic Ocean, Iglesias-Rodriguez et al. (2008) determined there had been a 40 percent increase in oceanic coccolith mass over the past 220 years, during which time the atmosphere's CO_2 concentration rose by approximately 90 ppm. They further found this response to be consistent with the results of several batch incubations of the far-ranging coccolithophore

species *Emiliania hyxleyi*, conducted while bubbling air of several different atmospheric CO_2 concentrations through the culture medium they employed for that purpose.

Working with materials derived from the same sediment core, Halloran et al. (2008) analyzed the size distribution of $CaCO_3$ particles in the less-than-10-µm sediment fraction over the past quarter-century. This analysis revealed "a changing particle volume since the late 20th century consistent with an increase in the mass of coccoliths produced by the larger coccolithophore species," which included *Oolithotus fragilis, Calcidicus leptoporus, Coccolithus pelagicus* var. *pelagicus,* and *Helicosphaera carteri*.

Commenting on their findings, Halloran et al. state their data suggest "in the real ocean the larger coccolithophore species increase their calcification in response to anthropogenic CO_2 release," and "such a calcification response could be attributed to an alleviation of CO_2 limitation in species that partly rely on the diffusive supply of dissolved carbon dioxide for photosynthesis, as demonstrated by a rise in photosynthetic efficiency with increasing carbon dioxide in cultures of *E. huxleyi* (Rost et al., 2003)."

Examining other phytoplankton, Lombard et al. (2010) studied the effects of ocean acidification on two planktonic foraminifera, which in the words of the authors, "are widespread calcifying protozoa, responsible for 32–80% of the global deep-ocean calcite fluxes (Schiebel, 2002)." Working with specimens of *Orbulina universa* collected by scuba divers off the coast of Catalina Island, California, and *Globigerinoides sacculifer* obtained near Puerto Rico, USA, Lombard et al. cultured them under high and low irradiances in filtered sea water whose pH and carbonate ion concentration—$[CO_3^{2-}]$—were manipulated by adding NaOH or HCl. Among other things, the data they collected in these experiments included "measurements of the initial and final size (µm), the survival time (days from collection to gametogenesis), and final weight of the shell (µg)," but only for "individuals that underwent gametogenesis and grew at least one chamber."

The four researchers report "under the IS92a 'business as usual' scenario as defined by the Intergovernmental Panel on Climate Change and projected for the year 2100," their results suggest "in 2100, the rate of calcification of *G. sacculife*r and *O. universa* could decline by 6–13% compared to recent rates." In addition, they state "the future increase in

temperature [predicted by the IPCC] could increase the production of calcite by foraminifera, counteracting the negative impact of ocean acidification." In addition, the results of the analysis of Tans (2009), illustrated in Figure 8.2.2, suggest (1) the true decline in oceanic pH by the year 2100 is more likely to be only about half of that projected by the IPCC and (2) this drop will begin to be ameliorated after 2100, gradually returning oceanic pH to present-day values after 2500.

In another experiment on foraminifers, Kuroyanagi et al. (2009) cultured asexually produced individuals of *Marginopora kudakajimensis*—a calcifying microorganism that contributes to both organic and inorganic carbon production in coral reefs—under carefully controlled laboratory conditions for a period of 71 days in glass jars containing approximately 110 ml of filtered natural seawater (control pH of about 8.2) and two less-basic pH conditions of about 7.9 and 7.7, created by additions of 0.1 N HCl.

In declining from the control pH of 8.2 to a pH of 7.9, the mean maximum shell diameter of the large foraminifer actually rose by 8.6 percent, while its mean shell weight rose by a much smaller and insignificant 0.7 percent. As the seawater's pH declined to 7.7, however, the organism's mean maximum shell diameter fell by 12.1 percent, and its mean shell weight fell by 49.3 percent.

Based on these results, Kuroyanagi et al. conclude that if oceanic pH remains within the range of 8.2 to 7.9, the "large foraminifers should be able to maintain present calcification rates," but they note any further drop in pH could lead to reduced rates of calcification. That said, although the IPCC's A2 scenario predicts a maximum pH decline of approximately 0.5 pH units by about AD 2270, the more recent analysis of Tans (2009) suggests a maximum pH drop of only about 0.14 unit at about AD 2090, after which pH begins to rise to asymptotically return to its current value after several hundred years. This latter projection suggests oceanic pH will not come close to creating a major decline in the calcification rate of *M. kudakajimensis*.
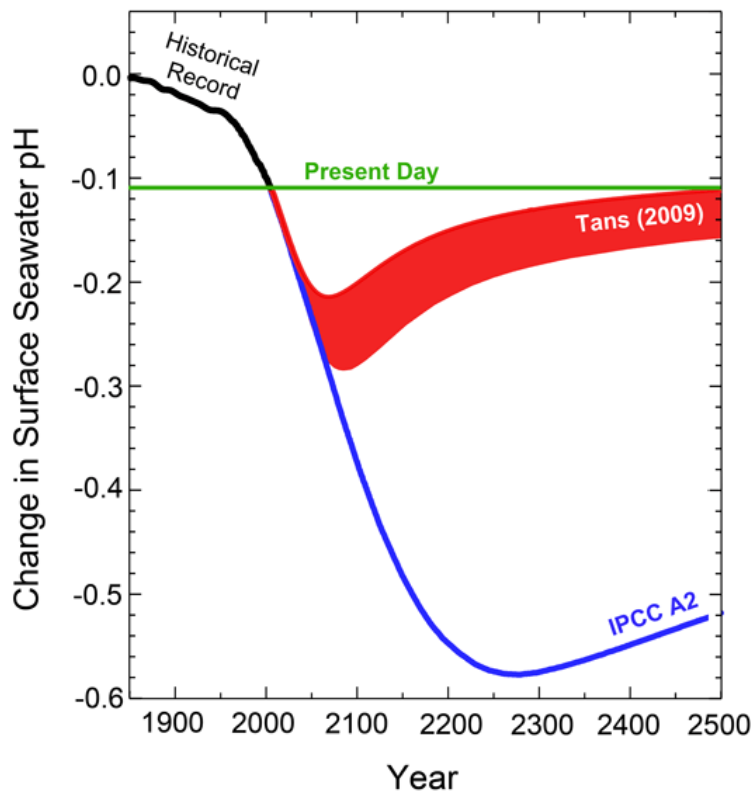
Figure 8.2.2. Change in surface seawater pH vs. time as observed for the prior century and a half and as calculated by the IPCC and Tans (2009) for the next five centuries.

We next report the results of two ocean acidification studies on phytoplankton communities. In prefacing their work, Wyatt et al. (2010) state "the assimilation of inorganic nutrients fuels phytoplankton growth," and, therefore, "any alteration in the bioavailability of these nutrients is likely to impact productivity and, by extension, climate regulation through the uptake of CO_2 by marine algae." They note "the reduction of surface ocean pH anticipated for the next century will alter the equilibrium coefficient between dissolved ammonia (NH_3(aq)) and ammonium (NH_4^+) shifting the equilibrium towards NH_4^+ (Zeebe and Wolf-Gladrow, 2001; Bell et al., 2007, 2008)," such that the future decease in ocean pH due to the ongoing rise in the air's CO_2 content could result in the transfer of more gaseous NH_3 from the overlying atmosphere to the ocean, as has been noted by Jacobson (2005).

To further explore this scenario, Wyatt et al. collected surface seawater samples from a coastal monitoring site in the western English Channel (WEC) from 17 March to 21 July 2008, which included two distinct phases of the annual spring phytoplankton bloom (a pre-bloom period of five weeks and the bloom proper of 11 weeks). In addition, they measured ambient pH for carbonate system estimates and dissolved inorganic nutrients, and they equilibrated the samples with CO_2-in-air mixtures that resulted in CO_2 concentrations of 380, 500, 760, and 1,000 ppm that led to pH values of 8.05, 8.01, 7.87, and 7.76, respectively, which are to be compared with the mean ambient value of 8.18.

The six scientists report their results indicated the phytoplankton community "was predominantly limited by the availability of inorganic nitrogen," and "during early and mid-summer, NH_X became the primary source of inorganic nitrogen." Interestingly, they also report "an overall increase in NH_X concentrations by 20% was observed between the present day CO_2 treatment (380 ppm) and 1000 ppm."

Given these findings, Wyatt et al. write, "as excess CO_2 dissociates in the oceans, the increased hydrogen ion concentration ionizes NH_3(aq) and decreases the ratio of NH_3(aq):NH_4^+," and this reduction in NH_3(aq) "would lead to an imbalance in the equilibrium between NH_3(aq) in the surface water and gaseous NH_3 in the overlying atmosphere resulting in the drawdown of atmospheric NH_3 to the surface ocean." Based on this finding, they further calculate that whereas the surface waters of the WEC "are a net source of 150 μmol/m^2/year of NH_3 to the

atmosphere at present (2009)," it is likely "the WEC will become a net sink of 300 μmol/m^2/year for atmospheric NH_3 as atmospheric CO_2 rises to 717 ppm and the surface pH decreases to 7.83," due to the increase in phytoplanktonic productivity driven by the increased transfer of gaseous NH_3 from the air to the surface waters of the WEC. This phenomenon would (1) boost the productivity of higher oceanic trophic levels, (2) help sequester more carbon at the bottom of the sea, and thereby (3) reduce the rate of increase in radiative forcing that is speculated to fuel global warming.

In a contemporaneous study of a phytoplankton community, Breitbarth et al. (2010) write as background for their report, "studies of artificial and natural iron input have demonstrated iron control of phytoplankton productivity and CO_2 drawdown over vast oceanic regions (Boyd et al., 2007; Blain et al., 2007; Pollard et al., 2009) and in coastal upwelling regions (Bruland et al., 2001; Hutchins and Bruland, 1998)," and they state "temporal control of iron on phytoplankton productivity was also observed in a Norwegian fjord system (Ozturk et al., 2002)."

Following the development of natural phytoplanktonic blooms in the Pelagic Ecosystem CO_2 Enrichment (PeECE III) study—where the blooms were monitored in mesocosms consisting of two-meter-diameter polyethylene bags submerged to a depth of ten meters in an adjacent fjord, where they were maintained in equilibrium with air possessing CO_2 concentrations of either 350, 700, or 1,050 ppm via aeration of the water column and the overlying atmosphere with air of the three CO_2 concentrations (Schulz et al., 2008), Breitbarth et al. measured dissolved iron (dFe) concentrations as well as levels and oxidation rates of Fe(II)—a necessary trace element (the ferrous species of iron) used by almost all living organisms—over the course of the study to determine whether ocean acidification may affect iron speciation in seawater.

The eight researchers report CO_2 perturbation and phytoplanktonic bloom development resulted in pH value ranges of 7.67–7.97, 7.82–8.06, and 8.13–8.26 at 1,050, 700, and 350 ppm CO_2, respectively. They state their measurements revealed significantly higher dFe concentrations in the high CO_2 treatment compared to the mid and low CO_2 treatments, and that the high-CO_2 mesocosms showed higher values of FE(II) compared to the lower CO_2 treatments.

Breitbarth et al. thus conclude "ocean acidification may lead to enhanced Fe-bioavailability

due to an increased fraction of dFe and elevated Fe(II) concentrations in coastal systems ... due to pH induced changes in organic iron complexation and Fe(II) oxidation rates," noting these phenomena "will result in increased turnover of Fe in surface seawater, potentially maintaining iron bioavailability given a sufficient supply of total Fe, since equilibrium partitioning eventually restores the biolabile Fe pools that have been depleted by biological uptake." They suggest "these processes may further fuel increased phytoplankton carbon acquisition and export at future atmospheric CO_2 levels," citing the work of Riebesell et al. (2007). They thus reach their final conclusion that "changes in iron speciation and the resulting potential negative feedback mechanism of phytoplankton productivity on atmospheric CO_2"— i.e., the drawdown of atmospheric CO_2 due to enhanced phytoplanktonic growth and transferal of the carbon thus removed from the atmosphere to the ocean depths—"need to be considered when assessing the ecological effects of ocean acidification."

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8.2.1.2. Macroalgae

Writing as background for their study, Jiang et al. (2010) note "seagrasses are flowering plants that thrive in shallow oceanic and estuarine waters around the world, and are ranked as one of the most ecologically and economically valuable biological systems on earth," citing the work of Beer et al. (2006). They state *Thalassia hemprichii* "is among the most widely-distributed seagrass species in an Indo-Pacific flora, dominating in many mixed meadows," citing the work of Short et al. (2007).

In conducting their analysis, the authors collected intact vegetative plants of *T. hemprichii* from Xincun Bay of Hainan Island, Southern China, which they transported to the laboratory and cultured in flow-through seawater aquaria bubbled with four different concentrations of CO_2 representative of (1) the present global ocean, with a pH of 8.10, (2) the projected ocean for 2100, with a pH of 7.75, (3) the projected ocean for 2200, with a pH of 7.50, and (4) the ocean characteristic of "an extreme beyond the current predictions" (a hundredfold increase in free CO_2, with a pH of 6.2).

The three researchers report the "leaf growth rate of CO_2-enriched plants was significantly higher than that in the unenriched treatment," that "nonstructural carbohydrates (NSC) of *T. hemprichii*, especially in belowground tissues, increased strongly with elevated CO_2," and "belowground tissues showed a similar response with NSC."

The Chinese scientists identify several implications of their findings that "CO_2 enrichment enhances photosynthetic rate, growth rate and NSC concentrations of *T. hemprichii*." With higher atmospheric CO_2 concentrations, they note, "colonization beyond current seagrass depth limits is possible"; the extra stored NSC "can be used to meet the carbon demands of plants during periods of low photosynthetic carbon fixation caused by severe environmental disturbance such as underwater light reduction"; it can enhance "rhizome growth, flowering shoot production and vegetative proliferation"; and it "may buffer the negative effects of transplant shock by increasing rhizome reserve capacity." They also write, "the globally increasing CO_2 may enhance seagrass survival in eutrophic coastal waters, where populations have been devastated by algal proliferation and reduced column light transparency," and "ocean acidification will stimulate seagrass biomass and productivity, leading

to more favorable habitat and conditions for associated invertebrate and fish species."

Also researching the potential effects of ocean acidification on macroalgae were Xu et al. (2010), who write, "*Gracilaria lemaneiformis* (Bory) Weber-van Bosse is an economically important red seaweed that is cultivated on a large scale in China due to the quantity and quality of agar in its cell walls." In addition, they state "much attention has been paid to the biofiltration capacity of the species (Yang et al., 2005, 2006; Zhou et al., 2006)," and that it has thus been suggested to be "an excellent species for alleviating coastal eutrophication in China (Fei, 2004)." Considering these important characteristics of this seaweed, the authors set out to examine how this aquatic plant might respond to elevated CO_2.

In conducting their experiment, plants were grown from thalli—collected at 0.5 m depth from a farm located in Shen'ao Bay, Nanao Island, Shantou (China)—for 16 days in 3-L flasks of natural seawater maintained at either natural (0.5 μM) or high (30 μM) dissolved inorganic phosphorus (Pi) concentrations in contact with air of either 370 or 720 ppm CO_2, while their photosynthetic rates, biomass production, and uptake of nitrate and phosphate were examined.

As best as can be determined from Xu et al.'s graphical representations of their results, algal photosynthetic rates in the natural Pi treatment were increased only by a non-significant 5 percent as a result of the 95 percent increase in the air's CO_2 concentration, and in the high Pi treatment they were increased by approximately 41 percent. In the case of growth rate or biomass production, on the other hand, the elevated CO_2 treatment exhibited a 48 percent increase in the natural Pi treatment, whereas in the high Pi treatment there was no CO_2-induced increase in growth, because the addition of the extra 29.5 μM Pi boosted the biomass production of the low-CO_2 natural-Pi treatment by approximately 83 percent, and additional CO_2 did not increase growth rates beyond that point.

The three Chinese researchers state "elevated levels of CO_2 in seawater increase the growth rate of many seaweed species despite the variety of ways in which carbon is utilized in these algae," noting "some species, such as *Porphyra yezoensis* Ueda (Gao et al., 1991) and *Hizikia fusiforme* (Harv.) Okamura (Zou, 2005) are capable of using HCO_3^-, but are limited by the current ambient carbon concentration in seawater," and "enrichment of CO_2 relieves this limitation and enhances growth." Regarding the

results they obtained with *Gracilaria lemaneiformis*, on the other hand—which they state "efficiently uses HCO_3^- and whose photosynthesis is saturated at the current inorganic carbon concentration of natural seawater (Zou et al., 2004)"—they write, "the enhancement of growth could be due to the increased nitrogen uptake rates at elevated CO_2 levels," which in their experiment were 40 percent in the natural Pi treatment, because "high CO_2 may enhance the activity of nitrate reductase (Mercado et al., 1999; Gordillo et al., 2001; Zou, 2005) and stimulate the accumulation of nitrogen, which could contribute to growth." Whatever strategy might be employed, these several marine macroalgae appear to be capable of benefiting greatly from increased atmospheric CO_2 concentrations.

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8.2.2. Effects on Marine Animals

8.2.2.1. Bivalves

In the introductory material to their paper on potential effects of predicted near-future increases in CO_2-driven ocean acidification on shell-producing calcification in a species of oyster, Watson et al. (2009) report over the past two centuries CO_2 emissions from deforestation and the burning of fossil fuels have increased atmospheric CO_2 concentrations from 280 to 380 ppm, citing NOAA/ESRL records produced and maintained by Pieter Tans. They additionally state the portion of this extra CO_2 that has been taken up by the planet's oceans has caused a 0.1 unit drop in the pH of their surface waters, which would appear to be correct. However, they predict there will be a further reduction in ocean pH of 0.3 to 0.5 units by 2100, citing the work of Haugan and Drange (1996), Orr et al. (2005), and Caldeira and Wickett (2005), while noting these predicted changes in ocean pH "are not only greater but far more rapid than any experienced in the last 24 million years,"

citing Blackford and Gilbert (2007), or "possibly the last 300 million years," citing Caldeira and Wickett (2003). But how likely are such predictions?

Consider the findings of Tans himself, who Watson et al. approvingly cite in regard to the CO_2 history they mention. In a paper published in *Oceanography*, Tans (2009) concluded the future trajectory of oceanic pH will likely be significantly different from that suggested by the scientists cited by Watson et al., while at the same time bravely criticizing the IPCC reports that also have accepted the highly inflated acidification predictions of those scientists. Indeed, whereas Watson et al. and the IPCC accept the claims of those who project a decline in pH somewhere in the range of 0.3 to 0.5 between now and the end of the century, Tans' projections yield a pH decline somewhere in the range of 0.09 to 0.17, which would be expected to have significantly reduced biological impacts compared to those suggested by the experimental work of Watson et al.

Based on the results of their experiments and the maximum decline in ocean-water pH they accept, Watson et al. predict a significant decline of 72 percent in Sydney rock oyster (*Saccostrea glomerata*) larval survival by the year 2100. However, utilizing Watson et al.'s data but with the maximum ocean-water pH decline calculated by Tans, one obtains a non-significant larval survival decline of only 14 percent, based on interpolation of the graphical results portrayed in Watson et al.'s paper. Similar assessments of changes in antero-posterior measurement yield a significant decline of 8.7 percent using Watson et al.'s assumptions about ocean pH, but a non-significant decline of only 1.8 percent according to Tans' pH calculations. Corresponding results for dorso-ventral measurement were a significant decline of 7.5 percent with Watson et al.'s pH values, but a non-significant decline of only 1.5 percent with Tans' values, and for larval dry mass there was a decline of 50 percent in Watson et al.'s analysis, but an actual increase (albeit non-significant) of 6 percent using Tans' pH analysis. Last, for empty shells remaining there was a significant decline of 90 percent in the Watson et al. study, but a non-significant decline of only 6 percent when Tans' pH projections were used.

Based on their experimental data and the ocean pH projections for the end of the century that are promoted by them and the IPCC, Watson et al. find what they characterize as "a dramatic negative effect on the survival, growth, and shell formation of the

early larval stages of the Sydney rock oyster." On the other hand, employing the pH values projected by Tans, there are no statistically significant reductions in any of the five biological parameters measured and evaluated by Watson et al.

In a separate effort designed to project potential CO_2-induced changes in estuarine calcification in the years ahead, larvae of two oyster species—the Eastern oyster (*Crassostrea virginica*) and the Suminoe oyster (*Crassostrea ariakensis*)—were grown by Miller et al. (2009) for up to 28 days in estuarine water in equilibrium with air of four different CO_2 concentrations (280, 380, 560, and 800 ppm), which were chosen to represent atmospheric conditions in the preindustrial era, the present day, and the years 2050 and 2100, respectively, as projected by the IS92a business-as-usual scenario of the IPCC, which were maintained by periodically aerating the different aquaria employed in the study with air containing 1 percent CO_2. Larval growth was assessed via image analysis, and calcification was determined by means of chemical analyses of calcium in the shells of the oyster larvae.

When the larvae of both species were cultured continuously from 96 hours post fertilization for 26 to 28 days while exposed to elevated CO_2 concentrations, the authors state they "appeared to grow, calcify and develop normally with no obvious morphological deformities, despite conditions of significant aragonite undersaturation." They write these findings "run counter to expectations that aragonite shelled larvae should be especially prone to dissolution at high pCO_2." More specifically, the authors state "both oyster species generated larval shells that were of similar mean thickness, regardless of pCO_2, O_{arag} [aragonite compensation point] or shell area," remarking they "interpret the pattern of similar shell thickness as further evidence of normal larval shell development." And because these two calcifying organisms appeared not to have suffered deleterious consequences, the four researchers concluded "biological responses to acidification, especially [in] calcifying biota, will be species specific and therefore much more variable and complex than reported previously."

In another study examining "the very earliest, and critical, process of fertilization," Havenhand and Schlegel (2009) collected specimens of the oyster *Crassostrea gigas*—which they obtained from a mixed mussel/oyster bed on the coast of western Sweden and kept within flow-through tanks of filtered sea water that they maintained at either (1) the normal ambient pH level or (2) a level reduced by about 0.35 units that was created by bubbling CO_2 through the water—and observed and measured the species' sperm-swimming behavior and fertilization kinetics. Their results indicated that in water of pH 8.15, mean sperm-swimming speeds were 92.1 ± 4.8µm/s, but in water of pH 7.8 they were slightly higher, at 94.3 ± 5.5µm/s, although the difference was not statistically significant. Mean fertilization success in water of pH 8.15 was 63.4 percent, whereas in water of pH 7.8 it was also slightly higher at 64.1 percent, although this difference, too, was not statistically significant.

Based on these findings, the Swedish scientists state "the absence of significant overall effects of pH on sperm swimming behavior and fertilization success is remarkable," and they emphasize the power analyses they conducted "showed clearly that these results were not due to inadequate statistical power." Moreover, they write, "the absence of significant effect is likely a true reflection of the responses of *Crassostrea gigas* gametes and zygotes from the Swedish west coast to levels of CO_2-induced acidification expected by the end of this century," a very encouraging finding.

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8.2.2.2. Cephalopods

In studying the common cuttlefish, *Sepia officinalis*, Gutowska et al. (2008) found it "is capable of not only maintaining calcification, but also growth rates and metabolism when exposed to elevated partial pressures of carbon dioxide." Over a six-week test period, they found "juvenile *S. officinalis* maintained calcification under ~4000 and ~6000 ppm CO_2, and grew at the same rate with the same gross growth efficiency as did control animals," gaining approximately 4 percent body mass daily and increasing the mass of their calcified cuttlebone by more than 500 percent. These findings led them to conclude specifically that "active cephalopods possess a certain level of pre-adaptation to long-term increments in carbon dioxide levels," and to conclude generally that our "understanding of the mechanistic processes that limit calcification must improve before we can begin to predict what effects future ocean acidification will have on calcifying marine invertebrates."

In another study examining the common cuttlefish (*Sepia officinalis*) and published one year later, Lacoue-Labarthe et al. (2009) monitored fertilized eggs of this species throughout their full development time at controlled temperature (16 or 19°C) and pH (8.1, 7.85, or 7.6) conditions. The latter values were maintained within ± 0.05 of a pH unit by periodically bubbling pure CO_2 into the bottles (which were continuously aerated with CO_2-free air), resulting in mean CO_2 concentrations of the air in contact with the surface of the water of either 400, 900, or 1,400 ppm.

This group of authors found "decreasing pH resulted in higher egg weight at the end of development at both temperatures ($p < 0.05$), with maximal values at pH 7.85 (1.60 ± 0.21 g and 1.83 ± 0.12 g at 16°C and 19°C, respectively)." In addition, they found "hatchlings were smaller when they developed at 16°C than at 19°C ($p < 0.05$)." They also observed zinc (Zn) accumulation "was higher at pH 7.85 during the full developmental period," when "high embryonic requirements for Zn are not fully covered by the maternal pool," so the higher accumulation of Zn "was associated with a greater rate of growth of both egg and embryo." Concurrently, there was also a greater accumulation of potentially detrimental silver in the tissues of the hatchlings; but any deleterious effects of the extra silver were apparently more than overcome by the positive effects of lowered pH on beneficial zinc accumulation, while toxic cadmium accumulation was actually reduced in the lower pH (or higher CO_2) treatments.

The seven scientists conclude their paper by noting "decreasing pH until 7.85," such as could be expected to occur in air enriched with carbon dioxide to a concentration of 900 ppm, "should lead to some possibly beneficial effects, such as a larger egg and presumably hatchling size and a better incorporation of the essential element[s] such as Zn in the embryonic tissue." These phenomena, in their words, "may improve the survival [of] the newly hatched juveniles."

Given the findings of both papers presented above, it would appear the ongoing rise in the air's CO_2 content would benefit cuttlefish.

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8.2.2.3. Miscellaneous

In a Brevia item published in *Science*, Checkley et al. (2009) "grew eggs and pre-feeding larvae of white sea bass (*Atractoscion nobilis*) under a range of CO_2 concentrations [380, 993, and 2,558 ppm] and measured the size of their sagittal otoliths," which, in the words of the authors, "are bony structures used by fish to sense orientation and acceleration and consist of aragonite-protein bilayers," or as the dictionary states, they are "small vibrating calcareous particles in ... the ears of some animals, especially of fishes." Noting atmospheric CO_2 enrichment has been calculated, on a purely chemical basis, to decrease the saturation state of carbonate minerals such as aragonite in the world's oceans, the six scientists "hypothesized that otoliths in eggs and larvae reared in seawater with elevated CO_2 would grow more slowly than they do in seawater with normal CO_2." To test this hypothesis they conducted their experiment.

"Contrary to expectations," in the words of Checkley et al., "the otoliths of fish grown in seawater with high CO_2, and hence lower pH and aragonite saturation, were significantly larger than those of fish grown under simulations of present-day conditions." More specifically, the researchers found "for 7- to 8-day-old fish grown under 993 and 2558 ppm CO_2, the areas of the otoliths were 7 to 9% and 15 to 17% larger, respectively, than those of control fish grown under 380 ppm CO_2."

As for why the otoliths were larger at a lower pH, the marine researchers went on to state young fish are "able to control the concentration of ions (H^+ and Ca^{2+}) ... in the endolymph surrounding the otolith," where "with constant pH, elevated CO_2 increases CO_3^{2-} concentration and thus the aragonite saturation state, accelerating formation of otolith aragonite."

Dupont et al. (2010) state, "echinoderms are among the most abundant and ecologically successful groups of marine animals (Micael et al., 2009), and are one of the key marine groups most likely to be impacted by predicted climate change events," presumably because "the larvae and/or adults of many species from this phylum form skeletal rods, plates, test, teeth, and spines from an amorphous calcite crystal precursor, magnesium calcite, which is 30 times more soluble than normal calcite (Politi et al., 2004)." This fact would normally be thought to make it much more difficult for them (relative to most other calcifying organisms) to produce calcification-dependent body parts.

Working with naturally fertilized eggs of the common sea star *Crossaster papposus*, which they collected and transferred to five-liter culture aquariums filled with filtered seawater (a third of which was replaced every four days), Dupont et al. tested this hypothesis by regulating the pH of the tanks to values of either 8.1 or 7.7 by adjusting environmental CO_2 levels to either 372 ppm or 930 ppm. During the testing period they documented (1) settlement success as the percentage of initially free-swimming larvae that affixed themselves to the aquarium walls, (2) larval length at various time intervals, and (3) degree of calcification.

The three researchers report just the opposite of what is often predicted actually happened, as the echinoderm larvae and juveniles were "positively impacted by ocean acidification." More specifically, they found "larvae and juveniles raised at low pH grow and develop faster, with no negative effect on survival or skeletogenesis within the time frame of the experiment (38 days)." In fact, they state the sea stars' growth rates were "two times higher" in the acidified seawater; and they remark, "*C. papposus* seem to be not only more than simply resistant to ocean acidification, but are also performing better."

Given these findings, the Swedish scientists concluded, "in the future ocean, the direct impact of ocean acidification on growth and development potentially will produce an increase in *C. papposus* reproductive success" and "a decrease in developmental time will be associated with a shorter pelagic period with a higher proportion of eggs reaching settlement," causing the sea stars to become "better competitors in an unpredictable environment." Not bad for a creature that makes its skeletal rods, plates, test, teeth, and spines from a substance that is 30 times more soluble than normal calcite.

Lastly, Rodolfo-Metalpa et al. (2010) worked with bryozoans or "moss animals"—a geologically important group of small animals that resemble corals and are major calcifiers, found on rocky shores in cool-water areas of the planet, where they comprise a significant component of the carbonate sediments in shallow sublittoral habitats, and where they form long-lived, three-dimensional structures that provide attachment sites for numerous epifauna and trap sediment and food for a variety of infauna—in what they describe as "the first coastal transplant experiment designed to investigate the effects of naturally acidified seawater on the rates of net calcification and dissolution of the branched calcitic

bryozoan *Myriapora truncata*." They did this by transplanting colonies of the species to normal (pH 8.1), high (pH 7.66), and extremely high (pH 7.43) CO_2 conditions at gas vents located just off Italy's Ischia Island in the Tyrrhenian Sea, where they calculated the net calcification rates of live colonies and the dissolution rates of dead colonies by weighing them before and after 45 days of *in situ* residence in May–June (when seawater temperatures ranged from 19 to 24°C) and after 128 days of *in situ* residence in July–October (when seawater temperatures ranged from 25–28°C).

Throughout the first and cooler observation period, "dead *M. truncata* colonies dissolved at high CO_2 levels (pH 7.66), whereas live specimens maintained the same net calcification rate as those growing at normal pH," the researchers write. At the extremely high CO_2 level, however, the net calcification rate of the live specimens was reduced to only about 20 percent of what it was at normal pH, but life continued. Throughout the second and warmer observation period, on the other hand, calcification ceased in both the normal and high CO_2 treatments, and in the extremely high CO_2 treatment, the transplants died.

Based on these findings the five scientists concluded, "at moderate temperatures," such as those to which they are currently adapted, "adult *M. truncata* are able to up-regulate their calcification rates and survive in areas with higher levels of pCO_2 than are predicted to occur due to anthropogenic ocean acidification, although this ability broke down below mean pH 7.4." This latter level, however, is below what even the IPCC predicts will occur in response to continued burning of fossil fuels, and far below what the more realistic analysis of Tans (2009) suggests.

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8.2.3. Effects on Marine Ecosystems

8.2.3.1 Coral Reefs

Several studies have investigated the response of corals to a decline in oceanic pH, and like the studies cited above, their results indicate the model-projected decline is highly exaggerated.

Suwa et al. (2010) employed controlled infusions of pure CO_2 to create mean pH values of 8.0, 7.6, and 7.3 in filtered seawater that flowed continuously through three sets of multiple tanks into which they had introduced the gametes of two *Acropora* coral species (A. *digitifera* and A. *tenuis*) they had collected during a natural spawning event. Seven days later they determined the percent that survived; after ten additional days, they documented the size of the developing polyps; and after 14 days they documented the percentage of polyps that had acquired zooxanthellae that the researchers had collected from the giant clam *T. crocea* and released into the several treatment tanks.

Results indicated "A. *digitifera* larval survival rate did not differ significantly among pH treatments," and the graphs of their data indicate survivorship in *A. tenuis* was about 18.5 percent greater in the lowest pH (highest CO_2) treatment than in the ambient seawater treatment. At the end of the subsequent ten-day study, however, polyp size was reduced in the lowest pH treatment, but by only about 14 percent, not too bad for an atmospheric CO_2 concentration of more than 2,000 ppm. And in the *A. tenuis* coral, this reduction in individual size was more than compensated by the even greater percentage increase in survivorship. In addition, after

only four days of being exposed to the zooxanthellae derived from giant clams, all polyps in all treatments had acquired a full complement of the symbiotic zooxanthella.

In discussing their findings, the seven scientists state "the survival of coral larvae may not be strongly affected by pH change," or "in other words," they continue, "coral larvae may be able to tolerate ambient pH decreases of at least 0.7 pH units." That, in fact, is something that will likely never occur, as it implies atmospheric CO_2 concentrations of more than 2,000 ppm. And in the unlikely event that such high concentrations ever were to happen, they would be a long, long time in coming, giving corals more than sufficient time to acclimate—and even evolve (Idso and Idso, 2009)—to cope with the slowly developing situation.

In another study, zooxanthellate colonies of the scleractinian coral *Astrangia poculata* were grown by Holcomb et al. (2010) in controlled laboratory conditions under all four combinations of ambient and elevated (5 μM NO_3^-, 0.3 μM PO_4^{-3}, and 2 nM Fe^{+2}) nutrients and ambient and elevated (~780 ppm) pCO_2 for a period of six months. Coral calcification rates were measured via two different techniques—both one month after the start of the experiment and again five months later—and the carbonate chemistry and saturation state of the seawater of each treatment were calculated from measured values of alkalinity, salinity, phosphate, and pCO$_2$.

The results of these operations indicated mean calcification rates of the studied corals were 2.1, 0.7, 1.4, and 1.3 g/m^2/day for the ambient, CO_2-treated, nutrient-treated, and CO_2-plus-nutrient-treated corals, respectively, so that relative to ambient conditions, calcification rates were reduced by the CO_2 treatment to approximately 33 percent of the ambient rate, but with the addition of nutrients bounced partway back to 62 percent of the ambient rate.

In light of their findings, Holcomb et al. conclude "nutritionally replete corals should be able to compensate for reduced saturation state under elevated pCO_2 conditions." As pCO_2 increases and seawater saturation state declines, for example, they write, the "availability of DIC [dissolved inorganic carbon] to the zooxanthellae will increase, potentially allowing increased photosynthesis which provides both alkalinity and energy to help drive calcification." Thus, if corals are experiencing carbon limitation, "elevated pCO_2 could even positively impact calcification."

It becomes clear, therefore, as the three researchers continue, that "saturation state alone is not an effective predictor of coral calcification." They note "the interaction between nutritional status of the coral, DIC availability, and saturation state may help to explain the wide range of calcification responses seen in published acidification and nutrient enrichment studies."

Two earlier studies reported similar findings. Atkinson et al. (1995) showed "nutritionally replete zooxanthellate corals in naturally low [aragonite] saturation-state seawaters are capable of accreting skeletons at rates comparable to those achieved by conspecifics in high-saturation-state seawaters." And Cohen and Holcomb (2009) reported "today, several reefs, including Galapagos, areas of Pacific Panama, and Jarvis (southern Line Islands), experience levels of aragonite saturation equivalent to that predicted for the open ocean under two times and three times pre-industrial CO_2 levels (Manzello et al., 2008; Kathryn Shamberger [PMEL/NOAA] and colleagues, *pers. comm.*, August 2009)," and "available data on coral colony growth rates on these reefs, albeit limited, suggest that they are equivalent to and sometimes even rival those of conspecifics in areas where aragonite saturation states are naturally high, such as the western Pacific warm pool."

Probably the most important deduction to flow from these observations is the fact, in the words of Cohen and Holcomb, that "naturally elevated levels of inorganic nutrients and, consequently, high levels of primary and secondary production, may already be facilitating high coral calcification rates in regions with naturally high dissolved CO_2 levels."

In another study, Kreif et al. (2010) collected two colonies of massive *Porites* corals (which form large multi-century-old colonies and calcify relatively slowly) and four colonies of the branching *Stylophora pistillata* coral (which is short-lived and deposits its skeleton rather rapidly) from a reef at the northern tip of the Red Sea. They grew fragments of these corals in 1,000-liter tanks through which they pumped Gulf of Eilat seawater adjusted to be in equilibrium with air of three different CO_2 concentrations (385, 1,904, and 3,970 ppm), which led to corresponding pH values of 8.09, 7.49, and 7.19 and corresponding aragonite saturation state (Ω_{arag}) values of 3.99, 1.25, and 0.65. After an incubation period of six months for *S. pistillata* and seven months for the *Porites* corals, several fragments were sampled and analyzed for a number of different coral properties. Then, 14 months

from the start of the experiment, fragments of each coral species from each CO_2 treatment were analyzed for zooxanthellae cell density, chlorophyll *a* concentration, and host protein concentration.

In the words of the seven scientists who conducted the study, "following 14 months incubation under reduced pH conditions, all coral fragments survived and added new skeletal calcium carbonate, despite Ω_{arag} values as low as 1.25 and 0.65." This was done, however, at a reduced rate of calcification compared to fragments growing in the normal pH treatment with a Ω_{arag} value of 3.99. Yet in spite of this reduction in skeletal growth, they report, "tissue biomass (measured by protein concentration) was found to be higher in both species after 14 months of growth under increased CO_2." And they further note the same phenomenon had been seen by Fine and Tchernov (2007), who, as they describe it, "reported a dramatic increase (orders of magnitude larger than the present study) in protein concentration following incubation of scleractinian Mediterranean corals (*Oculina patagonica* and *Madracis pharencis*) under reduced pH," stating "these findings imply tissue thickening in response to exposure to high CO_2." Also, in a somewhat analogous situation, Krief et al. report "a decrease in zooxanthellae cell density with decreasing pH was recorded in both species," but they state "this trend was accompanied by an increase in chlorophyll concentration per cell at the highest CO_2 level."

In discussing their findings, the Israeli, French, and U.K. researchers write, "the inverse response of skeleton deposition and tissue biomass to changing CO_2 conditions is consistent with the hypothesis that calcification stimulates zooxanthellae photosynthesis by enhancing CO_2 concentration within the coelenteron (McConnaughey and Whelan, 1997)," and they write, "since calcification is an energy-consuming process . . a coral polyp that spends less energy on skeletal growth can instead allocate the energy to tissue biomass," citing Anthony et al. (2002) and Houlbreque et al. (2004). Thus, they suggest "while reduced calcification rates have traditionally been investigated as a proxy of coral response to environmental stresses, tissue thickness and protein concentrations are a more sensitive indicator of the health of a colony," citing Houlbreque et al. (2004) in this regard as well.

In concluding their paper, Krief et al. state "the long acclimation time of this study allowed the coral colonies to reach a steady state in terms of their

physiological responses to elevated CO_2," and "the deposition of skeleton in seawater with $\Omega_{arag} < 1$ demonstrates the ability of both species to calcify by modifying internal pH toward more alkaline conditions." As a result, they further state "the physiological response to higher CO_2/lower pH conditions was significant, but less extreme than reported in previous experiments," suggesting "scleractinian coral species will be able to acclimate to a high CO_2 ocean even if changes in seawater pH are faster and more dramatic than predicted."

In further examining the complexities of this issue, Jury et al. (2010) write as background for their analysis, "physiological data and models of coral calcification indicate that corals utilize a combination of seawater bicarbonate and (mainly) respiratory CO_2 for calcification, not seawater carbonate," but "a number of investigators are attributing observed negative effects of experimental seawater acidification by CO_2 or hydrochloric acid additions to a reduction in seawater carbonate ion concentration and thus aragonite saturation state." Thus, they state there is "a discrepancy between the physiological and geochemical views of coral biomineralization." In addition, they report "not all calcifying organisms respond negatively to decreased pH or saturation state," and they state, "together, these discrepancies suggest that other physiological mechanisms, such as a direct effect of reduced pH on calcium or bicarbonate ion transport and/or variable ability to regulate internal pH, are responsible for the variability in reported experimental effects of acidification on calcification."

In an effort to shed more light on this conundrum, Jury et al. performed incubations with the coral *Madracis auretenra* (= *Madracis mirabilis sensu* Wells, 1973) in modified seawater chemistries, where, as they describe it, "carbonate parameters were manipulated to isolate the effects of each parameter more effectively than in previous studies, with a total of six different chemistries." Their results indicated among-treatment differences "were highly significant," and "the corals responded strongly to variation in bicarbonate concentration, but not consistently to carbonate concentration, aragonite saturation state or pH." They found, for example, that "corals calcified at normal or elevated rates under low pH (7.6–7.8) when the sea water bicarbonate concentrations were above 1800 µM," and, conversely, "corals incubated at normal pH had low

calcification rates if the bicarbonate concentration was lowered."

Jury et al. conclude, "coral responses to ocean acidification are more diverse than currently thought," and they question "the reliability of using carbonate concentration or aragonite saturation state as the sole predictor of the effects of ocean acidification on coral calcification." They state, "if we truly wish to decipher the response of coral calcification to ocean acidification, a firmer grasp of the biological component of biomineralization is paramount."

Lastly, Ries et al. (2010) investigated the impact of CO_2-induced ocean acidification on "the temperate scleractinian coral *Oculina arbuscula* by rearing colonies for 60 days in experimental seawaters bubbled with air-CO_2 gas mixtures of 409, 606, 903 and 2,856 ppm CO_2, yielding average aragonite saturation states (Ω_A) of 2.6, 2.3, 1.6 and 0.8." These operations indicated that "following the initial acclimation phase, survivorship in each experimental treatment was 100 percent," and, in regard to the corals' rates of calcification and linear extension, "no significant difference was detected relative to the control treatment ($\Omega_A = 2.6$) for corals reared under Ω_A of 2.3 and 1.6." The latter values correspond to pH reductions from current conditions of 0.08 and 0.26, respectively. It is enlightening to note the 0.26 pH reduction is approximately twice the maximum reduction derived from the analysis of Tans (2009) that would likely result from the burning of all fossil fuels in the crust of the Earth.

Given the above findings, the three researchers, in their words, "propose that the apparent insensitivity of calcification and linear extension within *O. arbuscula* to reductions in Ω_A from 2.6 to 1.6 reflects the corals' ability to manipulate the carbonate chemistry at their site of calcification." And it would further appear that ability should serve the corals well as the pH of the ocean declines in the future.

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8.2.4. Multiple Species

Two additional papers have examined the potential effects of ocean acidification and furthered our understanding of this phenomenon. The first, by Ries et al. (2009), explored the effects of lowering seawater pH on 18 oceanic species. The second study, by Hendriks et al. (2010), presented an ocean acidification meta-analysis in which the researchers calculated such effects on dozens of marine species.

Acknowledging "there is mounting concern over the impact that future CO_2-induced reductions in the $CaCO_3$ saturation state of seawater will have on marine organisms that construct their shells and skeletons from this mineral," Ries et al. (2009) set out to conduct an experiment in which they "reared 18 calcifying species for 60 days in isothermal (25°C) experimental seawaters equilibrated with average [atmospheric] CO_2 values of 409, 606, 903 and 2856 ppm, corresponding to modern CO_2, and ~2, 3 and 10 times pre-industrial levels (~280 ppm), respectively, and yielding average seawater saturation states of 2.5, 2.0, 1.5 and 0.7 with respect to aragonite." Then, "the organisms' net rates of calcification (total calcification minus total dissolution) under the various CO_2 treatments were estimated from changes in their buoyant weight and verified with dry weight measurements after harvesting."

According to the three Woods Hole Oceanographic Institution (USA) researchers, their study showed "in ten of the 18 species (temperate corals, pencil urchins, hard clams, conchs, serpulid worms, periwinkles, bay scallops, oysters, whelks, soft clams), net calcification decreased with increasing CO_2," and "in six of the ten negatively impacted species (pencil urchins, hard clams, conchs, periwinkles, whelks, soft clams) [they] observed net dissolution of the shell in the highest CO_2 treatment." However, as they continue, "in four of the 18 species (limpets, purple urchins, coralline red algae, calcareous green algae), net calcification increased relative to the control under intermediate CO_2 levels (605 and 903 ppm), and then declined at the highest CO_2 level (2856 ppm)." Last, they state "in three species (crabs, lobsters, and shrimps), net calcification was greatest under the highest level of CO_2 (2856 ppm)," and "one species, the blue mussel, exhibited no response to elevated CO_2."

In light of their many, diverse findings, Ries et al. concluded "the impact of elevated atmospheric CO_2 on marine calcification is more varied than previously thought," and so it is, with the reported responses ranging from negative to neutral to positive.

In another multiple-species study, Hendriks et al. (2010) assembled a database of 372 experimentally evaluated responses of 44 different marine species to ocean acidification that was induced by equilibrating seawater with CO_2-enriched air. At the time, this study represented the most comprehensive analysis ever conducted on this issue.

Of the 372 published reports they scrutinized, 154 assessed the significance of responses relative to controls; and of those reports, 47 reported no significant response, so "only a minority of studies," in their words, demonstrated "significant responses to acidification." And when the results of that minority group of studies were pooled, there was no significant mean effect. Nevertheless, the three researchers found some types of organisms and certain functional processes did exhibit significant responses to seawater acidification. However, since their analyses to this point had included some acidification treatments that were extremely high, they repeated their analyses for only those acidification conditions induced by atmospheric CO_2 concentrations of 2,000 ppm or less, the latter limiting concentration having been predicted to occur around the year 2300 by Caldeira and Wickett (2003).

In this second analysis, Hendriks et al. once again found the overall response, including all biological processes and functional groups, was not significantly different from that of the various control treatments, although calcification was reduced by 33 ± 4.5 percent and fertility by 11 ± 3.5 percent across groups, while survival and growth showed no significant overall responses. And when the upper limiting CO_2 concentrations were in the range of 731–759 ppm, or just below the value predicted by the IPCC (2007) for the end of the twenty-first century (790 ppm)—calcification rate reductions of only 25 percent were observed. What is more, the three researchers state this decline "is likely to be an upper limit, considering that all experiments involve the abrupt exposure of organisms to elevated pCO_2 values, while the gradual increase in pCO_2 that is occurring in nature may allow adaptive and selective processes to operate," citing the work of Widdicombe et al. (2008) and noting "these gradual changes take place on the scale of decades, permitting adaptation of organisms even including genetic selection."

Indeed, there is a large and accumulating volume of research that demonstrates rapid micro-

evolutionary processes operate in almost all of Earth's life forms, and these phenomena enable them to successfully cope with significant environmental changes at rates that correspond to those environmental changes (Balanya et al., 2006; Jump et al., 2006; Franks et al., 2007; Rae et al., 2007; Skelly et al., 2007; Van Doorslaer et al., 2007; Franks and Weis, 2008; Jump et al., 2008; Purcell et al., 2008; Alford et al., 2009; Bell and Gonzalez, 2009; Onoda et al., 2009; Van Doorslaer et al., 2009). Thus, species that respond negatively to dramatic step increases in the air's CO_2 content employed in many of the experiments analyzed by Hendriks et al. will likely be able to gradually adjust to, and successfully cope with, the restrained and slower rate at which the atmospheric CO_2 concentration of the real world will rise in the future.

Yet even this mitigating factor is not the end of the good news, for Hendriks et al. write "most experiments assessed organisms in isolation, rather than [within] whole communities," and they state the responses of other entities and processes within the community may well buffer the negative impacts of CO_2-indced acidification on Earth's corals. As an example, they note "sea-grass photosynthetic rates may increase by 50 percent with increased CO_2, which may deplete the CO_2 pool, maintaining an elevated pH that may protect associated calcifying organisms from the impacts of ocean acidification."

In describing another phenomenon that benefits corals, the researchers write, "seasonal changes in pCO_2 are in the range of 236–517 ppm in the waters of the northern East China Sea (Shim et al., 2007)," and "metabolically-active coastal ecosystems experience broad diel changes in pH, such as the diel changes of >0.5 pH units reported for sea grass ecosystems (Invers et al., 1997)," which they say represent "a broader range than that expected to result from ocean acidification expected during the 21st century." They remark these fluctuations also "offer opportunities for adaptation to the organisms involved."

Hendriks et al. additionally state the models upon which the ocean acidification threat is based "focus on bulk water chemistry and fall short of addressing conditions actually experienced by [marine] organisms," which are "separated from the bulk water phase by a diffusive boundary layer." They also note "photosynthetic activity"—such as that of the zooxanthellae that are hosted by corals—"depletes pCO_2 and raises pH (Kuhl et al., 1995) so the pH

actually experienced by organisms may differ greatly from that in the bulk water phase (Sand-Jensen et al., 1985)."

The insightful scientists then note "calcification is an active process where biota can regulate intracellular calcium concentrations," so that "marine organisms, like calcifying coccolithophores (Brownlee and Taylor, 2004), actively expel Ca^{2+} through the ATPase pump to maintain low intracellular calcium concentrations (Corstjens et al., 2001; Yates and Robbins, 1999)." And they state, "as one Ca^{2+} is pumped out of the cell in exchange for $2H^+$ pumped into the cell, the resulting pH and Ca^{2+} concentrations increase the $CaCO_3$ saturation state near extracellular membranes and appear to enhance calcification (Pomar and Hallock, 2008)," so much so, in fact, that they indicate "there is evidence that calcification could even increase in acidified seawater, contradicting the traditional belief that calcification is a critical process impacted by ocean acidification (Findlay et al., 2009)."

Hendriks et al. conclude the world's marine biota are "more resistant to ocean acidification than suggested by pessimistic predictions identifying ocean acidification as a major threat to marine biodiversity," noting this phenomenon "may not be the widespread problem conjured into the 21st century" by the IPCC. And in one final parting blow to the theory, Hendriks et al. state, "biological processes can provide homeostasis against changes in pH in bulk waters of the range predicted during the 21st century."

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8.2.5. Freshwater Acidification

Although many studies have examined the possible effects of declining ocean water pH, few have examined such effects for fresh water bodies. In one exception, Hargrave et al. (2009) "used free air CO_2 enrichment to compare effects of eCO_2 (i.e., double ambient ~720 ppm) relative to ambient CO_2 (aCO_2 ~360 ppm) on several ecosystem properties and functions in large, outdoor, experimental mesocosms

that mimicked shallow sand-bottom prairie streams." The results of this experiment indicated "eCO_2 decreased water-column pH," as the IPCC projects it also does in the world's oceans, thereby leading to acidification.

However, the three U.S. scientists discovered the all-important primary productivity of benthic algae "was about 1.6, 1.9, 2.5 and 1.3 times greater in the eCO_2 treatment on days 30, 45, 60 and 75, respectively." They also determined the carbon/phosphorus (C/P) ratio of the algae was on average 2 and 1.5 times greater in the eCO_2 treatment than in the aCO_2 treatment on days 45 and 90, respectively; and this result implies a reduced availability of phosphorus, which would supposedly make the algae less nutritious and, therefore, less beneficial for the ecosystem's consumers.

However, and quite to the contrary of this hypothesis, Hargrave et al. observed eCO_2 "had positive effects on benthic invertebrates, significantly increasing chironomid density, biomass, and average size." They note "chironomid density was about 3, 5 and 2.5 times greater in the eCO_2 treatment than in the aCO_2 treatment on days 30, 60 and 90, respectively"; "biomass was about 4, 3 and 3 times greater in the eCO_2 treatment than in the aCO_2 treatment on days 30, 60 and 90, respectively"; and "individual mass was about two times greater on days 30 and 60." Thus, "contrary to the dominating hypotheses in the literature," in the words of Hargrave et al., "eCO_2 might have positive, bottom-up effects on secondary production in some stream food webs."

Consequently, they conclude their experimental findings and "the large literature from terrestrial and marine ecosystems suggests that future [i.e., higher] atmospheric CO_2 concentrations are likely to have broad reaching effects on autotrophs and consumers across terrestrial and aquatic biomes," which effects could be positive, as were those observed in their study. Nevertheless, more research in freshwater ecosystems would be welcomed to explore these possibilities further.

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8.3 Simultaneous Aquatic Acidification and Warming

In the previous two sections of this chapter we examined the potential indirect (rising water temperatures) and direct (marine and freshwater acidification) threats claimed by the IPCC to result from Earth's rising atmospheric CO_2 concentration. In this section, we review studies that combine these two potential stressors to examine possible impacts of simultaneous aquatic acidification and warming.

We begin with the study of Grelaud et al. (2009), who note "coccolithophores are unicellular pelagic algae that represent a large part of the world ocean's nannophytoplankton and play a significant role in the carbon cycle as major producers of biogenic calcium carbonate," and "the inorganic fossil remains of coccolithophores consist of <20µm calcareous plates called coccoliths," the small size and large abundance of which "make it possible to sample marine sediment cores at mm to sub-mm intervals with ultra-high resolution." Against this backdrop and "in the context of modern global warming and ocean acidification due to anthropogenic CO_2 release," Grelaud et al. "investigated the morphometry (size, weight) of selected species of the order Isochrysidales (i.e., *E. huxleyi*, *G. muellerae* and *G. oceanica*) to understand how coccolithophores' carbonate mass is influenced by recent oceanographic global changes." They did this for sediment cores taken from "the deep center of the Santa Barbara Basin (SBB) on the North American Pacific margin in the interval from AD 1917 to 2004."

Based on their analysis, the three researchers report "morphometric parameters measured on *E. Huxleyi*, *G. muellerae* and *G. oceanica* indicate increasing coccolithophore shell carbonate mass from ~1917 until 2004 concomitant with rising pCO_2 and sea surface temperature in the region of the SBB." More specifically, they state "a >33% increase in mean coccolith weight was determined for the order Isochrysidales over 87 years from ~1917 until 2004." Given these findings, Grelaud et al. write, "the last century has witnessed an increasing net influx of atmospheric carbon dioxide into the world's oceans, a rising of pCO_2 of surface waters, and under-saturation with respect to aragonite, especially along the North American Pacific margin," which was the site of their study. These conditions, as they describe them, have been predicted by the IPCC "to result in reduced coccolithophore carbonate mass and a concomitant decrease in size and weight of coccoliths." As

indicated by Grelaud et al.'s study, however, just the opposite appears to be the case in the real world, even in places where the predicted calcification reductions are expected to be greatest. This also has been demonstrated to be the case by the work of Iglesias-Rodriguez et al. (2008), who observed—in the words of Grelaud et al.—"a 40% increase in average coccolith weight across the last 220 years, as recorded in a box core from the subpolar North Atlantic," and as has been further confirmed by the complimentary work of Halloran et al. (2008).

In a study of jellyfish, authors Winans and Purcell (2010) write, "scyphozoans have two main stages in their life cycles, the benthic polyps and pelagic jellyfish." The polyps reproduce asexually by budding polyps and through the process of strobilation, in which ephyrae (juvenile jellyfish) are produced by transverse fission. And, as they continue, "like many other marine invertebrates, jellyfish have statocysts, balance organs that enable them to sense gravity," and they state "inside these statocysts are numerous statoliths of trigonal crystals of calcium sulfate hemihydrate that are formed during strobilation."

Against this backdrop, the two researchers carried out an experiment designed to test the ability of jellyfish to respond to changes in water temperature and pH during their early life stages. Polyps produced by medusae collected from the moon jellyfish (*Aurelia labiata*) in Dyes Inlet, Washington (USA) were arbitrarily assigned (18 each) to one of six treatments constituting all combinations of two water temperatures (9 and 15°C) and three pH levels (7.2, 7.5, and 7.9), where they were allowed to develop under controlled conditions for 122 days.

The results of this undertaking indicated "polyp survival was 100% after 122 days in seawater in all six temperature and pH combinations." And because few polyps strobilated at 9°C and "temperature effects on budding were consistent with published results," the researchers state they "did not analyze data from those three treatments further." At 15°C, there were also no significant effects of pH on the numbers of ephyrae or buds produced per polyp or on the numbers of statoliths per statocyst. However, they state "statolith size was significantly smaller in ephyrae released from polyps reared at low pH."

Given the findings presented above, Winans and Purcell conclude "*A. labiata* polyps are quite tolerant of low pH, surviving and reproducing asexually even at the lowest tested pH," which degree of "acidification" is not expected to occur (even by the

IPCC) until about AD 2300. But to avoid coming up empty-handed with respect to potential bad news, they note "the effects of small statoliths on ephyra fitness are unknown," which means the phenomenon *could* bode poorly for Earth's jellyfish. On the other hand, they acknowledge many organisms "may be able to acclimate or adapt to slowly changing pH conditions." And in this context they report that in Puget Sound "pH fluctuates from 7.2 to 9.6 in 2.4-meter deep water over the span of a couple of days," stating "with such large pH fluctuations due to plant photosynthesis during the day and respiration at night, many organisms may be exposed to low pH conditions routinely."

In a contemporaneous study, Byrne et al. (2010a) examined the interactive effects of near-future (ca. AD 2070–2100) ocean warming (temperature increases of 2–6°C) and ocean acidification (pH reductions of 0.2–0.6) on fertilization in four intertidal and shallow subtidal echinoids (*Heliocidaris erythrogramma, Heliocidaris Tuberculata, Tripneustes gratilla, Centrostephanus rodgersii*), an asteroid (*Patiriella regularis*), and an abalone (*Haliotis coccoradiata*). They worked with batches of eggs collected from multiple females fertilized by sperm obtained from multiple males, all of which were maintained and employed in all combinations of three temperature and three pH treatments.

Their results indicated, in the words of the eight researchers, "there was no significant effect of warming and acidification on the percentage of fertilization." In light of their comprehensive findings, Byrne et al. state their results indicate "fertilization in these species is robust to temperature and pH/P_{CO2} fluctuation," while opining that their findings "may reflect adaptation to the marked fluctuation in temperature and pH that characterizes their shallow water coastal habitats." This interpretation further suggests other marine fauna in still other circumstances may likewise be capable of adapting to any warming and acidification that might possibly develop throughout the world's oceans during the remaining decades of the twenty-first century.

Also in 2010, and in another paper in which Byrne served as the lead author (Byrne et al. (2010b)), it was noted changes in seawater chemistry—such as a decline in pH—have the potential to negatively impact fertilization kinetics in free-spawning marine invertebrates, but that ocean warming could do the opposite and "may enhance

fertilization due to positive effects on sperm swimming speeds and heightened sperm-egg collisions," such that the net effect of both phenomena acting in unison could be negligible.

To explore the degree of likelihood of this scenario occurring in the real world, Byrne et al. (2010b) investigated the effects of projected near-future oceanic warming and acidification for conditions that have been predicted for southeast Australia within the timeframe of 2070–2100: an increase in sea surface temperature of 2 to 4°C and a decline in pH of 0.2 to 0.4. This they did in a fertilization study of the sea urchin *Heliocidaris erythrogramma* via multi-factorial experiments that incorporated a titration of sperm density (10–10^3 sperm per ml) across a range of sperm-to-egg ratios (10:1–1500:1).

The five Australian researchers found "across all treatments there was a highly significant effect of sperm density, but no significant effect of temperature or interaction between factors." In fact, they state, "low pH did not reduce the percentage of fertilization even at the lowest sperm densities used, and increased temperature did not enhance fertilization at any sperm density." In addition, they remark, "a number of ecotoxicology and climate change studies, where pH was manipulated with CO_2 gas, show that sea urchin fertilization is robust to a broad pH range with impairment only at extreme levels well below projections for ocean acidification by 2100 (pH 7.1–7.4, 2,000–10,000 ppm CO_2)," citing the work of Bay et al. (1993), Carr et al. (2006), and Kurihara and Shirayama (2004).

Interestingly, neither seawater warming nor seawater acidification (caused by contact with CO_2-enriched air) had either a positive or a negative effect on sea urchin fertilization, suggesting, as the five scientists concluded, that "sea urchin fertilization is robust to climate change stressors."

Also studying sea urchins that year were Brennand et al. (2010), who reared embryos of *Tripneustes gratilla* in flow-through chambers filled with filtered seawater maintained at all combinations of three different temperatures (24, 27, and 30°C) and three different pH values (8.15, 7.8, and 7.6), where the 24°C/pH 8.15 combination represented normal control conditions. After five days of such exposure, the growth and development of the larvae were assessed.

Brennand et al. report "larvae reared at pH 7.6 and pH 7.8 had smaller post oral arms when compared with those reared at control pH." However, they report "a +3°C warming diminished the negative effects of low pH/high CO_2," as was "seen in the similar post oral arm length of larvae treated at 27°C/pH 7.6 and 27°C/pH 7.8 and those reared in control temperature and pH." In addition, they state, "as total length of calcite rods is largely comprised of the post oral arms, this measure [of calcification] followed a similar pattern."

The results of this study suggest the negative effects of a 0.35 to 0.55 CO_2-induced decline in seawater pH on the growth and calcification of the sea urchin *Tripneustes gratilla* can be largely overcome by a 3°C increase in water temperature. And since the analysis of Tans (2009) suggests the maximum decline in seawater pH that will likely ever be produced by the burning of fossil fuels will be somewhere in the range of only 0.1 to 0.18 in the vicinity of AD 2100 (after which pH begins to rebound), there would seem to be little reason for concern about any negative impact of rising atmospheric CO_2 concentrations on this particular species of sea urchin, which is widely distributed throughout the Indo-Pacific region and is well-suited for production by aquaculture (Lawrence and Agatsuma, 2007; Juinio-Menez et al., 1998; Dworjanyn et al. 2007).

Shifting to a study of simultaneous aquatic acidification and warming on corals, Rodolfo-Metalpa et al. (2010) collected three live colonies of *Cladocora caespitosa* in the Bay of Villefranche (Ligurian Sea, France) at about 25 meters depth in July 2006 and three other colonies in February 2007. They divided the colonies into fragments and carefully removed single polyps that they attached to PVC plates and randomly assigned to aquariums that were continuously supplied with unfiltered seawater and maintained at ambient or elevated water temperature (T or T + 3°C) in equilibrium with air of ambient or elevated CO_2 concentration (400 or 700 ppm), subjecting them to "(1) mid-term perturbations (1 month) in summer and winter conditions of irradiance and temperature, and (2) a long-term perturbation (1 year), mimicking the seasonal changes in temperature and irradiance."

The results of their experimentation indicated that for the Mediterranean zooxanthellate coral, "an increase in CO_2, in the range predicted for 2100, does not reduce its calcification rate," and "an increase in CO_2, alone or in combination with elevated temperature, had no significant effect on

photosynthesis, photosynthetic efficiency and calcification." In addition, they report a 3°C rise in temperature in winter resulted in a 72 percent increase in gross photosynthesis and a significant increase in daytime calcification rate.

In light of their several significant findings, Rodolfo-Metalpa et al. conclude, "the conventional belief that calcification rates will be affected by ocean acidification may not be widespread in temperate corals." They note, for example, that Ries et al. (2009) reported the calcification rate of the temperate coral *Oculina arbuscula* is also unaffected by an increase in atmospheric CO_2 concentration of up to 840 ppm, and that a large decrease in calcification was found only at a CO_2 concentration in excess of 2,200 ppm. In addition, they write, "some marine invertebrates may be able to calcify in the face of ocean acidification or, contrary to what is generally expected, may increase their calcification rates as reported on the ophiourid brittlestar *Amphiura filiformis* (Wood et al., 2008), the seastar *Pisaster ochraceus* (Gooding et al., 2009) exposed to lower pH (7.8–7.3), the Caribbean coral *Madracis mirabilis* at pH 7.6 (Jury et al., 2010), and shown for coralline red algae, calcareous green algae, temperate urchins, limpets, crabs, lobsters and shrimp (Ries et al., 2009)." In addition, they write there are many cases where "rates of photosynthesis are either not affected (e.g. Langdon et al., 2003; Reynaud et al., 2003; Schneider and Erez, 2006; Marubini et al., 2008) or slightly increased (e.g. Langdon and Atkinson, 2005) at the level of CO_2 expected in 2100."

Also studying corals, Kiessling (2009)—who hails from the Museum fur Naturkunde of the Leibniz Institute for Research on Evolution and Biodiversity at Berlin's Humboldt University—reviewed the then-current state of knowledge of the long-term effects of changes in oceanic temperature and the atmosphere's CO_2 concentration on the vigor of the planet's coral reefs. He reports, "on geologic timescales, there is little evidence for climate change affecting reefs in a linear fashion" and "changes in mean global temperature as reconstructed from stable oxygen isotopes and the distribution of non-reef climate-sensitive sediments do not correspond to changes in reef abundance or latitudinal distribution," citing some of his own analyses of the subject (Kiessling, 2001a, 2002). And he states "reports linking reef expansions and declines to climate change fail to explain why other changes in temperature did not lead to a similar response in reefs and why the reported (fairly modest) temperature changes would have such a dramatic effect."

With respect to ocean acidification, the German researcher states "just like temperature," it is currently receiving much attention as "a control of reef development," but "the boom and bust pattern of reefs and hyper-calcifiers is difficult to explain with inferred long-term changes in the saturation state of ocean water, at least if the major trigger is atmospheric pCO_2," because "previous analyses failed to find any significant cross-correlation between changes in pCO_2 and changes in reef attributes," citing Kiessling (2001b, 2002).

As a result of these and many other observations, Kiessling concludes "neither climate nor sea-level nor chemical changes in the oceans can elucidate the waxing and waning of reefs" throughout their history on Earth, and their "boom and bust pattern" is "impossible to explain by linear responses to physicochemical changes." Furthermore, Kiessling states, "ecologically complex reef systems have been around for hundreds of millions if not billions of years," and "geologic models of CO_2 concentrations in the atmosphere suggest that these were much greater during most of Earth's history than today," which further suggests something other than CO_2-induced global warming and ocean acidification must have been responsible for their prior "boom and bust" pattern of behavior.

Another example of these complexities is seen in the paper of De'ath et al. (2009), who detected a 14 percent drop in *Porites* calcification rate on the Great Barrier Reef from 1990 to 2005 (actually from 1970 to 2005, if one goes by their graph of the phenomenon, reproduced below) and declared that decline to be "unprecedented in at least the past 400 years," which is indeed what their data show. But if one follows their calcification history back in time a mere 33 more years, from 1605 to 1572, when the air's CO_2 concentration was more than 100 ppm less than what it is today and, therefore, was supposedly much healthier for corals (if one assumes the IPCC's claim to be correct)—the coral calcification rate at that earlier time is seen to have been approximately 23 percent lower than what it was at its twentieth-century peak.
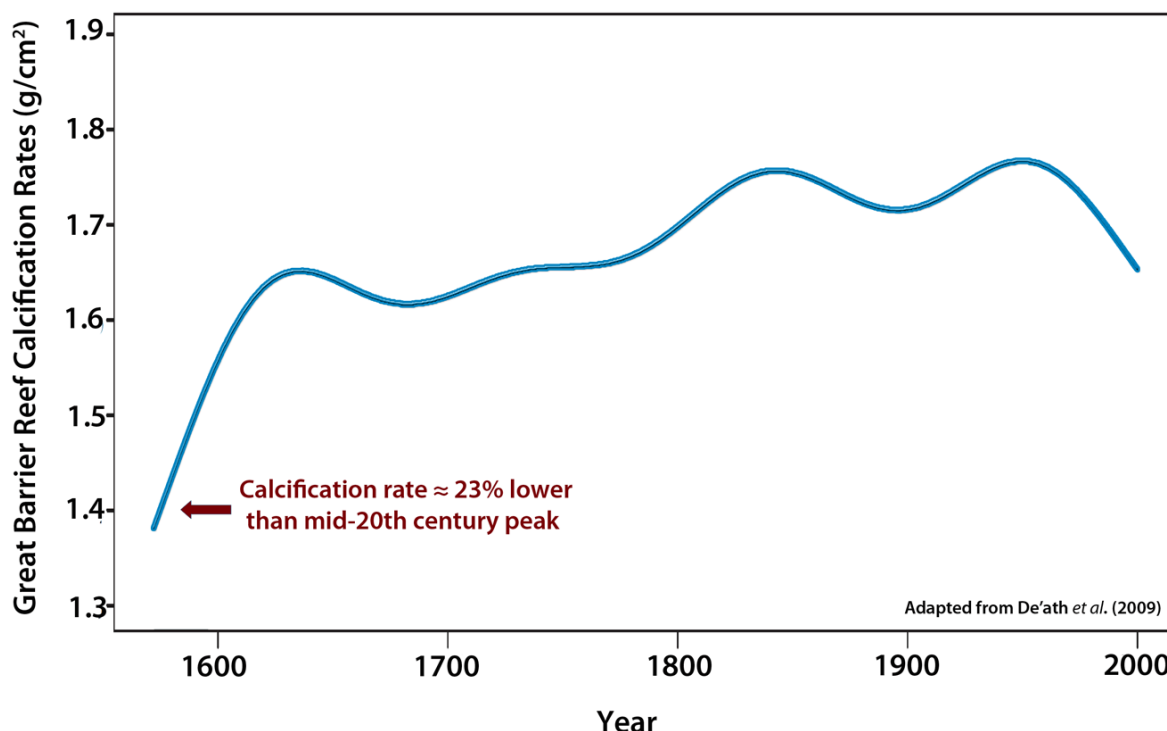
Figure 8.3.1. Calcification rates of *Porites* corals from the Great Barrier Reef over the period 1572-2001. Adapted from De'ath et al. (2009).

Another way of looking at De'ath et al.'s data is to realize that from 1572 to 1970 *Porites* calcification rates on the Great Barrier Reef rose, by about 27 percent, as atmospheric CO_2 concentration and air temperature rose concurrently, after which calcification rates declined, but by a much smaller 14 percent, as these same air temperature and CO_2 trends continued, further obfuscating the issue and presumably causing the researchers from the Australian Institute of Marine Science to state "the causes for the Great Barrier Reef-wide decline in coral calcification of massive *Porites* remain unknown."

Clearly, the effects of simultaneous ocean acidification and warming are more complex than the IPCC seems to believe.

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