6

Aquatic Life

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Key Findings

The key findings of this chapter, which challenge the alarming and negative projections of United Nations' Intergovernmental Panel on Climate Change (IPCC), are presented in the bullet points below.

- Multiple studies from multiple ocean regions confirm ocean productivity tends to increase with temperature. Subjects of this research include phytoplankton and macroalgae, corals, crustaceans, and fish.
- Rising seawater temperature is conducive to enhanced coral calcification, leading some experts

to forecast coral calcification will increase by about 35% beyond pre-industrial levels by 2100, and no extinction of coral reefs will occur in the future.

- Many aquatic species demonstrate the capability to adjust their individual critical thermal maximum (the upper temperature at which the onset of behavioral incapacitation occurs) upwards in response to temperature increases of the amount forecast by IPCC.
- Aquatic life has survived decadal, centennial, and millennial-scale climate oscillations that have

persisted for millions of years. Evidence indicates they are well-equipped to adapt to forecasted increases in temperature, if necessary.

- Caution should be applied when interpreting results from laboratory-based studies of lower seawater pH levels. Such studies often are incapable, or fall far short, of mimicking conditions in the real world, and thus they frequently yield results quite different than what is observed in nature.
- Rising atmospheric CO₂ levels do not pose a significant threat to aquatic life. Many aquatic species have shown considerable tolerance to declining pH values predicted for the next few centuries, and many have demonstrated a likelihood of positive responses in empirical studies.
- The projected decline in ocean pH levels in the year 2100 (as compared to preindustrial times) may be significantly overstated, amounting to only half of the 0.4 value IPCC predicts.
- The natural variability of oceanic pH is often much greater than the change in pH levels forecast by IPCC.
- Natural fluctuations in pH may have a large impact on the development of resilience in marine populations, as heterogeneity in the environment with regard to pH and pCO_2 exposure may result in populations that are acclimatized to variable pH or extremes in pH.
- For those aquatic species showing negative responses to pH declines in experimental studies, there are adequate reasons to conclude such responses will be largely mitigated through phenotypic adaptation or evolution during the many decades to centuries the pH concentration is projected to fall.

Introduction

Some observers have suggested rising atmospheric carbon dioxide (CO_2) concentrations may harm aquatic life via global warming, in which the temperatures of the world's water bodies rise, and through the absorption of additional CO_2 from the air into water, thereby lowering the pH of the waters to which aquatic life is accustomed. IPCC projects

marine and freshwater species will be negatively affected by these processes and will experience future declines, in some instances so severe as to cause species extinctions.

In contrast, the material presented in this chapter, representing the findings of hundreds of peerreviewed research analyses, suggests a much better future is in store for Earth's aquatic life. Many laboratory and field studies have demonstrated growth and developmental improvements in response to higher temperatures and reduced water pH levels. Other research has illustrated the capability of marine and freshwater species to tolerate and adapt to rising temperature and pH decline of the planet's water bodies. When such observations are considered, the pessimistic projections of IPCC give way to considerable optimism with respect to the future of the planet's marine life.

This chapter begins by summarizing research on the impact of rising ocean temperatures on phytoplankton and macroalgae, corals, crustaceans, fish, and other marine species. Researchers have found repeatedly that many species benefit rather than from rising temperatures, suffer including temperature increases forecast by IPCC. Section 6.2 examines research on the effects of warmer temperatures on freshwater species. Much less research has been conducted in this area, but it too highlights beneficial effects of warming on phytoplankton, several species of fish, and freshwater mussels.

Section 6.3 addresses the threat of so-called "ocean acidification." The phrase is an improper choice because natural seawater is basic (alkaline), with an average pH level typically around 8.1, and the oceans will never become acidic (below 7.0) due to IPCC's worst-case scenarios of future anthropogenic CO₂ emissions. The prospect of oceans and lakes becoming "acidic" is frightening to the general public, and rightly so. While many scientists conducting research in this area use the term, perhaps to attract public attention to their work, more accurate and less judgmental phrases are "lower oceanic pH," "lower seawater pH levels," and "ocean pH reduction." The research summarized in this section makes it clear that rising atmospheric CO₂ levels do not pose as significant a threat to aquatic life as claimed by IPCC. Many aquatic species have shown considerable tolerance to declining pH values predicted for the next few centuries, and many have demonstrated a likelihood of positive responses in empirical studies.

Section 6.4 summarizes research on freshwater

"acidification." The number of studies examining this topic is dramatically smaller than the number concerning oceans, but those highlighted here reveal findings typically more positive than negative.

Section 6.5 investigates research on the combined effects of rising temperatures and falling pH levels on marine plants and animals. Research in this area is not as plentiful, but what exists is generally reassuring: Many studies show the combination of higher temperatures and falling pH levels to be beneficial, not harmful, to marine life.

6.1 Ocean Warming

According to IPCC, global warming will warm the planet's oceans, resulting in catastrophic effects on marine plants and animals. In a draft of the Summary for Policymakers of its contribution to IPCC's Fifth Assessment Report, Working Group II claims "Openocean net primary production is projected to redistribute and to fall globally by 2100 under RCP8.5. Climate change adds to threats of overfishing and other non-climatic stressors, thus complicating marine management regimes (*high confidence*)" (IPCC 2014-II, p. 9). More warnings along these lines appear in Working Group II's draft full report, as shown by excerpts presented at the beginning of Section 6.1.2 below.

IPCC's frequent description of the modern rise in global temperature as "unprecedented" suggests there already should be signs of negative impacts on oceanic productivity and marine life, but a review of the scholarly literature on this subject reveals just the opposite: Productivity is rising and species are flourishing, except in cases where human activities such as over-fishing, pollution, generation of silt, and other damaging practices are to blame. The studies highlighted in this section yield little evidence to support IPCC's point of view.

6.1.1 Phytoplankton and Macroalgae

This section examines research on the impacts of ocean warming on marine phytoplankton and macroalgae. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings.

• Multiple studies from multiple ocean regions confirm ocean productivity tends to increase with temperature.

- Several observation-based analyses reveal phytoplankton productivity has increased over the past several decades in response to the instrumental-era rise in temperature.
- Evidence suggests marine plants are wellequipped to adapt and evolve to forecasted increases in future temperature, as they have done so in responding to decadal, centennial, and millennial-scale climate oscillations that have persisted for millions of years.

Sarmiento et al. (2004) conducted a massive computational study employing six coupled climate model simulations to determine the biological response of the global ocean to climate warming they simulated from the beginning of the Industrial Revolution to the year 2050. Based on vertical velocity, maximum winter mixed-layer depth, and sea-ice cover, they defined six biomes and calculated how their surface geographies would change in response to their calculated changes in global climate. Next, they used satellite ocean color and climatological observations to develop an empirical model for predicting surface chlorophyll concentrations from the final physical properties of the world's oceans as derived from their global warming simulations. They then used three primary production algorithms to estimate the response of oceanic primary production to climate warming based on their calculated chlorophyll concentrations. The 13 scientists from Australia, France, Germany, Russia, the United Kingdom, and the United States arrived at a global warming-induced increase in global ocean primary production ranging from 0.7 to 8.1%.

In addition to Sarmiento et al.'s model-based study, a number of real-world observations also suggest IPCC's concerns about future declines in ocean productivity in response to rising temperatures are unfounded. Goes et al. (2005) analyzed seven years (1997-2004) of satellite-derived ocean surface phytoplankton productivity data, as well as associated sea surface temperatures (SSTs) and winds in the Arabian Sea. They report for the region located between 52 to 57°E and 5 to 10°N, "the most conspicuous observation was the consistent year-byyear increase in phytoplankton biomass over the 7year period." This change was so significant that by the summer of 2003, they write, "chlorophyll a concentrations were >350% higher than those observed in the summer of 1997." They also report the increase in chlorophyll a was "accompanied by an intensification of sea surface winds, in particular of

the zonal (east-to-west) component," noting these "summer monsoon winds are a coupled atmosphereland-ocean phenomenon, whose strength is significantly correlated with tropical SSTs and Eurasian snow cover anomalies on a year-to-year basis." They write, "reduced snow cover over Eurasia strengthens the spring and summer land-sea thermal contrast and is considered to be responsible for the stronger southwest monsoon winds." They note "the influence of southwest monsoon winds on phytoplankton in the Arabian Sea is not through their impact on coastal upwelling alone but also via the ability of zonal winds to laterally advect newly upwelled nutrient-rich waters to regions away from the upwelling zone." They conclude, "escalation in the intensity of summer monsoon winds. accompanied by enhanced upwelling and an increase of more than 350% in average summertime phytoplankton biomass along the coast and over 300% offshore, raises the possibility that the current warming trend of the Eurasian landmass is making the Arabian Sea more productive."

Drinkwater (2006) examined marine ecosystems of the North Atlantic, determining "in the 1920s and 1930s, there was a dramatic warming of the air and ocean temperatures in the northern North Atlantic and the high Arctic, with the largest changes occurring north of 60°N." This warming "led to reduced ice cover in the Arctic and subarctic regions and higher sea temperatures," as well as northward shifts of multiple marine ecosystems. This early twentieth century warming "contributed to higher primary and secondary production," Drinkwater writes, and "with the reduced extent of ice-covered waters, more open water allow[ed] for higher production than in the colder periods."

McGregor et al. (2007) state, "coastal upwelling occurs along the eastern margins of major ocean basins and develops when predominantly along-shore winds force offshore Ekman transport of surface waters, which leads to the ascending (or upwelling) of cooler, nutrient-rich water." They note these regions of coastal upwelling account for about 20% of the global fish catch while constituting less than 1% of the area covered by the world's oceans. To better understand this productivity-enhancing phenomenon of great practical and economic significance, they studied its long-term history along the northwest coast of Africa-in the heart of the Cape Ghir upwelling system off the coast of Morocco-by analyzing two sediment cores having decadal-or-better resolution that extend from the late Holocene to the end of the twentieth century-from 520 BC to AD 1998.

The four researchers found an anomalous cooling of sea surface temperatures during the twentieth century, which they say "is consistent with increased upwelling." They note, the "upwelling-driven sea surface temperatures also vary out of phase with millennial-scale changes in Northern Hemisphere temperature anomalies and show relatively warm conditions during the Little Ice Age and relatively cool conditions during the Medieval Warm Period."

McGregor *et al.* offer an explanation for how this happens, posing a scenario that starts with an impetus for warming that leads to near-surface air temperatures over land becoming warmer than those over the ocean. The greater warming over the land "deepens the thermal low-pressure cell over land while a higher-pressure center develops over the slower-warming ocean waters." As this occurs, "winds blow clockwise around the high and anticlockwise around the continental low." With the coast representing the boundary between the two centers, the resulting wind is "oriented alongshore and southward (equator-ward), which thus drives the upwelling and negative sea surface temperature anomalies."

McGregor *et al.* say similar anti-phased thermal behavior—the cooling of coastal waters that leads to enhanced coastal upwelling during periods of hemispheric or global warming—has been observed in the Arabian Sea and along the Iberian margin, as well as in parts of the California Current and the Peru-Chile Current. This suggests as global warming enhances the upwelling of cooler nutrient-rich waters along the eastern margins of major ocean basins, it helps to significantly enhance global-ocean primary productivity, which leads to an increase in globalocean secondary productivity, as represented by the global fish catch.

Boyd *et al.* (2007) reported somewhat analogous findings in their review of iron enrichment experiments conducted between 1993 and 2005. These experiments conclusively demonstrate, they write, "phytoplankton grow faster in warmer open-ocean waters, as predicted by algal physiological relationships." These findings indicate total ocean productivity should have benefited immensely from twentieth century global warming and likely will continue to benefit from continued global warming.

Marasovic *et al.* (2005) analyzed monthly observations of basic hydrographic, chemical, and biological parameters, including primary production, made since the 1960s at two oceanographic stations, one near the coast of Croatia (Kastela Bay) and one in the middle Adriatic Sea. They found mean annual

primary production in Kastela Bay averaged about 430 mg C m⁻² d⁻¹ over the period 1962–1972, exceeded 600 mg C m^{$^{-2}$} d^{$^{-1}$} in 1972–1982, and rose to more than 700 mg C m⁻² d⁻¹ in 1982–1996, accompanied by a similar upward trend in percent oxygen saturation of the surface water. The initial value of primary production in the open sea was much less (approximately 150 mg C m^{-2} d⁻¹), but it began to follow the upward trend of the Kastela Bay data after about one decade. Marasovic et al. conclude, "even though all the relevant data indicate that the changes in Kastela Bay are closely related to an increase of anthropogenic nutrient loading, similar changes in the open sea suggest that primary production in the Bay might, at least partly, be due to global climatic changes," which are "occurring in the Mediterranean and Adriatic Sea open waters" and may be directly related to "global warming of air and ocean" because "higher temperature positively affects photosynthetic processes."

Raitsos et al. (2005) investigated the relationship between Sea-viewing Wide Field-of-view Sensor (SeaWiFS) chlorophyll a measurements in the Central Northeast Atlantic and North Sea (1997-2002) and simultaneous measurements of the Phytoplankton Color Index (PCI) collected by the Continuous Plankton Recorder survey, an upper-layer plankton monitoring program that has operated in the North Sea and North Atlantic Ocean since 1931. By developing a relationship between the two databases over their five years of overlap, the scientists were able to produce a Chl-a history for the Central Northeast Atlantic and North Sea for the period 1948-2002. Of this record they say "an increasing trend is apparent in mean Chl-a for the area of study over the period 1948-2002." They report "there is clear evidence for a stepwise increase after the mid-1980s, with a minimum of 1.3 mg m^{-3} in 1950 and a peak annual mean of 2.1 mg m⁻³ in 1989 (62% increase)." Alternatively, the data may represent a steadier long-term upward trend upon which is superimposed a decadal-scale oscillation. In a final comment on their findings, they note, "changes through time in the PCI are significantly correlated with both sea surface temperature and Northern Hemisphere temperature," citing Beaugrand and Reid (2003).

Antoine *et al.* (2005) applied revised dataprocessing algorithms to two ocean-sensing satellites, the Coastal Zone Color Scanner (CZCS) and SeaWiFS, over the periods 1979–1986 and 1998– 2002, respectively, to provide an analysis of the decadal changes in global oceanic phytoplankton biomass. The results showed "an overall increase of the world ocean average chlorophyll concentration by about 22%" over the two decades under study.

Hirawake et al. (2005) analyzed chlorophyll a data obtained from Japanese Antarctic Research Expedition cruises made on the Southern Ocean by the Fuji and Shirase icebreakers between Tokyo and Antarctica from 15 November to 28 December of nearly every year between 1965 and 2002 in a study of interannual variations of phytoplankton biomass, calculating results for the equatorial region between 10°N and 10°S, the Subtropical Front (STF) region between 35°S and 45°S, and the Polar Front (PF) region between 45°S and 55°S. They found an increase in chl a "in the waters around the STF and the PF, especially after 1980 around the PF in particular," and "in the period between 1994 and 1998, the chl a in the three regions exhibited rapid gain simultaneously." They also found "significant correlations between chl a and year through all of the period of observation around the STF and PF, and the rates of increase are 0.005 and 0.012 mg chl $a \text{ m}^{-3} \text{ y}^{-1}$, respectively." They report the satellite data of Gregg and Conkright (2002) "almost coincide with our results." The Japanese scientists note, "simply considering the significant increase in the chl a in the Southern Ocean, a rise in the primary production as a result of the phytoplankton increase in this area is also expected."

Sepulveda *et al.* (2005) presented "the first reconstruction of changes in surface primary production during the last century from the Puyuhuapi fjord in southern Chile, using a variety of parameters (diatoms, biogenic silica, total organic carbon, chlorins, and proteins) as productivity proxies." Noting the fjord is located in "a still-pristine area," they state it is "suitable to study changes in past export production originating from changes in both the paleo-Patagonian ice caps and the globally important Southern Ocean."

They found the productivity of the Puyuhuapi fjord "was characterized by a constant increase from the late 19th century to the early 1980s, then decreased until the late 1990s, and then rose again to present-day values." For the first of these periods (1890–1980), they report "all proxies were highly correlated (r > 0.8, p < 0.05)" and "all proxies reveal an increase in accumulation rates." From 1980 to the present, the pattern differed among the various proxies. The researchers state, "considering that the top 5 cm of the sediment column (~10 years) are diagenetically active, and that bioturbation by benthic organisms may have modified and mixed the sedimentary signal, paleo-interpretation of the period 1980–2001 must be taken with caution." Their work provides substantial solid evidence that, for the first 90 years of the 111-year record, surface primary production in the Puyuhuapi fjord rose dramatically, and with lesser confidence it appears to have leveled out over the past two decades.

While IPCC worries recent "unprecedented" increases in mean global air temperature and CO₂ concentration have been bad for the biosphere, Sepulveda et al. present yet another case of an ecosystem apparently thriving in such conditions. Nevertheless, claims of impending ocean productivity declines have not ceased, and the study of Behrenfeld et al. (2006) is often cited as support of such claims. Working with NASA's Sea-viewing Wide Field-ofview Sensor (SeaWiFS), the team of 10 U.S. scientists calculated monthly changes in net primary production (NPP) from similar changes in upperocean chlorophyll concentrations detected from space over the past decade. They report this period was dominated by an initial NPP increase of 1,930 teragrams of carbon per year (Tg C yr^{-1}), which they attributed to the significant cooling of "the 1997 to 1999 El Niño to La Niña transition," and they note this increase was "followed by a prolonged decrease averaging 190 Tg C yr⁻¹," which they attributed to subsequent warming.

The researchers' explanation for the means by which changing temperatures drove the two trends in NPP is based on their presumption a warming climate increases the density contrast between warmer surface waters and cooler underlying nutrient-rich waters. The enhanced stratification that occurs with warming, they say, "suppresses nutrient exchange through vertical mixing," which decreases NPP by reducing the supply of nutrients to the surface waters where photosynthesizing phytoplankton predominantly live. The scientists suggest "surface cooling favors elevated vertical exchange," by contrast, which increases NPP by enhancing the supply of nutrients to the ocean's surface waters, which have a greater concentration of phytoplankton than the underlying waters do because of light requirements for photosynthesis.

Real-world observations raise questions about that explanation. From approximately the middle of 2001 to the end of the data series in early 2006 (which accounts for more than half the data record), there has been, if anything, a slight increase in global NPP. Does this observation mean there has been little or no net global warming since mid-2001? Or does it mean the global ocean's mean surface temperature declined over that five-year period? Neither alternative accords with the model-based projections of CO₂-induced climate warming.

The relationship between global warming and oceanic productivity may not be nearly as strong as what Behrenfeld et al. suggest. They leave themselves significant wiggle room in this regard, stating, "modeling studies suggest that shifts in ecosystem structure from climate variations may be as [important as] or more important than the alterations in bulk integrated properties reported here," noting some "susceptible ecosystem characteristics" that might shift include "taxonomic composition, physiological status, and light absorption by colored dissolved organic material." Given enough time, then, the phenomena Behrenfeld et al. describe could result in important "shifts in ecosystem structure" that could compensate, or even overcompensate, for what might initially appear to be negative warming-induced consequences.

Another reason for not concluding too much from the Behrenfeld *et al.* oceanic NPP dataset is that it may be of too short a duration to reveal what might be occurring on a longer timescale throughout the world's oceans, or its position in time may prevent the detection of greater short-term changes of the opposite sign that may have occurred a few years earlier or might occur in the near future. The central regions of the world's major oceans were long thought to be essentially vast biological deserts (Ryther, 1969), but several studies of primary photosynthetic production conducted in those regions in the 1980s (Shulenberger and Reid, 1981; Jenkins, 1982; Jenkins and Goldman, 1985; Reid and Shulenberger, 1986; Marra and Heinemann, 1987; Laws et al., 1987; Venrick et al., 1987; Packard et al., 1988) yielded results that suggest marine productivity at that time was at least twice as great as it likely was for a long time before 1969, causing many scientists of that day to speculate "the ocean's deserts are blooming" (Kerr, 1986).

Of even greater interest, perhaps, the 1970–1988 dataset of Jones *et al.* (1999) indicates Earth underwent a linear-regression-derived global warming of 0.333° C; the database of the Global Historical Climatology Network indicates the planet experienced a similarly calculated global warming of 0.397° C. The mean of these two values (0.365° C) is nearly twice as great as the warming that occurred over the post-1999 period studied by Behrenfeld *et al.*, yet this earlier much larger warming—which Behrenfeld *et al.*'s work suggests should have produced a major decline in ocean productivity—was accompanied by a huge increase in ocean produc-

tivity. It would appear Behrenfeld *et al.* got the causeand-effect relationship between global warming and ocean productivity exactly backwards.

Since publication of the Behrenfeld et al. study, other researchers have found no cause for alarm with respect to ocean productivity and rising global temperatures. Arrigo et al. (2008) write, "between the late 1970s and the early part of the 21st century, the extent of Arctic Ocean sea ice cover has declined during all months of the year, with the largest declines reported in the boreal summer months, particularly in September $(8.6 \pm 2.9\% \text{ per decade}),"$ citing Serreze et al. (2007). To "quantify the change in marine primary productivity in Arctic waters resulting from recent losses of sea ice cover," the "implemented a primary productivity authors algorithm that accounts for variability in sea ice extent, sea surface temperature, sea level winds, downwelling spectral irradiance, and surface chlorophyll a concentrations," and "was parameterized and validated specifically for use in the Arctic (Pabi et al., 2008) and utilizes forcing variables derived either from satellite data or NCEP reanalysis fields."

Arrigo *et al.* determined "annual primary production in the Arctic increased yearly by an average of 27.5 Tg C per year since 2003 and by 35 Tg C per year between 2006 and 2007." Thirty percent of the increase was attributable to decreased minimum summer ice extent, and 70% was due to a longer phytoplankton growing season. Arrigo *et al.* conclude if the trends they discovered continue, "additional loss of ice during Arctic spring could boost productivity >3-fold above 1998–2002 levels." If the 26% increase in annual net CO₂ fixation in the Arctic Ocean between 2003 and 2007 continues, they state, "this would represent a weak negative feedback on climate change."

Smith and Comiso (2008) employed phytoplankton pigment assessments, surface temperature estimates, modeled irradiance, and observed sea ice concentrations—all derived from satellite data—and incorporated them into a vertically integrated production model to estimate primary productivity trends according to the technique of Behrenfeld *et al.* (2002). The two authors state "the resultant assessment of Southern Ocean productivity is the most exhaustive ever compiled and provides an improvement in the quantitative role of carbon fixation in Antarctic waters."

Over the nine years (1997–2006) analyzed in the study, "productivity in the entire Southern Ocean showed a substantial and significant increase," and

this increase can be calculated from the graphical representation of their results as $\sim 17\%$ per decade. The two researchers note "the highly significant increase in the productivity of the entire Southern Ocean over the past decade implies that long-term changes in Antarctic food webs and biogeochemical cycles are presently occurring," and these changes are positive.

Peck *et al.* (2010) note the loss of glaciers and ice shelves at the Antarctic Peninsula 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." 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), which 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 10-year time series of chlorophyll depth profiles (1997–2007) from a near-shore site in northern Marguerite Bay developed by Clarke *et al.* (2008), Peck *et al.* reconstructed the magnitude of new oceanic production that developed around the Antarctic Peninsula as sea ice progressively gave way to open water.

The five researchers with the British Antarctic Survey report 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." They state if only 15% 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," and "over 9 Mtonnes of carbon would be locked up in biological communities in the water column or on the sea bed." They suggest over a period of tens, hundreds, or thousands of years, "this process may act as a climate control mechanism."

Brown *et al.* (2011) investigated the widespread assumption the Bering Sea is "rapidly warming and losing sea ice" by employing "satellite-derived sea ice concentration, sea surface temperature, and ocean color data as input to a primary productivity algorithm to take stock of environmental change and primary production" in this region. As the three U.S. researchers report, "rather than declining," they found mean annual sea ice extent in the Bering Sea "has exhibited no significant change over the satellite sea ice record (1979-2009)," because significant warming during the satellite sea surface temperature record (1982-2009) "is mainly limited to the summer months." In addition, and despite certain hotspots of primary production and a strong pulse in the spring, they also determined "the rate of annual areanormalized primary production in the Bering Sea $(124 \text{ g C per } m^2 \text{ per year})$ is below the global mean (140 g C per m² per year)." By "comparing warm, low-ice years (2001-2005) with cold, high-ice years (1998–2000 and 2006–2007)," they conclude "Bering Sea primary productivity is likely to rise under conditions of future warming and sea ice loss." That rise could be substantial, as they report, "basin-wide annual primary production ranged from 233 to 331 Tg C per year under the influence of highly variable sea ice and temperature conditions."

Chavez *et al.* (2011) reviewed the concepts and methods used to estimate ocean primary production (PP), after which they used the modern global instrumental record of sea surface temperature (SST) to analyze the principal modes of interannual to multidecadal climate and ocean variability. They then compared spatiotemporal patterns derived from *in situ* and satellite time-series of PP with the known timeseries of climate and ocean variability, to identify the processes responsible for the observed patterns in PP. They introduced paleoclimate studies into their work to broaden the temporal context and "lead into speculation regarding century-scale variability."

Based on the first part of their analysis, the three researchers from the Monterey Bay Aquarium Research Institute of Moss Landing, California (USA) write, "general conclusions from the satellite and *in situ* time-series presented here are that PP is increasing globally," and they note global marine PP appears to have risen over the past several decades in association with multidecadal variations in climate. They report data from Continuous Plankton Recorder surveys conducted in the north Atlantic depict "increases in chlorophyll from the 1950s to the present," citing McQuatters-Gollop *et al.* (2007).

In the second part of their analysis, Chavez *et al.* report ocean sediment cores containing an "undisturbed history of the past" have been analyzed for variations in PP over timescales that include the Little Ice Age (LIA, ~1400–1800; Gutierrez *et al.*, 2009). Based on reconstructed flux rates of total organic carbon (Sifeddine *et al.*, 2008); diatoms, silica, and fish scales; bones; and vertebrae, they determined during the LIA the ocean off Peru had "low PP, diatoms and fish," but "at the end of the LIA, this condition changed abruptly to the low subsurface oxygen, eutrophic upwelling ecosystem that today produces more fish than any region of the world's oceans (Chavez *et al.*, 2008)." The researchers conclude, "in coastal environments, PP, diatoms and fish and their associated predators are predicted to decrease and the microbial food web to increase under global warming scenarios," citing Ito *et al.* (2010). However, they write, "present-day trends and the sedimentary record seem to indicate that the opposite might occur."

Tremblay et al. (2011) note the Canadian Beaufort Shelf and adjacent bays make up a small part of the Arctic Ocean but are of "prime social, economical and cultural importance" for coastal communities because they are "hotspots of marine productivity and staging" and "feeding areas for large aggregations of resident and migrant marine birds and mammals," citing Carmack and MacDonald (2002). Wondering what would happen to the productivity of this important coastal region if it were to warm further, Tremblay et al. set out to compare time series of ice cover, wind forcing, and satellite-based assessments of photosynthetic carbon production for the years 2002–2008 with corresponding in situ measurements of salinity, nutrients, new production, biological stocks, and biogenic fluxes obtained during overwintering surveys in 2003–2004 and 2007–2008.

In 2007–2008, the 15 researchers report, in areas where ice was no longer present due to enhanced seasonal warming, there was significant wind-induced upwelling of growth-promoting nitrates, which were brought up from deep and dark waters into the euphotic zone, where photosynthesis occurs. As a result of this fertilization effect, the herbivorous copepod *Calanus glacialis*—which they say is "the key link between diatom production and apex consumers on Arctic shelves," citing Soreide *et al.* (2010)—experienced a total abundance "3 to 33 times higher than in 2003 during mid-fall and 1.6 to 13 fold higher than in 2004 during early summer."

On the region's central shelf, they observed "sedimentary chlorophyll *a* was over 20-fold higher than at any station not influenced by upwelling," and "benthic carbon demand was among the highest ever observed in the Arctic ocean," citing Clough *et al.* (2005). The end result of these related phenomena was the "repeated instances of ice ablation and upwelling during fall 2007 and summer 2008 multiplied the production of ice algae, phytoplankton, zooplankton and benthos by 2 to 6 fold."

Tremblay *et al.* conclude the phenomena they observed are "likely to prevail with the increasingly deep and frequent seaward retreat of the central ice pack and the greater incidence of upwelling-favorable winds," as described in detail by Yang (2009), and "new production is also bound to rise as winds gain in intensity and upwelling draws deeper into the nutrient-rich, upper Pacific halocline."

McMinn and Martin (2013) note "most algae regularly experience periods of darkness ranging from a few hours to a few days," during which time "they are unable to photosynthesize, and so must consume stored energy products." The scientists note "some organisms such as polar algae and some microalgal cysts and spores are exposed to darkness for months to years, and these must use alternative strategies to survive." McMinn and Martin-who work at the University of Tasmania's Institute for Marine and Antarctic Studies-reviewed the scientific literature on this subject and found "some taxa, such as dinoflagellates, form cysts and become dormant," while "others use physiological methods or adopt mixotrophy," and "the longest documented survival of more than a century was for dinoflagellates buried in sediments in a Norwegian fjord." In the future, they opine, polar microalgae will have to survive "the same period of seasonal darkness but at higher temperatures, and this will require a greater drawdown of stored energy." McMinn and Martin report "recent experimental work has shown that both Arctic [Martin et al., 2012] and Antarctic [Reeves et al., 2011] phytoplankton are able to survive increases of up to 6°C in the dark." Because such a temperature increase is "unlikely to be experienced in a few centuries as a result of climate change," polar microalgae should be safe for a long, long time to come

According to Aberle *et al.* (2012), in places such as the Baltic Sea a "temporal match of zooplankton peaks with the spring phytoplankton bloom is required to provide an efficient energy transfer up the food web at the start of the growing season," but some scientists have predicted "warming will affect the different trophic levels unequally" and result in a counterproductive "temporal mismatch between predators and their prey." Aberle *et al.* conducted a set of indoor mesocosm experiments "to analyze time-lags between phytoplankton and microzooplankton during the spring succession of Baltic Sea plankton in relation to changing temperature [0 and 6°C above the decadal mean] and light conditions," along with "model simulations using a modified Rosenzweig and MacArthur (1963) predator-prey model incorporating temperaturedependent growth, grazing and mortality rates of autotrophic and heterotrophic components."

The five German scientists say "during the experiments, we observed reduced time-lags between the peaks of phytoplankton and protozoan biomass in response to warming," adding "warming induced a shift in micro-zooplankton phenology leading to a faster species turnover." The models they employed also "predicted reduced time-lags between the biomass peaks of phytoplankton and its predators (both micro-zooplankton and copepods) with warming." Aberle *et al.* conclude their study shows "instead of a mismatch, warming might lead to a stronger match between protist grazers and their prey."

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, 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. The five French scientists found "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." They found "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 warmer is better, a maxim exemplified in the current case by the greater productivity of the tropical ocean during the warmer period and the ocean's continuous upward trend in the diversity of phytoplanktonic species throughout the period of warming.

Cermeño (2011) states "micro-organisms dominate terrestrial, aquatic and aerial ecosystems and largely rule our planet's life by playing pivotal roles in global biogeochemical cycles," citing Staley and Fuhrman (2002) and Falkowski *et al.* (2008). He declares these facts indicate "life on Earth is microbe dependent." Cermeño used records of climatic variability and microfossil data from the world's oceans covering the past 65 million years to "explore the linkage between the rate of climate change and the probability of extinction, origination and net diversification of marine planktonic diatoms and calcareous nannoplankton," analyzing the evolutionary dynamics of the two phytoplankton groups throughout the 65million-year period of study and comparing the results with the climate change record.

Cermeño states his findings demonstrate "the probability of extinction of microbial plankton species did not increase during periods of enhanced climatic instability over the past 65 million years." He savs his results show "exceptional climatic contingencies, such as those occurring across the Late Palaeocene-Eocene and the Eocene-Oligocene boundary transitions, caused substantial morphological diversification." Cermeño concludes, "to the extent that contemporaneous trends in climate change have analogies with the climates of the geological period analyzed here, my results suggest that these microbial plankton groups will persist in the future ocean, perhaps even expanding their ranges of morphological diversity."

Cannariato et al. (1999) provide additional evidence marine biota are well-equipped to adapt to rising temperatures. They investigated the character, magnitude, and speed of responses of benthic foraminifera to millennial-scale climate oscillations manifest in data obtained from an ocean sediment core in the Santa Barbara Basin of the Northeast Pacific that covered the most recent 60,000 years. Although a number of rapid climatic switches were noted throughout the record, representing periods of "extreme environmental variability," the scientists found no extinctions, and the benthic ecosystems "appear to be both resilient and robust in response to rapid and often extreme environmental conditions." Although faunal turnovers occurred within decades, they did so "without extinction or speciation."

Ladah *et al.* (1999) examined the density and population structure of giant kelp "forests" located near Bahia Tortugas, Baja California, Mexico, before, during, and after the 1998 El Niño. At the height of the extreme warming event, sea surface temperatures (SSTs) were 3°C higher than the previous 10-year average for this region, and they led to the complete disappearance of the giant kelp that historically had inhabited the area. However, when the SST anomalies subsided, the giant kelp were once again found to be growing there, and from evidence derived from population structure data and the rapidity with which the plants reestablished themselves, Ladah *et al.* deduced "a microscopic stage that was not visible during dive surveys survived the stressful conditions of ENSO and caused the recruitment event, supporting the hypothesis that a bank of microscopic forms can survive conditions stressful to macroscopic algae." They note there was independent evidence to suggest "microscopic stages may subsist in nature under low light intensities in a semi-dormant state until conditions become favorable."

In a follow-up study published several years later, Ladah and Zertuche-Gonzalez (2004) found a second and more likely predominant means by which the return of the giant kelp was made possible. Although all giant kelp growing at 15 m depth or shallower died during the peak warmth of the El Niño, the pair of researchers discovered there were numerous large fertile adults located between 25 and 40 m depth unaffected by the high surface water temperatures. Although the upper 15 meters of these plants died and sloughed off, regenerated fronds reached the surface of the sea by the fall of 1998.

The two scientists write, "survival in deep water during this extreme El Niño may have been due to local hydrography, such as internal waves bringing cool nitrate-rich water into the deeper regions of the shelf from below the thermocline, providing a refugium against the warm temperatures, low nutrients, and heavy wave action associated with warming events." They also note "the increased light that often occurs after canopy removal apparently resulted in ... recruitment events ... from newly produced spores from nearby fertile individuals surviving in deeper waters." They conclude "deepwater populations may regularly survive El Niño warming in this region due to internal wave activity. and go undetected due to the depth at which they occur and the sloughing of the shallow (<15 m) biomass "

Zheng et al. (2012) state dinoflagellates "are generally believed to prefer warm temperatures and presumably may do better in the face of temperature increases," noting Prorocentrum donghaiense was able to grow at temperatures ranging from 10 to 27°C and achieved its maximum specific growth rate at the latter temperature (Xu et al., 2010). For P. minimum, they note, "growth rates increased from 0.25/day at 4°C to 0.98/day at 20°C," citing Lomas and Gilbert (1999a,b). They report the composition of phytoplankton exposed to a temperature rise in the vicinity of a nuclear power plant's thermal effluent "tipped toward dinoflagellates both in terms of species number and cell abundance (Li et al., 2011)," probably because "some dinoflagellates were found to produce heat-shock proteins to stabilize protein secondary structure in response to thermal stress

(Alexandrov, 1994)." They further note, "heat shock protein 70 was induced in *Alexandrium tamarense* when subjected to a 10°C jump from its acclimated temperature of 20°C (Kobiyama *et al.*, 2010)."

Zheng et al. studied the effects of temperature shock on the growth of the dinoflagellate Polarella glacialis, "by monitoring its physiological and biochemical responses to temperature rises from 4°C to 10 and 15°C" while examining the growth rate and expression of two important genes for this alga. The three researchers state, "it is noteworthy that in the present study the cultures were directly transferred from 4°C to 10 and 15°C without progressive intermediate steps," and in response to these sudden temperature shifts, "the cultures first experienced a period of declination, then cell density tended to become stable, a sign that a part of the cell population survived." Zheng et al. conclude, "if the species can survive such heat shock in the long term, there is good opportunity that it can be transported from polar regions to temperate or even warmer waters," which perhaps explains why "taxa closely related to this species occur in temperate aquatic environments (Lin et al., 2009, 2010)." If P. glacialis and related species can do that, they should have no problem coping with projected global warming.

Clark et al. (2013) used "a quantitative genetic breeding design to establish whether there is a heritable variation in thermal sensitivity in two populations of a habitat-forming intertidal macroalga, Hormosira banksii (Turner) Descaisne," in which "gametes from multiple parents were mixed and growth and photosynthetic performance were measured in the resulting embryos, which were incubated under control and elevated temperatures (20°C and 28°C)." The four researchers report "significant interactions between male genotype and temperature in one population indicated the presence of genetic variation in thermal sensitivity," such that "selection for more tolerant genotypes thus has the ability to result in the evolution of increased thermal tolerance." They found "genetic correlations between embryos grown in the two temperatures were positive, indicating that those genotypes that performed well in elevated temperature also performed well in control temperature." Clark et al. conclude their "finding of genetic variation in thermal tolerance of H. banksii embryos suggests resilience to thermal stresses."

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6.1.2 Corals

Perhaps no other species of marine life is projected by IPCC to experience as much hardship and degradation in response to rising temperatures as corals. Several statements from a draft of Working Group II's contribution to IPCC's *Fifth Assessment Report* illustrate these concerns:

The frequency and magnitude of coral bleaching and mortality will increase in the next few decades (*very high confidence*).

Under the A1B CO_2 emission scenario, 99% of the grid cells experience at least one severe bleaching event over 2090–2099.

Half of the coral reefs may avoid high frequency bleaching through 2100 assuming hypothetical

acclimation and/or adaptation (*limited evidence*, *low agreement*).

— Chapter 5, Coastal Systems and Low-Lying Areas, Working Group II, IPCC *Fifth Assessment Report*, draft dated March 28, 2013, p. 19.

It is *very likely* that coral reef ecosystems will not survive changes in sea temperature beyond an additional increase of 1°C.

Combining the known sensitivity of coral reefs within the Caribbean and Coral Triangle subregions, with the exposure to higher temperatures that are projected under medium (RCP4.5) to high (RCP8.5) scenarios, reveals that both coral reef rich regions are *virtually certain* to experience levels of thermal stress that cause coral bleaching every 1–2 years by the mid to late part of this century (*robust evidence, high levels of agreement, very high confidence*).

The frequency of mass mortality events (DHM > 5; Figure 30–11 A,C) climbs towards events that occur every 1–2 years by mid to late of this century under low to high climate change scenarios (*robust evidence, high levels of agreement, very high confidence*).

Mass mortality events that impact coral reefs will result in changes to community composition in the short term (2010–2039) and a continuing downward trend in reef building coral stocks in the longer term.

— Chapter 30, The Ocean, Working Group II, IPCC *Fifth Assessment Report*, draft dated March 28, 2013, p. 35.

There is *robust evidence* and *high agreement* that coral reefs are one of the most vulnerable marine ecosystems.

Even under optimistic assumptions regarding corals being able to rapidly adapt to thermal stress, one-third (9–60%, 68% uncertainty range) of the world's coral reefs are projected to be subject to long-term degradation under the RCP3-PD scenario. Under the RCP4.5 scenario, this fraction increases to two-thirds (30–88%, 68% uncertainty range).

If present day corals have residual capacity to acclimatize and/or adapt, half of the coral reefs may avoid high frequency bleaching through 2100 (*limited evidence, limited agreement*). Evidence of

corals adapting rapidly, however, to climate change is missing or equivocal.

— Technical Summary, Working Group II, IPCC *Fifth Assessment Report*, draft dated March 28, 2013, pp. 67–68.

This section examines the future of Earth's corals in response to possible global warming, beginning with a review of the literature on the many suspected causes of coral bleaching, almost all of which have been attributed (often implausibly) to CO₂-induced global warming. Thereafter, the discussion turns to the possibility corals can adapt to the various environmental threats they face, followed by an examination of whether the widespread bleaching events seen in recent decades are indeed caused by global warming. The discussion concludes with a brief examination of an indirect temperature-related threat to corals-rising sea levels-which IPCC predicts will occur to a significant degree over the twenty-first century and beyond as global warming melts large portions of the ice presently stored in the world's glaciers and ice sheets.

This survey offers a much different perspective on the future of Earth's corals than that predicted by IPCC. Though rising temperatures have challenged and may continue to challenge Earth's corals, a large body of evidence indicates many corals can adapt to and even overcome the temperature-related challenges they are projected to face in response to CO_2 -induced global warming. In reaching its overly pessimistic conclusions about corals, IPCC has clearly and improperly ignored the weight of the many research findings summarized here.

6.1.2.1 Causes of Coral Bleaching

This section reviews studies examining the causes of coral bleaching. The key findings are as follows:

- Many studies attribute high sea water temperatures as the primary cause of coral bleaching. However, the crucial link between temperature and coral reef bleaching may not reside in the absolute temperature of the water surrounding the corals but in the rapidity with which the temperature either rises above or falls below the temperature regime to which the corals are normally adapted.
- A number of studies have provided evidence inconsistent with the global-warming-induced coral

bleaching hypothesis, pointing to other important factors and causes of coral bleaching, including solar irradiance, a solar radiation-temperature stress synergism, changes in salinity, bacterial infections, increased sedimentation, and exposure to toxicants.

• Many sources of coral stress and survival have little or nothing to do with rising CO₂ concentrations or temperatures.

Coral bleaching ranks among the more frequently cited negative consequences projected to result from CO_2 -induced global warming. A loss of color in certain reef-building corals occurs when algal symbionts, or zooxanthellae, living within the host corals are subjected to various stresses and expelled from them, resulting in a loss of photosynthetic pigments from the coral colony. If the stress is mild, or short in duration, the affected corals often recover and regain their normal complement of zooxanthellae. If the stress is prolonged, or extreme, the corals eventually die, being deprived of their primary food source.

One of the most frequently cited causes of coral bleaching is anomalously high water temperature (Linden, 1998). The origin of this attribution can be traced to the strong El Niño event of 1982–1983, in which widespread bleaching was reported in corals exposed to unusually high surface water temperatures (Glynn, 1988). Since then, a number of other such observations have been made (Cook *et al.*, 1990; Glynn 1991; Montgomery and Strong, 1994; Brown *et al.*, 1996), and several laboratory studies have demonstrated elevated seawater temperatures can indeed induce bleaching in corals (Hoegh-Guldberg and Smith, 1989; Jokiel and Coles, 1990; Glynn and D'Croz, 1990).

Anomalously *low* seawater temperatures also have been identified with coral bleaching (Walker *et al.*, 1982; Coles and Fadlallah, 1990; Muscatine *et al.*, 1991; Gates *et al.*, 1992; Saxby *et al.*, 2003; Hoegh-Guldberg and Fine 2004; Yu *et al.*, 2004; Kemp *et al.*, 2011). These observations suggest the crucial link between temperature and coral reef bleaching may not be in the absolute temperature of the water surrounding the corals, but in the rapidity with which the temperature varies from the temperature regime to which the corals are normally adapted.

Winter *et al.* (1998), for example, studied relationships between coral bleaching and nine temperature indices, concluding, although "prolonged heat stress may be an important precondition for

bleaching to occur," sharp temperature changes act as the "immediate trigger." Jones (1997) reported coral bleaching on a portion of Australia's Great Barrier Reef just after average daily sea water temperature rose by 2.5°C over a brief period of eight days. Kobluk and Lysenko (1994) observed severe coral bleaching after an 18-hour *decline* of 3°C in seawater temperature. Because the corals studied by the latter researchers had experienced massive bleaching two years earlier as a result of an anomalous 4°C *increase* in water temperature, the authors conclude coral bleaching is more a function the rapidity of a temperature change than of the absolute magnitude or sign of the change, of heating or cooling.

Podesta and Glynn (1997) provided further evidence seawater temperatures *per se* are not the critical factors in coral bleaching. They examined a number of temperature-related indices of surface waters near Panama over the period 1970–1994. Their analysis revealed for the two years of highest maximum monthly sea surface temperature, 1972 and 1983, coral bleaching was reported only in 1983; 1972 produced no bleaching whatsoever, even though water temperatures that year were just as high as they were in 1983.

Another prominent cause of coral bleaching is solar radiation, a link dating back more than a century to when MacMunn (1903) postulated ultraviolet radiation could damage corals. It wasn't until half-acentury later that scientists began to confirm this suspicion (Catala-Stucki, 1959; Siebeck, 1988; Gleason and Wellington, 1995).

Many investigators of the solar irradiance-coral reef bleaching link have studied the phenomenon by transplanting reef corals from deep to shallow waters. Gleason and Wellington (1993), for example, transplanted samples of the reef-building coral Montastrea annularis from a depth of 24 meters to depths of 18 and 12 meters. Using sheets of acrylic plastic to block out ultraviolet radiation on some of the coral samples, they found the shielded corals experienced less bleaching than the unshielded corals, and the unshielded corals at the 12-meter depth had significantly lower amounts of zooxanthellae and chlorophyll per square centimeter than all other treatment and control groups. Similarly, Hoegh-Guldberg and Smith (1989) reported bleaching in the corals Stylophora pistillata and Seriatopora hystrix when they were moved from a depth of 6 meters to 1.2 meters. Vareschi and Fricke (1986) obtained similar results when moving *Plerogyra sinuosa* from a depth of 25 meters to 5 meters. As in the case of temperature stress, Glynn (1996) notes artificially

reduced light levels also have been observed to cause coral bleaching.

A number of laboratory studies have provided additional evidence for a link between intense solar irradiance and coral reef bleaching, but identifying a specific wavelength or range of wavelengths as the cause of the phenomenon has proven difficult. Fitt and Warner (1995), for example, reported the most significant decline in symbiont photosynthesis in the coral *Montastrea annularis* occurred when it was exposed to ultraviolet and blue light, but other studies have reported coral bleaching to be most severe at shorter ultraviolet wavelengths (Droller *et al.*, 1994; Gleason and Wellington, 1995). Still others have found it to be most strongly expressed at longer photosynthetically active wavelengths (Lesser and Shick, 1989; Lesser *et al.*, 1990; Brown *et al.*, 1994).

As additional studies provided evidence for a solar-induced mechanism of coral reef bleaching (Brown *et al.*, 1994; Williams *et al.*, 1997; Lyons *et al.*, 1998), some also provided evidence for a synergism of solar radiation and temperature stress (Gleason and Wellington, 1993; Rowan *et al.*, 1997; Jones *et al.*, 1998). Researchers have found a number of situations, for example, in which corals underwent bleaching when changes in both of these parameters combined to produce particularly stressful conditions (Lesser *et al.*, 1990; Glynn *et al.*, 1992; Brown *et al.*, 1995), such as during periods of low wind velocity and calm seas, which favor the intense heating of shallow waters and concurrent strong penetration of solar radiation.

This two-parameter interaction has much to recommend it as a primary cause of coral bleaching. It is the mechanism favored by Hoegh-Guldberg (1999), who claimed, in one of the strongest attempts made to that point in time to portray global warming as the cause of bleaching in corals, "coral bleaching occurs when the photosynthetic symbionts of corals (zooxanthellae) become increasingly vulnerable to damage by light at higher than normal temperatures."

The story is considerably more complicated than that. In a review paper on coral bleaching, Brown (1997) listed several potential causes, including elevated seawater temperature, decreased seawater temperature, intense solar radiation, the combination of intense solar radiation and elevated temperature, reduced salinity, and bacterial infections. In a similar review, Meehan and Ostrander (1997) added increased sedimentation and exposure to toxicants.

With respect to seawater salinity, Meehan and Ostrander (1997) note, as with temperature, both high and low values have been observed to cause coral bleaching. Low values typically occur as a result of seawater dilution caused by high precipitation or storm runoff; high values are much rarer, typically occurring only near desalinization plants.

A number of studies also have described the role of bacterial infections in causing coral reef bleaching (Ritchie and Smith, 1998). This phenomenon, too, may have a connection to high seawater temperatures. In a study of the coral Oculina patagonica and the bacterial agent Vibrio AK-1, for example, Kushmaro et al. (1996, 1997) conclude bleaching of colonies of this coral along the Mediterranean coast has its origin in bacterial infection, and that warmer temperatures may lower the resistance of the coral to infection and/or increase the virulence of the bacterium. In subsequent studies of the same coral and bacterium, Toren et al. (1998) and Kushmaro et al. (1998) further demonstrated this high temperature effect may operate by enhancing the ability of the bacterium to adhere to the coral.

Kushmaro et al. (1998) comment on the "speculation that increased seawater temperature, resulting from global warming or El Niño events, is the direct cause of coral bleaching." Against this presumption, they cite several studies of coral bleaching events not associated with any major sea surface temperature anomalies, and they explicitly state, "it is not yet possible to determine conclusively that bleaching episodes and the consequent damage to reefs is due to global climate change." Likewise, Toren et al. (1998) note the extensive bleaching that occurred on the Great Barrier Reef during the summer of 1982 was not associated with any major sea surface temperature increase, and "several authors have reported on the patchy spatial distribution and spreading nature of coral bleaching." They note this observation conflicts with the global-warminginduced coral bleaching hypothesis. Instead, they write, "the progression of observable changes that take place during coral bleaching is reminiscent of that of developing microbial biofilms," a point that will later be seen to be of great significance.

High rates of sedimentation have been demonstrated to lead to coral bleaching (Wesseling *et al.*, 1999), and most historical increases in sedimentation rates are clearly human-induced. Umar *et al.* (1998), for example, listed such contributing anthropogenic activities as deforestation, agricultural practices, coastal development, construction, mining, drilling, dredging, and tourism. Nowlis *et al.* (1997) discussed "how land development can increase the risk of severe damage to coral reefs by sediment runoff during storms." However, it has been difficult to determine just how much these phenomena have varied over the past few centuries.

McCulloch et al. (2003) recreated a 250-year record of sediment transfer to Havannah Reef-a site on the inner Great Barrier Reef of northern Queensland, Australia-by flood plumes from the Burdekin River. They found sediments suspended in the Burdekin River contain barium (Ba), which is desorbed from the particles that carry it as they enter the ocean, where growing corals incorporate it into their skeletons along with calcium (Ca). When more sediment is carried to the sea by periodic flooding and more gradual longer-term changes in land use that exacerbate soil erosion, the resultant increases in sediment load are recorded in the Ba/Ca ratio of coral skeleton material. McCulloch et al. measured Ba/Ca ratios in a 5.3-meter-long coral core from Havannah Reef that covered the period from about 1750 to 1985, as well as in some shorter cores from Havannah Reef and nearby Pandora Reef that extended the proxy sediment record to 1998.

The results revealed before the time of European settlement, which began in the Burdekin catchment in 1862, there was "surprisingly little evidence for flood-plume related activity from the coral Ba/Ca ratios." Soon after, land clearance and domestic grazing intensified, and the soil became more vulnerable to monsoon-rain-induced erosion. By 1870, baseline Ba/Ca ratios had risen by 30%, and "within one to two decades after the arrival of European settlers in northern Queensland, there were already massive impacts on the river catchments that were being transmitted to the waters of the inner Great Barrier Reef." During subsequent periods of flooding, the transport of suspended sediment to the reef increased by five- to ten-fold over what had been characteristic of pre-European settlement times.

In a companion article, Cole (2003) report corals from East Africa "tell a similar tale of erosion exacerbated by the imposition of colonial agricultural practices in the early decades of the twentieth century." There, similar coral data from Malindi Reef, Kenya, indicate "a low and stable level of barium before about 1910 which rises dramatically by 1920, with a simultaneous increase in variance," which was also evident in the Australian data.

Cole concludes "human activity, in the form of changing land use, has added sedimentation to the list of stresses experienced by reefs." As land-use intensification is a widespread phenomenon, she notes, "many reefs close to continents or large islands are likely to have experienced increased delivery of sediment over the past century," which suggests the stress levels produced by this phenomenon are likely to have increased over the past century as well. Cole concludes as coastal populations continue to rise, "this phenomenon is likely to expand."

A number of poisonous substances are known to induce coral bleaching. Some—such as herbicides, pesticides, and even excess nutrients that make their way from farmlands to the sea (Simkiss, 1964; Pittock, 1999)—are of human origin. Other poisons originate in the sea itself, many the result of metabolic waste products of other creatures (Crossland and Barnes, 1974) and some a by-product of the coral host itself (Yonge, 1968). Each of these toxicants presents the coral community with its own distinct challenge.

Taken together, these findings identify a number of sources of stress on coral survival and growth that have little or nothing to do with rising CO_2 concentrations or temperatures. They also clearly indicate human population growth and economic development have predisposed coral reefs to incidences of bleaching and subsequent mortality via a gradual intensification of near-coastal riverine sediment transport rates.

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6.1.2.2 Responses to Temperature-Related Stresses

Considering the many threats to the health of corals outlined in the previous section, many have questioned how these repositories of underwater biodiversity could possibly escape irreversible bleaching and death. In response to such concerns, Glynn (1996) noted, "numerous reef-building coral species have endured three periods of global warming, from the Pliocene optimum (4.3–3.3 million years ago) through the Eemian interglacial (125 thousand years ago) and the mid-Holocene (6000–5000 years ago), when atmospheric CO_2 concentrations and sea temperatures often exceeded those of today." Glynn observed "an increase in sea warming of less than 2°C would result in a greatly increased diversity of corals in certain high latitude locations."

Living organisms are resilient. Various life forms can tolerate temperatures from below freezing to the boiling point of water; others inhabit niches where light intensity varies from complete darkness to full sunlight. Given time to adapt, nearly all living organisms can learn to survive in conditions well outside their normal zones of environmental tolerance. As Gates and Edmunds (1999) note, numerous studies indicate "corals routinely occupy a physically heterogeneous environment," which "suggests they should possess a high degree of biological flexibility." Their successful responses to the different threats that cause coral bleaching prove that flexibility and are examined in the subsections below.

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6.1.2.2.1 Thermal Adaptation

The studies reviewed in this section examine the concept of thermal adaptation, which refers to the ability of corals to adapt to temperature stresses in the future of similar or even greater magnitude than what they have experienced in the past. The key findings are presented in the bullet points below followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- As living entities, corals are not only affected by the various elements of their environment, they also react or respond to them. When changes in environmental factors pose a challenge to their continued existence, they sometimes take major defensive or adaptive actions, including thermal adaptation, to ensure their survival.
- Multiple studies demonstrate corals are thermally adapting to rising sea water temperatures. Bleaching at many reefs is either reduced or no longer occurs at temperatures that previously caused it.

- Cold water coral species also have been shown to display resilience in adapting to temperature increases as large as 5°C.
- Coral genera most susceptible to thermal stress sometimes display the greatest increase in thermal tolerance.
- Genotypic analyses suggest "the physiological plasticity of the host and/or symbiotic components" plays an important role in thermal adaptation.
- There is "a growing body of evidence to support the notion that corals inhabiting more thermally unstable habitats outperform conspecifics from reefs characterized by more stable temperatures when exposed to elevated temperatures."
- "Previous exposure to an environmentally variable microhabitat adds substantially to coral-algal thermal tolerance, beyond that provided by heat-resistant symbionts alone." Similarly, the thermal adaptive capacity of some corals "is likely facilitated by a combination of short-term acclimation in individuals during acute environmental conditions (e.g., recurrent bleaching events) and long-term adaptation among coral populations to chronic environmental conditions (e.g., extreme temperatures)."
- "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."

Fang *et al.* (1997) experimented with samples of *Acropora grandis* taken from the hot water outlet of a nuclear power plant near Nanwan Bay, Taiwan. In 1988, the year the power plant began full operation, the coral samples were completely bleached within two days of exposure to a temperature of 33°C. Two years later, however, "samples taken from the same area did not even start bleaching until six days after exposure to 33°C temperatures," illustrating their ability to thermally adapt.

Middlebrook *et al.* (2008) reported similar findings. They collected multiple upward-growing branch tips of the reef-building coral *Acropora aspera* from three large colonies at the southern end of Australia's Great Barrier Reef and placed them on racks immersed in running seawater within four 750-liter tanks maintained at the mean local ambient temperature (27°C) and exposed to natural reef-flat summer daily light levels. Two weeks before a simulated bleaching event—where water temperature was raised to a value of 34°C for six days—they boosted the water temperature in one of the tanks to 31° C for 48 hours, and in another tank they boosted it to 31° C for 48 hours one week before the simulated bleaching event. In the third tank they had no preheating treatment, and in the fourth tank they used no pre-heating nor any simulated bleaching event. At different points throughout the study, they measured photosystem II efficiency, xanthophyll and chlorophyll *a* concentrations, and *Symbiodinium* densities.

Middlebrook et al. found the symbionts of the corals exposed to the 48-hour pre-bleaching thermal stress "were found to have more effective photoprotective mechanisms," including "changes in nonphotochemical quenching and xanthophyll cycling." They determined "these differences in photoprotection were correlated with decreased loss of symbionts, with those corals that were not prestressed performing significantly worse, losing over 40% of their symbionts and having a greater reduction in photosynthetic efficiency," whereas "prestressed coral symbiont densities were unchanged at the end of the bleaching." Middlebrook et al. say their study "conclusively demonstrates that thermal stress events two weeks and one week prior to a bleaching event provide significantly increased thermal tolerance to the coral holobiont, suggesting that short time-scale thermal adaptation can have profound effects on coral bleaching."

In another laboratory-based study, Bellantuono *et al.* (2012) "tested the response of *Acropora millepora* to thermal preconditioning by exposing coral nubbins to 28°C (3°C below bleaching threshold) for 10 days, prior to challenging them with water temperatures of 31°C for 8 days," while "in another treatment (non-preconditioned), corals were exposed to 31°C without prior exposure to the 28°C treatment." They conducted these procedures in a set of "transparent tanks plumbed into flowing sea water, with four replicate tanks for each treatment."

The three researchers discovered short-term preconditioning to higher-than-ambient temperatures (but still 3°C below the experimentally determined bleaching threshold) for 10 days provided thermal tolerance for the scleractinian coral and its symbionts. Based on various genotypic analyses they conducted, they determined "the acclimatization of this coral species to thermal stress does not come down to simple changes in *Symbiodinium* symbiont shuffling and/or the bacterial communities that associate with

reef-building corals bacterial shuffling." These findings, Bellantuono *et al.* write, suggest "the physiological plasticity of the host and/or symbiotic components appears to play an important role in responding to ocean warming." They describe realworld examples of this phenomenon possibly playing a crucial role in preserving corals exposed to extreme warm temperatures in the past (Fang *et al.*, 1997; Middlebrook *et al.*, 2008; Maynard *et al.*, 2008b).

South of Malta in the Mediterranean Sea, Naumann et al. (2013) collected live specimens of two scleractinian cold-water coral (CWCs) species, Dendrophyllia cornigera and D. dianthus. They transferred the specimens into two identically equipped and darkened 100-L flow-through aquaria through which Mediterranean subsurface seawater was continuously pumped from a 50-meter depth and supplied to the tanks at a rate of about one liter per minute. They maintained this water at a temperature of $12.5 \pm 0.1^{\circ}$ C for approximately 30 months before initiating the primary phase of their experiment, which was to increase the temperature of one of the aquariums by 0.5° C per day up to $17.5 \pm 0.1^{\circ}$ C, thereafter maintaining it for a further 87 days, while conducting "daily visual assessments of coral health (i.e. tentacle protrusion, suspension feeding and mortality/survival) and monthly growth measurements by the buoyant weight technique (Davies, 1989)," ultimately translating the latter into coral dry weight data.

The three researchers write, "over the entire experimental period, both CWC species showed neither differences in tentacle protrusion and suspension feeding nor mortality at ambient (12.5°C) or elevated (17.5°C) seawater temperatures." They state, "D. cornigera specimens developed a nonquantified number of new polyps at both temperatures suggesting efficient thermal acclimatization." They report "D. dianthus exhibited growth rates for ambient and elevated temperatures of $0.23 \pm 0.08\%$ per day and $0.19 \pm 0.06\%$ per day, whereas D. cornigera grew at $0.05 \pm 0.01\%$ per day under ambient and $0.14\% \pm 0.07\%$ per day under elevated temperature conditions." Their findings "suggest that D. dianthus and D. cornigera may be capable of surviving in warmer environments than previously reported, and thus challenge temperature as the paramount limiting environmental factor for the occurrence of some CWC species."

Multiple researchers have confirmed the phenomenon of thermal adaptation in corals in response to real-world temperature-related stresses. Brown *et al.* (2002) conducted a 17-year study of

coral reef flats at Ko Phuket, Thailand, assessing reef changes in response to elevated sea temperatures in 1991, 1995, 1997, and 1998. Although the authors state many corals bleached "during elevated sea temperatures in May 1991 and 1995," they report "no bleaching was recorded in 1997." In addition, they write, "in May 1998 very limited bleaching occurred although sea temperatures were higher than previous events in 1991 and 1995 (Dunne and Brown, 2001)." When bleaching did take place, they note, "it led only to partial mortality in coral colonies, with most corals recovering their color within 3–5 months of initial paling."

Riegl (2003) reviewed what was known at the time about the responses of coral reefs to hightemperature-induced bleaching, focusing primarily on the Arabian Gulf, which they note "has recently experienced high-frequency recurrences of temperature-related bleaching (1996, 1998, 2002)." Riegl reports in each of the three high-temperature years, sea surface temperature (SST) anomalies of 2 to 2.5°C above average in situ measured summer maximum SSTs persisted from April to September, and local maxima of in situ measured SSTs were 35.5°C in 1996 and 37°C in 2002. In response to these high-temperature events, Acropora, which during the 1996 and 1998 events always bleached first and suffered heaviest mortality, bleached less than all other corals in 2002 at Sir Abu Nuair (an offshore island of the United Arab Emirates) and recovered along the coast of Dubai between Jebel Ali and Ras Hasyan. Riegl states, "the unexpected resistance of Sir Abu Nuair Acropora to bleaching in 2002 might indicate support for the hypothesis of Baker (2001) and Baker et al. (2002) that the symbiont communities on recovering reefs of the future might indeed be more resistant to subsequent bleaching." and "the Arabian Gulf perhaps provides us with some aspects which might be described as a 'glimpse into the future,' with ... hopes for at least some level of coral/zooxanthellae adaptation."

Jimenez and Cortes (2003a) documented coral cover variability in the Pacific between 1992 and 2001, when the El Niño warming events of 1991– 1992 (weak) and 1997–1998 ("the strongest in recorded history") affected coral communities along the Costa Rican central Pacific coast, after which they reported their observations and those of other scientists pertaining to these and earlier warming events caused by the El Niños of 1982–1983 (very strong) and 1986–1987 (moderate). The authors report there was a "paucity of bleaching and mortality in the study area in 1987 despite sea temperature anomalies similar to or higher than in other years in which bleaching and mortality occurred," and this situation "may have been the result of the higher cloud cover and runoff which, in combination, decreased solar radiation stress." They suggest "similar atmospheric conditions during 1998 may explain the considerably small number of corals that bleached that year in the upwelling area of [Costa Rica's] Golfo de Papagayo," where they report "few corals bleached, even though sea temperature anomalies were higher than in autumn 1997."

As to the 1997–1998 El Niño, considered to be "the strongest event on record (McPhaden, 1999; Enfield, 2001)," the authors report "mortality of entire colonies associated with this event was remarkably low in Costa Rica, less than 6% (Jimenez *et al.*, 2001)," and "only one coral species, *Psammocora stellata*, disappeared at one locality (Cambutal) after the 1997–1998 warming event." This disappearance "did not have an effect on the percent of total cover, which was not significantly dissimilar to previous years." They report "this species was not affected in Mexico by the 1997–1998 warming episode (Carriquiry *et al.*, 2001)."

Jimenez and Cortes note conspecific corals "have shown differences in susceptibility to bleach, mortality rates and recovery capabilities (Brown, 1997; Hoegh-Guldberg, 1999; Marshall and Baird, 2000; Fitt et al., 2001; Glynn et al., 2001)," which may "reflect corals' adaptation to local conditions, different warming intensities at each locality, thermal acclimation, and presence of several clades of symbionts." They state moderate warming events "may positively affect coral reef communities," noting "increases in growth rates, reproductive activity and recruitment pulses have been observed after some El Niño episodes (Glynn et al., 1991, 1994: Feingold, 1995: Guzman and Cortes, 2001: Vargas-Angel et al., 2001; Jimenez and Cortes, 2003b)."

Guzman and Cortes (2007) note coral reefs of the eastern Pacific Ocean "suffered unprecedented mass mortality at a regional scale as a consequence of the anomalous sea warming during the 1982–1983 El Niño." At Cocos Island (5°32'N, 87°04'W), in particular, where they conducted a survey of three representative reefs in 1987, they found remaining live coral cover was only 3% of what it had been before the great El Niño four years earlier (Guzman and Cortes, 1992). Based on this finding and the similar observations of other scientists at other reefs, they predicted "the recovery of the reefs' framework would take centuries, and recovery of live coral cover, decades." In 2002, nearly 20 years after the disastrous coral-killing warming, they returned to see how correct they were after their initial assessment of the El Niño damage, quantifying "the live coral cover and species composition of five reefs, including the three previously assessed in 1987."

Regarding thermal tolerance, the most interesting aspect of their study was the occurrence of a second major El Niño between the two assessment periods. Guzman and Cortes state "the 1997–1998 warming event around Cocos Island was more intense than all previous El Niño events," noting temperature anomalies "above 2°C lasted 4 months in 1997–1998 compared to 1 month in 1982–83." Nevertheless, they report, "the coral communities suffered a lower and more selective mortality in 1997–1998, as was also observed in other areas of the eastern Pacific (Glynn *et al.*, 2001; Cortes and Jimenez, 2003; Zapata and Vargas-Angel, 2003)," indicating some type of thermal adaptation occurred after the 1982–1983 El Niño.

Maynard *et al.* (2008a) question the wisdom of "popularizing predictions based on essentially untested assumptions," among which they list IPCC-held claims, "all corals live close to their thermal limits" and "corals cannot adapt/acclimatize to rapid rates of change."

In discussing the first of these "untested assumptions," the three Australian researchers say "predictions that reefs will disappear as a result of global warming are based, at least in part, on the assumption corals are living close to their maximum thermal limits." However, they note, "the severity of bleaching responses varies dramatically within and among taxa," citing McClanahan *et al.* (2009), 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 report little is known about the sensitivity of coral population response to climateinduced changes in growth, mortality, and fecundity, but they state 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 (2002), and Hughes *et al.* (2003).

The three researchers clearly accept there is "an

adaptive response," in contradiction of the second untested assumption Maynard *et al.* (2008a) discuss, stating "a number of studies suggest that bleaching mortality rates have declined and thermal tolerance has increased in some regions." They report, for example, "mortality rates in the Eastern Pacific were significantly lower in 1998 when compared with 1982 and 1983 (Glynn *et al.*, 2001)," and "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."

The Australian scientists say there is "circumstantial evidence for ongoing evolution of temperature tolerance between both species and reefs," citing 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 declare "there is growing evidence that such shuffling can increase thermal tolerance, at least in the short term (Berkelmans and van Oppen, 2006)." Thus 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."

Adjeroud et al. (2009) observed coral reefs of the Tiahura outer reef sector at the western end of the north shore of Moorea, French Polynesia, a region they say is "largely free of direct anthropogenic disturbances." They describe the results of detailed observations made there periodically since the early 1970s and annually since 1991. This history, they write, "constitutes one of the longest records of coral reef dynamics." Concentrating on the period of detailed annual observations (1991 onward), the 10 researchers report a significant decline in coral cover followed the two disturbances of 1991 (a major bleaching event and a cyclone), when "coral cover (pooled among genera) declined from $51.0 \pm 9.5\%$ in early 1991 to $24.2 \pm 14.4\%$ in 1992, and $22.5 \pm 9.3\%$ in 1993." This decline, they write, was "among the most rapid of this magnitude recorded following natural disturbances." In contrast, they found "the bleaching events of 1994, 2002 and 2003 had no detectable effects on coral cover, even though the thermal anomalies causing these events and their short-term impacts in terms of bleaching prevalence were similar to the 1991 bleaching event."

Adjeroud *et al.* say their results reveal "corals can recover rapidly following a dramatic decline," noting

similar recoveries of coral cover have been documented at several other locations, citing Connell (1997), Halford *et al.* (2004), Emslie *et al.* (2008), and Sheppard *et al.* (2008). They state their work "supports the hypothesis that some reefs will undergo gradual changes in structure of their coral communities in response to major stress rather than collapse abruptly," citing Loya *et al.* (2001), Hughes *et al.* (2003), and Wakeford *et al.* (2008).

Maynard et al. (2008b) analyzed the bleaching severity of three genera of corals (Acropora, Pocillopora, and Porites) along five sites in the central section of Australia's Great Barrier Reef in late February and March of 1998 and 2002. Regarding the influence of temperature, the four researchers report "the amount of accumulated thermal stress (as degree heating days) in 2002 was more than double that in 1998 at four of the five sites," and "average surface irradiance during the 2002 thermal anomaly was 15.6-18.9% higher than during the 1998 anomaly." They found "in 2002, bleaching severity was 30-100% lower than predicted from the relationship between severity and thermal stress in 1998, despite higher solar irradiances during the 2002 thermal event." In addition, "coral genera most susceptible to thermal stress (Pocillopora and Acropora) showed the greatest increase in tolerance."

Maynard *et al.* state their findings are "consistent with previous studies documenting an increase in thermal tolerance between bleaching events (1982– 1983 vs. 1997–1998) in the Galapagos Islands (Podesta and Glynn, 2001), the Gulf of Chiriqi, the Gulf of Panama (Glynn *et al.*, 2001), and on Costa Rican reefs (Jimenez *et al.*, 2001)." They also note "Dunne and Brown (2001) found similar results ... in the Andaman Sea, in that bleaching severity was far reduced in 1998 compared to 1995 despite seatemperature and light conditions being more conducive to widespread bleaching in 1998."

The Australian scientists say "the range in bleaching tolerances among corals inhabiting different thermal realms suggests that at least some coral symbioses have the ability to adapt to much higher temperatures than they currently experience in the central Great Barrier Reef," citing Coles and Brown (2003) and Riegl (1999, 2002). They note, "even within reefs there is a significant variability in bleaching susceptibility for many species (Edmunds, 1994; Marshall and Baird, 2000), suggesting some potential for a shift in thermal tolerance based on selective mortality (Glynn *et al.*, 2001; Jimenez *et al.*, 2001) and local population growth alone." Their results suggest "a capacity for acclimatization or adaptation." Maynard *et al.* (2008b) conclude "there is emerging evidence of high genetic structure within coral species (Ayre and Hughes, 2004)," suggesting "the capacity for adaptation could be greater than is currently recognized." As Skelly *et al.* (2007) state, "on the basis of the present knowledge of genetic variation in performance traits and species' capacity for evolutionary response, it can be concluded that evolutionary change will often occur concomitantly with changes in climate as well as other environmental changes."

Focusing more on such evolutionary possibilities, Meyer *et al.* (2009) "performed controlled crosses between three genetically distinct colonies of the branching coral *Acropora millepora*," and then "compared the families of larvae (which in this species naturally lack symbionts) for several physiological traits." They conducted this work at two water temperatures—the standard culturing temperature of 28°C and an elevated temperature of 32°C—as well as an even higher temperature of 34°C maintained for two full days.

Results of the U.S., Canadian, and Australian researchers' analysis confirmed the existence of phenotypic variance for several pertinent thermal and dispersive factors among the families of coral they studied. This finding, they write, "suggests the existence of considerable heritable variation in natural coral populations," and this 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)." 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."

Grimsditch *et al.* (2010) say "it has been shown that it is possible for colonies to acclimatize to increased temperatures and high irradiance levels so that they are able to resist bleaching events when they occur." They note "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."

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, and 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). They found "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." This result suggests, they write, "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."

Osborne *et al.* (2011) note "coral decline is frequently described as ongoing with the integrity and persistence of the reef system threatened by a number of different stressors," citing Bellwood *et al.* (2004), and "climate change is widely regarded as the single greatest threat to coral reef ecosystems." They also note "the scale and extent of bleaching on the GBR [Great Barrier Reef] since 1998 is unprecedented (Oliver *et al.*, 2009)," "coral disease is an emerging stressor that was first recorded on the GBR in the early 1990s (Willis *et al.*, 2004; Lough, 2007)," and various harmful environmental disturbances "appear to be increasing in frequency and severity."

To quantify the trend in live coral cover of the Great Barrier Reef between 1995 and 2009, which IPCC contends was the warmest decade-and-a-half experienced by the planet in the past millennium, the scientists surveyed coral communities annually on 47 reefs in six latitudinal sectors across 1300 km of the GBR, surveying between two and five reefs in each sub-region. They did so at three sites on the northeast flank of each reef, with each site consisting of five 50-m transects marked by steel rods at depths between six and nine meters. They note "percent cover of live hard coral was estimated from a randomly selected sequence of images taken along the transects using a point-sampling technique in a quincunx pattern (Adbo *et al.*, 2004)."

They found "coral cover increased in six subregions and decreased in seven sub-regions," with some of the changes "being very dynamic and others changing little." With respect to the entire reef system, they report "overall regional coral cover was stable (averaging 29% and ranging from 23% to 33% across years) with no net decline between 1995 and 2009." They state they found "no evidence of consistent, system-wide decline in coral cover since 1995." In spite of the purportedly unprecedented negative influences arrayed against them over the past decade-and-a-half, GBR corals appear to have held their own, adapting to the purported onslaught of stresses and maintaining a stable presence.

According to Oliver and Palumbi (2011), "the vast majority of studies that investigate the effects of fluctuating thermal regimes on thermal tolerance have examined daily thermal cycles in which the hottest temperatures lasted on the timescale of hours," and in eight of 10 such studies-performed on taxa as diverse as corals, crustaceans, fish, and amphibians-"organisms that were acclimated to a daily fluctuating thermal regime showed thermal tolerance or tolerance-relevant gene expression (e.g., heat shock proteins) that was equal to, or greater than, that of organisms acclimated to a thermal regime held constant at the maximum temperature of the fluctuating regime," citing Hutchison and Ferrance (1970), Otto (1974), Sastry (1979), Thorp and Wineriter (1981), Threader and Houston (1983), Podrabsky and Somero (2004), Schaefer and Ryan (2006), and Putnam et al. (2010).

Studying back-reef pools in American Samoa that differ in diurnal thermal variation, Oliver and Palumbi experimentally heat-stressed Acropora hyacinthus corals from a thermally moderate lagoon pool and a more thermally variable pool that naturally experienced two- to three-hour high temperature events during summer low tides. They compared coral mortality and photosystem II photochemical efficiency of colony fragments collected from each of these lagoons that they exposed to either ambient (28.0°C) or elevated (31.5°C) water temperatures. The two researchers report in the heated treatment, "moderate pool corals showed nearly 50% mortality whether they hosted heat-sensitive or heat-resistant symbionts," whereas "variable pool corals, all of which hosted heat-resistant symbionts, survived well, showing low mortalities statistically indistinguishable from controls held at ambient temperatures." Also in the heated treatment, they state, "moderate pool corals hosting heat-sensitive algae showed rapid rates of decline in algal photosystem II photochemical efficiency," whereas those "hosting heat-resistant algae showed intermediate levels of decline." They found "variable pool corals hosting heat-resistant algae showed the least decline."

Oliver and Palumbi say their results suggest "previous exposure to an environmentally variable microhabitat adds substantially to coral-algal thermal tolerance, beyond that provided by heat-resistant symbionts alone," indicating a latent potential of Earth's corals to adapt to warmer temperatures than scientists believed possible in the past, should they gradually begin to experience recurring daily episodes of greater warmth in a gradually warming world.

In a study designed to investigate how coral assemblages in the Persian Gulf might cope with global warming via reproductive biology, Bauman et al. (2011) examined six locally common coral species on two shallow reef sites in Dubai, United Arab Emirates, in 2008 and 2009, to investigate their patterns of reproduction, focusing primarily on the timing and synchrony of spawning. They found the reproductive biology of the six coral species in the southern Persian Gulf "appears to be well adapted to extreme annual environmental fluctuations" and is "remarkably similar to conspecifics elsewhere in the Indo-Pacific (Baird et al., 2009a,b)." They also found "the adaptive capacity of corals in the Persian Gulf is likely facilitated by a combination of short-term acclimation in individuals during acute environmental conditions (e.g., recurrent bleaching events) and longterm adaptation among coral populations to chronic environmental conditions (e.g., extreme temperatures)."

Bauman *et al.* state their work "confirms that corals are capable of reproductive activities under extreme environmental conditions," as Coles and Fadlallah (1991) and Coles and Brown (2003) also found. They conclude "coral populations can survive and proliferate in extreme conditions that are projected to occur in many other regions of the world by the end of this century," noting, "the recovery of these coral assemblages following mortality induced by a number of recent temperature-related bleaching events (1996, 1998 and 2002) suggests these assemblages are also resilient to extreme fluctuations in water temperature," citing Riegl (1999, 2003) and Burt *et al.* (2008).

Serrano *et al.* (2013) investigated the adaptation of corals to temperature-related stresses through range expansion or migration. The team of researchers state, "despite the evidence that some coral species appear to be responding to climatic warming by expanding their distributions toward the poles (Wooddroffe, 2011), it has been argued that latitudinal migration is unlikely to occur rapidly enough to respond to the current projected temperature change $(3-6^{\circ}C)$ over the next 100 years (IPCC, 2007)) due to the significant distance involved (i.e., the latitudinal temperature gradient is ~1.5°C/1000 km), the effects of temperature on reproduction, and the decrease in carbonate ion concentrations at high latitudes." Serrano *et al.* analyzed a long-term, large-scale observational dataset to characterize the dynamics of a hermatypic coral (*Oculina patagonica*) in regard to its "recent northward range shift along the coast of Catalonia," while examining "the main factors that could have influenced this spread," which they did "by monitoring 223 locations including natural and artificial habitats along >400 km of coastline over the last 19 years (1992–2010)."

The six Spanish scientists report Oculina patagonica "increased from being present in one location in 1992 to occur on 19% of the locations in 2010, and exhibited an acceleration of its spreading over time driven by the joint action of neighborhood and long-distance dispersal." They further note the "northward expansion has occurred at the fastest rate (22 km per year) reported for a coral species thus far." Serrano et al. write, "a coral species with particular biological characteristics that allow it to withstand the temperature challenge that accompanies northward migration as well as the natural and anthropogenic side effects that this type of migration involves (i.e., competition with macroalgae, high sediment loads, turbidity, water chemistry) has accomplished a successful northward expansion and may be able to keep pace with the global warming prediction of \sim 3°C over the next 100 years."

Yamano et al. (2011) report "although most studies of climate change effects on corals have focused on temperature-induced coral bleaching in tropical areas, poleward range shifts and/or expansions may also occur in temperate areas, as suggested by geological records and present-day evewitnesses in several localities," citing Greenstein and Pandolfi (2008) and Precht and Aronson (2004). Yamano et al. collected records of coral species occurrence from eight temperate regions of Japan along a latitudinal gradient, where they obtained what they describe as "the first large-scale evidence of the poleward range expansion of modern corals, based on 80 years of national records ... where century-long measurements of in situ sea-surface temperatures have shown statistically significant rises."

They found "four major coral species categories, including two key species for reef formation in tropical areas, showed poleward range expansions since the 1930s, whereas no species demonstrated southward range shrinkage or local extinction," adding "the speed of these expansions reached up to 14 km per year," which they say "is far greater than that for other species." They note, "in regions with poleward current flows (east coast of the United States [Precht and Aronson, 2004], east coast of South America, east coast of Africa and east coast of Australia [Figueira and Booth, 2010]) the speed would be much greater."

The Japanese scientists conclude their results, "in combination with recent findings suggesting range expansions of tropical coral-reef associated organisms, strongly suggest that rapid, fundamental modifications of temperate coastal ecosystems could be in progress." They suggest "temperate areas may serve as refugia for tropical corals in an era of global warming."

Van Woesik et al. (2012) examined the response of more than 30,000 coral colonies at 80 sites in Palau during a regional thermal-stress event in 2010, to determine "whether any habitats were comparatively resistant to thermal stress." The six scientists discovered "bleaching was most severe in the northwestern lagoon, in accordance with satellitederived maximum temperatures and anomalous temperatures above the long-term averages," noting corals there "suffered the most extensive bleaching and the highest mortality." But "in the bays where temperatures were higher than elsewhere, bleaching and mortality were low." They suggest "constant exposure to high temperatures, and high vertical attenuation of light caused by naturally high suspended particulate matter buffered the corals in bays from the 2010 regional thermal-stress event." Van Woesik et al. conclude their study shows "reefs around bays were more resistant to regional thermal stress than patch and outer reefs," and "nearshore reefs in the bays are therefore valuable refuges to buffer coral-reef ecosystems against climate changeinduced disturbances." Those bays "should be given high conservation status because they provide refugia for coral populations as the oceans continue to warm."

Carilli *et al.* (2012) note "observations indicating that mass bleaching events have recently become more common, combined with projected increases in heat stress, have prompted dire predictions for the future of coral reefs under unabated greenhouse gas emissions scenarios," citing Hoegh-Guldberg (1999) and Donner *et al.* (2005). They point out, "there is evidence that corals may adapt to better withstand heat stress via a number of mechanisms," as "corals might acquire more thermally-resistant symbionts (Buddemeier and Fautin, 1993; Rowan, 2004), or might increase their own physiological mechanisms to reduce bleaching susceptibility by producing oxidative enzymes (Coles and Brown, 2003) or photoprotective compounds (Salih *et al.*, 2000)." They emphasize there is evidence suggesting the susceptibility of a given coral or reef to bleaching depends on the thermal history of that coral or reef (Thompson and Van Woesik, 2009; Donner, 2011; Brown *et al.*, 2002).

Carilli *et al.* "collected cores from massive *Porites sp.* corals in the Gilbert Islands of Kiribati to determine how corals along a natural gradient in temperature variability responded to recent heat stress events" and "examined changes in coral skeletal growth rates and partial mortality scars (Carilli *et al.*, 2010) to investigate the impact of the bleaching event in 2004 (Donner, 2011) on corals from different temperature variability regimes."

The three researchers—from Australia, Canada, and the United States—discovered the spatial patterns in skeletal growth rates and partial mortality scars found in corals from the central and northern islands suggest "corals subject to larger year-to-year fluctuations in maximum ocean temperature were more resistant to a 2004 warm-water event," and "a subsequent 2009 warm event had a disproportionately larger impact on those corals from the island with lower historical heat stress." Carilli *et al.* conclude, "coral reefs in locations with more frequent warm events may be more resilient to future warming."

Penin *et al.* (2013) "compared variations in spatial and taxonomic patterns between two bleaching events at the scale of an island (Moorea Island, French Polynesia)," where "nine stations involving three locations (Haapiti, Tiahura, and Viapahu) and three depths (6, 12, and 18 m) have been routinely surveyed for various scientific purposes since 2001," as described by Penin *et al.* (2007a, 2010). They measured bleaching intensity "two weeks following the first signs of bleaching (Penin *et al.*, 2007b)" for six coral genera (*Acropora, Montipora, Montastrea, Pavona, Pocillopora,* and *Porites*) at each of the nine stations in 2002 and 2007. The six coral genera accounted for 88% of the total coral assemblage.

Their measurements showed the "thermal stress was similar between the two years studied," but "the bleaching intensity was lower in 2007 (25–49%) than in 2002 (39–72%)" and "the response to elevated temperature was delayed in the latter year." They note "the outer slopes at Moorea Island are located in an oligotrophic oceanic environment and are not under terrestrial influence, which makes it unlikely that there was any effect of nutrients on the response of the corals, as has been proposed for other reef eco-

systems (Wooldridge and Done, 2009)." The three researchers conclude "it is likely that the observed decrease in stress response was the result of acclimatization of the coral/algal holobionts (Berkelmans *et al.*, 2004; Maynard *et al.*, 2008) or an influx of thermo-tolerant colonies between 2002 and 2007." They note several "similar decreases in susceptibility to thermal stress have been documented between successive bleaching events, including between 1991 and 1994 at Moorea Island (Adjeroud *et al.*, 2002), between 1998 and 2002 on the Great Barrier Reef in Australia (Maynard *et al.*, 2008b), and between 1982–83 and 1997–98 in Panama (Glynn *et al.*, 2001), Costa Rica (Jimenez *et al.*, 2001), and at the Galapagos Islands (Podesta and Glynn, 2001)."

Mayfield et al. (2013) write, "recent work has found that pocilloporid corals from regions characterized by unstable temperatures, such as those exposed to periodic upwelling, display a remarkable degree of phenotypic plasticity," and "some recent works have shown that not all corals bleach, or even manifest signs of stress, at elevated temperatures predicted to characterize reefs in the coming decades (Barshis et al., 2013)." They also note "corals from highly variable temperature environments of both American Samoa (Oliver and Palumbi, 2011) and southern Taiwan (Mayfield et al., 2011, 2013) have previously been shown to withstand exposure to temperatures (e.g., 30–31°C) that induce bleaching or even mortality in conspecifics from other regions (Jokiel and Coles, 1990; Brown, 1997)."

To "uncover the long-term impacts of elevated temperature exposure to corals from reefs that experience episodic upwelling," Mayfield et al. conducted a mesocosm-based experiment in which P. damicornis specimens collected from an upwelling coral reef on Houbihu (a small embayment within Nanwan Bay, southern Taiwan) were exposed for nine months to nearly 30°C, a temperature that the corals normally encounter in situ for just a few hours per vear (Mayfield et al., 2012). The three researchers write, "upon nine months of exposure to nearly 30°C, all colony (mortality and surface area), polyp (Symbiodinium density and chlorophyll a content), tissue (total thickness), and molecular (gene expression and molecular composition)-level parameters were documented at similar levels between experimental corals and controls incubated at 26.5°C, suggesting that this species can readily acclimate to elevated temperatures that cause significant degrees of stress, or even bleaching and mortality, in conspecifics of other regions of the Indo-Pacific."

Mayfield et al. state, "there is now a growing

body of evidence to support the notion that corals inhabiting more thermally unstable habitats outperform conspecifics from reefs characterized by more stable temperatures when exposed to elevated temperatures," citing Coles (1975), Castillo and Helmuth (2005), and Oliver and Palumbi (2011). They also report, "in other systems, provocative gene expression changes, such as the constitutive upregulation of genes involved in thermotolerance (e.g., *hsps*; Heath *et al.*, 1993; Feder, 1996), underlie the capacity for organisms to inhabit high and/or variable temperature environments," as Barshis *et al.* (2013) also documented in corals.

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6.1.2.2.2 Symbiont Shuffling

The studies reviewed in this section examine symbiont shuffling, the ability of corals to replace the zooxanthellae expelled during a stress-induced bleaching episode with one or more varieties of zooxanthellae more tolerant of that particular stress. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings.

- Zooxanthellae that reside within the cells of host corals are highly diverse, comprising perhaps hundreds of species, of which several are typically found in each species of coral.
- Many corals respond to stress by replacing the zooxanthellae expelled during a stress-induced bleaching episode with one or more varieties of zooxanthellae more tolerant of that stress.
- Coral bleaching is an adaptive strategy for "shuffling" symbiont genotypes to create associations better adapted to new environmental conditions, as opposed to "a breakdown of a stable relationship that serves as a symptom of degenerating environmental conditions."
- Multiple studies confirm the strategy of symbiont shuffling is occurring in nature.
- Symbiont shuffling "represents a mechanism for rapid acclimatization of the holobiont to environmental change."

Although once considered to be members of the single species *Symbiodinium microadriacticum*, the zooxanthellae that reside within membrane-bound vacuoles in the cells of host corals are highly diverse, comprising perhaps hundreds of species, with each species of coral typically possessing several of these species (Trench, 1979; Rowan and Powers, 1991; Rowan *et al.*, 1997). One way corals respond to stress is to replace the zooxanthellae expelled by the coral host during a stress-induced bleaching episode with one or more varieties of zooxanthellae more tolerant of that particular stress.

Rowan et al. (1997) suggest this phenomenon

occurs in many of the most successful Caribbean corals that act as hosts to dynamic multispecies communities of symbionts, and "coral communities may adjust to climate change by recombining their existing host and symbiont genetic diversities," thereby reducing the amount of damage that might be expected from another occurrence of anomalously high temperatures. Buddemeier and Fautin (1993) propose coral bleaching is an adaptive strategy for "shuffling" symbiont genotypes to create associations better adapted to new environmental conditions. Kinzie (1999) suggests coral bleaching "might not be simply a breakdown of a stable relationship that serves as a symptom of degenerating environmental conditions," but also "may be part of a mutualistic relationship on a larger temporal scale, wherein the identity of algal symbionts changes in response to a changing environment."

The findings of Rowan and Knowlton (1995) and Gates and Edmunds (1999) provide additional evidence of this process of replacing less-stresstolerant symbionts with more-stress-tolerant ones. The process seems to be successful, for as Glynn (1996) observed, "despite recent incidences of severe coral reef bleaching and mortality, no species extinctions have yet been documented."

These observations accord well with the experimental findings of Fagoonee et al. (1999), who suggest coral bleaching events "may be frequent and part of the expected cycle." Gates and Edmunds (1999) report "several of the prerequisites required to support this hypothesis have now been met"; after describing them in some detail, they conclude "there is no doubt that the existence of multiple Symbiodinium clades, each potentially exhibiting a different physiological optima, provide corals with the opportunity to attain an expanded range of physiological flexibility which will ultimately be reflected in their response to environmental challenge." This phenomenon may explain the paradox posed by Pandolfi (1999): "a large percentage of living coral reefs have been degraded, yet there are no known extinctions of any modern coral reef species." This result is exactly what would be expected if periods of stress lead to the acquisition of more-stress-resistant zooxanthellae by coral hosts.

Hoegh-Guldberg (1999) challenged the symbiont shuffling hypothesis by noting the stress-induced replacement of less-stress-tolerant varieties of zooxanthellae by more-stress-tolerant varieties "has never been observed." Although that was true at the time it was written, subsequent studies have produced the long-sought proof that transforms the hypothesis into fact.

Baker (2001) transplanted corals of different combinations of host and algal symbiont from shallow (2–4 m) to deep (20–23 m) water and vice versa. After eight weeks, nearly half of the corals transplanted from deep to shallow water had experienced partial or severe bleaching, whereas none of the corals transplanted from shallow to deep water bleached. After one year, and despite even more bleaching at shallow depths, upward transplants showed no mortality, but nearly 20% of downward transplants had died.

The symbiont shuffling hypothesis explains Baker's results as follows. The corals transplanted upwards were presumed to have adjusted their algal symbiont distributions, via bleaching, to favor moretolerant species, whereas the corals transplanted downward were assumed to have not done so, since they did not bleach. Baker suggests these findings "support the view that coral bleaching can promote rapid response to environmental change by facilitating compensatory change in algal symbiont communities." Without bleaching, he continues, "suboptimal host-symbiont combinations persist, leading eventually to significant host mortality." Baker proposed coral bleaching may "ultimately help reef corals to survive." It may also explain why reefs, though depicted by IPCC as environmentally fragile, have survived the large environmental changes experienced throughout geologic time.

Adjeroud et al. (2002) provided additional evidence for the veracity of the symbiont shuffling hypothesis through their study of the interannual variability of coral cover on the outer slope of the Tiahura sector of Moorea Island, French Polynesia, between 1991 and 1997, which focused on the impacts of bleaching events caused by thermal stress when sea surface temperatures rose above 29.2°C. Soon after the start of their study, they observed a severe decline in coral cover following a bleaching event that began in March 1991, which was followed by another bleaching event in March 1994. They report the latter bleaching event "did not have an important impact on coral cover," even though "the proportion of bleached colonies ... and the order of susceptibility of coral genera were similar in 1991 and 1994 (Gleason, 1993; Hoegh-Guldberg and Salvat, 1995)." Between 1991 and 1992 total coral cover dropped from 51.0 to 24.2%, but "coral cover did not decrease between 1994 and 1995."

Adjeroud *et al.* note a "possible explanation of the low mortality following the bleaching event in 1994 is that most of the colonies in place in 1994

were those that survived the 1991 event or were young recruits derived from those colonies," and "one may assume that these coral colonies and/or their endosymbiotic zooxanthellae were phenotypically and possibly genotypically resistant to bleaching events," exactly what the symbiont shuffling hypothesis would predict. They say "this result demonstrates the importance of understanding the ecological history of reefs (i.e., the chronology of disturbances) in interpreting the specific impacts of a particular disturbance."

Brown *et al.* (2002) published the results of a 17year study of coral reef flats at Ko Phuket, Thailand, in which they assessed coral reef changes in response to elevated water temperatures in 1991, 1995, 1997, and 1998. They write, "many corals bleached during elevated sea temperatures in May 1991 and 1995, but no bleaching was recorded in 1997." They report, "in May 1998 very limited bleaching occurred although sea temperatures were higher than previous events in 1991 and 1995 (Dunne and Brown, 2001)"; when bleaching did take place, "it led only to partial mortality in coral colonies, with most corals recovering their color within 3–5 months of initial paling.

Riegl (2003) reviewed what is known about the responses of real-world coral reefs to hightemperature-induced bleaching, focusing primarily on the Arabian Gulf, which experienced high-frequency recurrences of temperature-related bleaching in 1996, 1998, and 2002. Acropora, which during the 1996 and 1998 events always bleached first and suffered heaviest mortality, bleached less than all other corals in 2002 at Sir Abu Nuair (an offshore island of the United Arab Emirates) and recovered along the coast of Dubai between Jebel Ali and Ras Hasyan. Riegl writes, "the unexpected resistance of Sir Abu Nuair Acropora to bleaching in 2002 might indicate support for the hypothesis of Baker (2001) and Baker et al. (2002) that the symbiont communities on recovering reefs of the future might indeed be more resistant to subsequent bleaching," and "the Arabian Gulf perhaps provides us with some aspects which might be described as a 'glimpse into the future,' with ... hopes for at least some level of coral/zooxanthellae adaptation."

Kumaraguru *et al.* (2003) assessed the damage inflicted on a number of coral reefs within Palk Bay (located on the southeast coast of India just north of the Gulf of Mannar) by a major warming event that produced monthly mean sea surface temperatures of 29.8 to 32.1°C from April through June 2002, after which they studied the degree of recovery of the reefs. They determined "a minimum of at least 50% and a maximum of 60% bleaching were noticed among the six different sites monitored." They continue, "the corals started to recover quickly in August 2002 and as much as 52% recovery could be noticed." By comparison, they note, "recovery of corals after the 1998 bleaching phenomenon in the Gulf of Mannar was very slow, taking as much as one year to achieve similar recovery." The Indian scientists state, "the process of natural selection is in operation, with the growth of new coral colonies, and any disturbance in the system is only temporary." They conclude, "the corals will resurge under the sea."

Rowan (2004) described how he measured the photosynthetic responses of two zooxanthellae genotypes or clades—Symbiodinium C and Symbiodinium D-to increasing water temperature and found the photosynthetic prowess of the former decreased at higher temperatures whereas that of the latter increased. He notes "adaptation to higher temperature in Symbiodinium D can explain why Pocillopora spp. hosting them resist warm-water bleaching whereas corals hosting Symbiodinium C do not," and "it can also explain why Pocillopora spp. living in frequently warm habitats host only Symbiodinium D, and, perhaps, why those living in cooler habitats predominantly host Symbiodinium *C*." These observations, he concludes, "indicate that symbiosis recombination may be one mechanism by which corals adapt, in part, to global warming."

Baker *et al.* (2004) "undertook molecular surveys of *Symbiodinium* in shallow scleractinian corals from five locations in the Indo-Pacific that had been differently affected by the 1997–98 El Niño-Southern Oscillation (ENSO) bleaching event." Along the coasts of Panama, they surveyed ecologically dominant corals in the genus *Pocillopora* before, during, and after ENSO bleaching, finding "colonies containing *Symbiodinium* in clade D were already common (43%) in 1995 and were unaffected by bleaching in 1997, while colonies containing clade C bleached severely." They found "by 2001, colonies containing clade D had become dominant (63%) on these reefs."

After describing similar observations in the Persian (Arabian) Gulf and the western Indian Ocean along the coast of Kenya, Baker *et al.* summarize say their results indicate "corals containing thermally tolerant *Symbiodinium* in clade D are more abundant on reefs after episodes of severe bleaching and mortality, and that surviving coral symbioses on these reefs more closely resemble those found in high-temperature environments," where clade D predom-

inates. They conclude by noting the symbiont changes they observed "are a common feature of severe bleaching and mortality events," and they predict "these adaptive shifts will increase the resistance of these recovering reefs to future bleaching."

Lewis and Coffroth (2004) described a controlled experiment in which they induced bleaching in a Caribbean octocoral (*Briareum* sp.) and then exposed it to exogenous *Symbiodinium* sp. containing rare variants of the chloroplast 23S ribosomal DNA (rDNA) domain V region (cp23S-genotype), after which they documented the symbionts' repopulation of the coral, whose symbiont density had been reduced to less than 1% of its original level by the bleaching. In an analogous study, Little *et al.* (2004) investigated the acquisition of symbionts by juvenile *Acropora tenuis* corals growing on tiles they attached to different portions of reef at Nelly Bay, Magnetic Island (an inshore reef in the central section of Australia's Great Barrier Reef).

Lewis and Coffroth state their results show "the repopulation of the symbiont community involved residual populations within *Briareum* sp., as well as symbionts from the surrounding water," noting "recovery of coral-algal symbioses after a bleaching event is not solely dependent on the *Symbiodinium* complement initially acquired early in the host's ontogeny," but "these symbioses also have the flexibility to establish new associations with symbionts from an environmental pool." Similarly, Little *et al.* report, "initial uptake of zooxanthellae by juvenile corals during natural infection is nonspecific (a potentially adaptive trait)," and "the association is flexible and characterized by a change in (dominant) zooxanthella strains over time."

Lewis and Coffroth conclude "the ability of octocorals to reestablish symbiont populations from multiple sources provides a mechanism for resilience in the face of environmental change." Little *et al.* conclude the "symbiont shuffling" observed by both groups "represents a mechanism for rapid acclimatization of the holobiont to environmental change."

Chen *et al.* (2005) reported on their study of the seasonal dynamics of *Symbiodinium* algal phylotypes via bimonthly sampling over an 18-month period of *Acropora palifera* coral on a reef flat at Tantzel Bay, Kenting National Park, southern Taiwan, in an attempt to detect real-world symbiont shuffling. They found two levels of symbiont shuffling in host corals: between *Symbiodinium* phylotypes C and D, and among different variants within each phylotype. The most significant changes in symbiont composition occurred at times of significant increases in seawater

temperature during late spring and early summer, perhaps as a consequence of enhanced stress experienced at that time, leading Chen *et al.* to state their work revealed "the first evidence that the symbiont community within coral colonies is dynamic ... involving changes in *Symbiodinium* phylotypes."

Van Oppen et al. (2005) sampled zooxanthellae from three common species of scleractinian corals at 17 sites along a latitudinal and cross-shelf gradient in the central and southern sections of the Great Barrier Reef four to five months after the major bleaching event of 2002, recording the health status of each colony at the time of its collection and identifying its zooxanthella genotypes, of which there are eight distinct clades (A-H) with clade D being the most heat-tolerant. They found "there were no simple correlations between symbiont types and either the level of bleaching of individual colonies or indicators of heat stress at individual sites." They write, "there was a very high post-bleaching abundance of the heat tolerant symbiont type D in one coral population at the most heat-stressed site."

The Australian researchers say they suspect the post-bleaching abundance of clade D zooxanthellae at the high heat-stress site was due to "a proliferation in the absolute abundance of clade D within existing colonies that were previously dominated by clade C zooxanthellae." In the four to five months before sampling them, the writers note, "mixed C-D colonies that had bleached but survived may have shifted (shuffling) from C-dominance to D-dominance, and/or C-dominated colonies may have suffered higher mortality during the 2002 bleaching event" and subsequently been repopulated by a predominance of clade D genotypes.

Berkelmans and van Oppen (2006) investigated the thermal acclimatization potential of *Acropora millepora* corals at Australia's Great Barrier Reef to rising temperatures through transplantation and experimental manipulation. They found the adult corals "are capable of acquiring increased thermal tolerance and that the increased tolerance is a direct result of a change in the symbiont type dominating their tissues from *Symbiodinium* type C to D." Two years later, working with an expanded group of authors (Jones *et al.*, 2008), the two researchers reported similar findings following the occurrence of a natural bleaching event.

Before that bleaching event, Jones *et al.* report, "A. *millepora* at Miall reef associated predominantly with *Symbiodinium* type C2 (93.5%) and to a much lesser extent with *Symbiodinium* clade D (3.5%) or mixtures of C2 and D (3.0%)." During the bleaching
event, they report, "the relative difference in bleaching susceptibility between corals predominated by C2 and D was clearly evident, with the former bleaching white and the latter normally pigmented," whereas corals harboring a mix of Symbiodinium C2 and D were "mostly pale in appearance." Three months after the bleaching event, they observed "a major shift to thermally tolerant type D and C1 symbiont communities ... in the surviving colonies"; the latter types had not been detected in any of the corals before bleaching. They report, "this shift resulted partly from a change of symbionts within coral colonies that survived the bleaching event (42%) and partly from selective mortality of the more bleaching-sensitive C2-predominant colonies (37%)." All of the colonies that harbored low levels of D-type symbionts before the bleaching event survived and changed from clade C2 to D predominance.

Jones et al. write, "as a direct result of the shift in symbiont community, the Miall Island A. millepora population is likely to have become more thermotolerant," as they note "a shift from bleachingsensitive type C2 to clade D increased the thermal tolerance of this species by 1-1.5°C." They say their results "strongly support the reinterpreted adaptive bleaching hypothesis of Buddemeier et al. (2004), which postulates that a continuum of changing environmental states stimulates the loss of bleachingsensitive symbionts in favor of symbionts that make the new holobiont more thermally tolerant." They state their observations "provide the first extensive colony-specific documentation and quantification of temporal symbiont community change in the field in response to temperature stress, suggesting a population-wide acclimatization to increased water temperature."

Lien et al. (2007) examined the symbiont diversity in a scleractinian coral. *Oulastrea crispata*. throughout its entire latitudinal distribution range in the West Pacific, from tropical peninsular Thailand (<10°N) to high-latitudinal outlying coral communities in Japan (>35°N). Those results convincingly demonstrate, the six scientists write, "that phylotype D is the dominant Symbiodinium in scleractinian corals throughout tropical reefs and marginal outlying non-reefal coral communities." They learned this particular symbiont clade "favors 'marginal habitats' where other symbionts are poorly suited to the stresses, such as irradiance, temperature fluctuations, sedimentation, etc." As a major component of the symbiont repertoire of most scleractinian corals in most places, the apparent near-universal presence of Symbiodinium phylotype D thus provides, Lien et al.

write, "a flexible means for corals to routinely cope with environmental heterogeneities and survive the consequences (e.g., recover from coral bleaching)."

Also in 2007, Mieog et al. (2007) utilized a newly developed real-time polymerase chain reaction assay, which they say "is able to detect Symbiodinium clades C and D with >100-fold higher sensitivity compared to conventional techniques." to test 82 colonies of four common scleractinian corals (Acropora millepora, Acropora tenuis, Stylophora pistillata, and Turbinaria reniformis) from 11 locations on Australia's Great Barrier Reef for evidence of the presence of background Symbiodinium clades. They found "ninety-three percent of the colonies tested were dominated by clade C and 76% of these had a D background." The latter symbionts, they write, "are amongst the most thermotolerant types known to date," being found "on reefs that chronically experience unusually high temperatures or that have recently been impacted by bleaching events, suggesting that temperature stress can favor clade D." Mieog et al. conclude the clade D symbiont backgrounds detected in their study may act as a safety net, "allowing corals to become more thermo-tolerant through symbiont shuffling as seawater temperatures rise due to global warming." They suggest symbiont shuffling is likely to play a role in the way "corals cope with global warming conditions," leading to new competitive hierarchies and, ultimately, "the coral community assemblages of the future."

Despite the hope symbiont shuffling provides that corals will be able to cope with any future global warming, whether anthropogenic or natural—some researchers have claimed few coral symbioses host more than one type of symbiont, which has led some commentators to argue symbiont shuffling is not an option for most coral species to survive the coming thermal onslaught of global warming. That claim has been shown to be incorrect.

Working with samples of the widely distributed massive corals *Porites lobata* and *Porites lutea*— collected from Kaneohe Bay, Hawaii—Apprill and Gates (2007) compared the identity and diversity of *Symbiodinium* symbiont types obtained using cloning and sequencing of internal transcribed spacer region 2 (ITS2) with those obtained using the more commonly applied downstream analytical techniques of denaturing gradient gel electrophoresis (DGGE). The results revealed "a total of 11 ITS2 types in *Porites lobata* and 17 in *Porites lutea* with individual colonies hosting from one to six and three to eight ITS2 types for *P. lobata* and *P. lutea*, respectively." The two authors

report, "of the clones examined, 93% of the *P. lobata* and 83% of the *P. lutea* sequences are not listed in GenBank," noting they resolved "sixfold to eightfold greater diversity per coral species than previously reported."

In a "perspective" that accompanied Apprill and Gates' paper, van Oppen (2007) wrote, "the current perception of coral-inhabiting symbiont diversity at nuclear ribosomal DNA is shown [by Apprill and Gates] to be a significant underestimate of the wide diversity that in fact exists." These findings, in her words, "have potentially far-reaching consequences in terms of our understanding of Symbiodinium diversity, host-symbiont specificity and the potential corals to acclimatize to environmental of perturbations through changes in the composition of their algal endosymbiont community."

Baird *et al.* (2007) also discount the argument symbiont shuffling is not an option for most coral species, because it is the sub-clade that must be considered within this context, citing studies that indicate "there are both heat tolerant and heat susceptible sub-clades within both clades C and D *Symbiodinium.*" Hence, the more relevant question becomes: How many coral species can host more than one sub-clade? The answer is that most, if not all, likely do. As Baird *et al.* note, "biogeographical data suggest that when species need to respond to novel environments, they have the flexibility to do so."

Although most prior research into how and when such sub-clade changes might occur has been on adult colonies switching symbionts in response to warming-induced bleaching episodes, Baird *et al.* suggest "change is more likely to occur between generations," because initial coral infection typically occurs in larvae or early juveniles, which are much more flexible than adults. They note, "juveniles of *Acropora tenuis* regularly harbor mixed assemblages of symbionts, whereas adults of the species almost invariably host a single clade," and larvae of *Fungia scutaria* ingest symbionts from multiple hosts, although they generally harbor but one symbiont as adults.

The Australian researchers say there is no need for an acute disturbance, such as bleaching, to induce clade or sub-clade change. Instead, if ocean temperatures rise in the future, they foresee juveniles naturally hosting more heat-tolerant sub-clades and maintaining them into adulthood.

In a further assessment of the size of the symbiont diversity reservoir, especially among juvenile coral species, Pochon *et al.* (2007) collected more than 1,000 soritid specimens over a depth of 40 meters on

a single reef at Gun Beach on the island of Guam, Micronesia, throughout an entire year. They studied the specimens by means of molecular techniques to identify unique internal transcribed spacer–2 (ITS–2) types of ribosomal DNA (rDNA), in a project selfdescribed as "the most targeted and exhaustive sampling effort ever undertaken for any group of *Symbiodinium*-bearing hosts."

Pochon *et al.* identified 61 unique symbiont types in only three soritid host genera, making the Guam *Symbiodinium* assemblage the most diverse derived to date from a single reef. They report, "the majority of mixed genotypes observed during this survey were usually harbored by the smallest hosts." The authors speculate "juvenile foraminifera may be better able to switch or shuffle heterogeneous symbiont communities than adults," so as juveniles grow, "their symbiont communities become 'optimized' for the prevailing environmental conditions," suggesting this phenomenon "may be a key element in the continued evolutionary success of these protests in coral reef ecosystems worldwide."

The work of Mumby (1999), who analyzed the population dynamics of juvenile corals in Belize both before and after a massive coral bleaching event in 1998, supports that statement. Although 70 to 90% of adult coral colonies were severely bleached during the event, only 25% of coral recruits exhibited signs of bleaching. One month after the event, they concluded "net bleaching-induced mortality of coral recruits ... was insignificant," demonstrating the ability of juvenile corals to successfully weather such bleaching events.

Fitt *et al.* (2009) note the various *Symbiodinium* clades that comprise the algal symbiont found in their coral host have been thought "to exert a major influence on the ability of reef-building corals to survive high-temperature stress." They add that if the host itself plays a role in this process, "the hypothesis that corals simply shuffle or swap their *Symbiodinium* for clades that are more thermally tolerant does not tell the whole story." In fact, it suggests corals may be even more adept at coping with rising temperatures than scientists previously believed.

Fitt *et al.* studied a number of coral host and *Symbiodinium* properties and processes in two ubiquitous Indo-Pacific reef corals known to be either very susceptible (*Stylophora pistillata*) or resistant (*Porites cylindrica*) to heat stress, exposing them to seawater temperatures of either 28°C (normal ambient) or 32°C (elevated) for five days before returning them to the normal ambient temperature. The 16 scientists report finding "both physiological

and biochemical differences of both symbiont and host origin in the response to high-temperature stress." They say "hypotheses that talk only in terms of the thermal characteristics of the symbiont may miss critical information concerning questions surrounding the thermal tolerance of corals in the coming century." They note "there are dynamic photoprotective mechanisms in both the host and zooxanthellae that include ultraviolet radiation absorbing mycosporine-like amino acids (Shick and Dunlap, 2002; Lesser, 2004), excess excitation energy dissipation in photosystem II via the xanthophyll cycle (Brown et al. 1999; Gorbunov et al., 2001), the expression of heat-shock proteins and other stress markers (Black et al., 1995; Downs et al., 2000; Lesser and Farrell, 2004), the up-regulation of antioxidant enzymes (Lesser, 1996; Lesser and Farrell, 2004; Lesser, 2006), host energy reserve utilization (Porter et al., 1989; Grottoli et al., 2004, 2006), and heterotrophic plasticity (Grotolli et al., 2006)." All of these phenomena, they write, "presumably have underlying influences on any response to thermal stress, and hence, contribute to the overall differences within and between species in regard to their bleaching sensitivity." This diverse group of phenomena that can help both the coral host and its algal symbionts adjust to rising temperatures indicate Earth's corals are well-equipped to deal with whatever further warming may come their way.

Silverstein *et al.* (2012) state many reef-building corals "have been shown to respond to environmental change by shifting the composition of their algal symbiont (genus *Symbiodinium*) communities," and "these shifts have been proposed as a potential mechanism by which corals might survive climate stressors, such as increased temperatures." They say "conventional molecular methods suggest this adaptive capacity may not be widespread because few (~25%) coral species have been found to associate with multiple *Symbiodinium* clades." They hasten to add, "these methods can fail to detect low abundance symbionts (typically less than 10–20% of the total algal symbiont community)."

To determine whether additional *Symbiodinium* clades might be present but undetected in various corals using conventional discovery and identification techniques, Silverstein *et al.* "applied a high-resolution, real-time PCR [polymerase chain reaction] assay to survey *Symbiodinium* (in clades A-D) from 39 species of phylogenetically and geographically diverse scleractinian corals." This survey, they write, "included 26 coral species thought to be restricted to hosting a single *Symbiodinium* clade," referring to the

latter corals as symbiotic specialists.

The three U.S. scientists say they "detected at least two Symbiodinium clades (C and D) in at least one sample of all 39 coral species tested," and "all four Symbiodinium clades were detected in over half (54%) of the 26 symbiotic specialist coral species." They report, "on average, 68% of all sampled colonies within a given coral species hosted two or more symbiont clades." Silverstein et al. conclude, "the ability to associate with multiple symbiont clades is common in scleractinian (stony) corals," and in regard to coral-algal symbiosis, "specificity is rarely absolute." They conclude "the potential for reef corals to adapt or acclimatize to environmental change via symbiont community shifts may therefore be more phylogenetically widespread than has previously been assumed."

Cumbo *et al.* (2013) note "coral reefs thrive in part because of the symbiotic partnership between corals and *Symbiodinium*," but "the point at which symbiosis is established (i.e., larva vs. juvenile) remains uncertain, as does the source of free-living *Symbiodinium* in the environment." They investigated "the types of symbionts taken up by *Acropora* larvae exposed to sediments collected from three different locations on the Great Barrier Reef, and compared this to the *Symbiodinium* types within adult cnidarians for each location." In addition, they "tested whether the *Symbiodinium* types changed during ontogeny by comparing types within the larvae, juvenile and adults of the same species at each location."

The three researchers report, "Symbiodinium clearly reside in the sediments of shallow reef communities and are capable of initiating symbiosis with aposymbiotic coral larvae," and "the larvae of many species of corals are promiscuous, associating with multiple Symbiodinium types independent of coral species or location." Cumbo et al. say their findings suggest "as sea surface temperatures rise, the promiscuity of larvae could benefit corals by allowing them to acquire symbionts with the greatest heat tolerance in each new generation (LaJeunesse et al., 2004; Baird et al., 2007)." In addition, although "this mechanism of acclimatization will most likely be restricted to species that show horizontal transmission of symbionts," they note such species account for approximately 85% of all species.

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6.1.2.2.3 Other Stress Response Strategies

The studies reviewed in this section examine other stress response strategies known to operate in corals under stressful conditions. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings.

- Some corals increase their expression of heat shock proteins that help repair heat-damaged constituents of their bodies as another strategy to cope with heat stress.
- The coral probiotic hypothesis, or bacterial shuffling, posits that many corals rearrange their bacterial populations in a manner akin to symbiont shuffling as another response to environmental stress.
- Corals employ other strategies of coping with and adapting to environmental stresses, further suggesting they will be able to continue to cope with the many environmental threats they face now and may face in the future.

In addition to thermal acclimation and symbiont shuffling, corals have other means to cope with and adapt to environmental stresses. One such mechanism is the production of heat shock proteins that help repair heat-damaged constituents of their bodies (Black *et al.*, 1995; Hayes and King, 1995; Fang *et al.*, 1997). Sharp *et al.* (1997), for example, demonstrated sub-tidal specimens of *Goniopora djiboutiensis* typically have much lower constitutive levels of a 70-kD heat shock protein than do their intertidal conspecifics, and they have shown corals transplanted from subtidal to intertidal locations (where temperature extremes are greater and more common) typically increase their expression of this heat shock protein.

Roberts et al. (1997) reported similar results in field work with Mytilus californianus. Gates and Edmunds (1999) observed an increase in the 70-kD heat shock protein after six hours of exposure of Montastraea franksi to a 2-3°C increase in temperature, followed by another heat shock protein increase at the 48-hour point of exposure to elevated water temperature. They state the first of these protein increases "provides strong evidence that changes in protein turnover during the initial exposure to elevated temperature provides this coral with the biological flexibility to acclimatize to the elevation in sea water temperature," and the second increase "indicates another shift in protein turnover perhaps associated with an attempt to acclimatize to the more chronic level of temperature stress."

Reshef *et al.* (2006) discussed another adaptive bleaching mechanism, developing a case for what they call the coral probiotic hypothesis, which might also be referred to as bacterial shuffling. This concept, they write, "posits that a dynamic relationship exists between symbiotic microorganisms and environmental conditions which brings about the selection of the most advantageous coral holobiont." It is analogous to the adaptive bleaching hypothesis of Buddemeier and Fautin (1993), or what was referred to in the preceding section as symbiont shuffling, in which corals exposed to some type of stress-such as that induced by exposure to unusually high water temperatures or solar irradiance-first lose their dinoflagellate symbionts (bleach) and then regain a new mixture of zooxanthellae better suited to the stress conditions. The two phenomena work in precisely the same way, in one case by the corals rearranging their zooxanthellae populations (symbiont shuffling) and in the other by the corals rearranging their bacterial populations (bacterial shuffling).

The team of Israeli researchers looked for examples of corals developing resistance to emerging diseases. Corals lack an adaptive immune system they possess no antibodies (Nair *et al.*, 2005)—and therefore can protect themselves against specific diseases in no other way than to adjust the relative sizes of the diverse bacterial populations associated with their mucus and tissues so as to promote the growth of those types of bacteria that tend to mitigate most effectively against the specific disease that happens to be troubling them.

Reshef et al. described the discovery that bleaching of Oculina patagonica corals in the Mediterranean Sea was caused by the bacterium Vibrio shiloi, together with the finding that bleaching of Pocillopora damicornis corals in the Indian Ocean and Red Sea was the result of an infection with Vibrio coralliilyticus. They report "during the last two years O. patagonica has developed resistance to the infection by V. shiloi," "V. shiloi can no longer be found on the corals," and "V. shiloi that previously infected corals are unable to infect the existing corals." They write, "by some unknown mechanism, the coral is now able to lyse the intracellular V. shiloi and avoid the disease." Because corals lack the ability to produce antibodies and have no adaptive immune system, the only logical conclusion to be drawn from these observations is that bacterial shuffling must be at work

The Israeli scientists note "Hoegh-Guldberg (1999, 2004) has predicted that coral reefs will have only remnant populations of reef-building corals by the middle of this century," based on "the assumption that corals cannot adapt rapidly enough to the predicted temperatures in order to survive." They report considerable evidence has been collected in support of the adaptive bleaching hypothesis, and they emphasize the hundreds of different bacterial species associated with corals "give the coral holobiont an enormous genetic potential to adapt rapidly to changing environmental conditions." They state, "it is not unreasonable to predict that under appropriate selection conditions, the change could take place in days or weeks, rather than decades required for classical Darwinian mutation and selection," and "these rapid changes may allow the coral holobiont to use nutrients more efficiently, prevent colonization by specific pathogens and avoid death during bleaching by providing carbon and energy from photosynthetic prokaryotes," of which they say there is "a metabolically active, diverse pool" in most corals.

Another example of adaptation to stress comes from studies of corals that exhibit a "zonation" of their symbiont taxa with depth, where symbiont algae that are less tolerant of intense solar radiation grow on corals at greater depths below the ocean surface (Rowan and Knowlton, 1995; Rowan et al., 1997). Researchers also have demonstrated zooxanthellae in corals possess a number of light-quenching mechanisms that can be employed to reduce the negative impacts of excess light (Hoegh-Guldberg and Jones, 1999; Ralph et al., 1999). Both the coral host and its symbionts also have the capacity to produce amino acids that act as natural "sunscreens" (Hoegh-Guldberg, 1999); and they can regulate their enzyme activities to enhance internal scavenging systems that remove noxious oxygen radicals produced in coral tissues as a result of high light intensities (Dykens and Shick, 1984; Lesser et al., 1990; Matta and Trench, 1991; Shick et al., 1996).

Another means corals can use to lessen the stress of solar irradiance is coral tissue retraction. Brown et al. (1994) studied the phenomenon in the scleractinian coral Coeloseris mayeri at coral reefs in Phuket, Thailand by examining the retraction and recovery of coral tissues over a tidal cycle. They found extreme tissue retraction occurred approximately 85 minutes after initial sub-aerial coral exposure. Tissue retraction did not involve any reduction in chlorophyll concentration or algae symbiont abundance; the tissues expanded over the coral skeletons to pre-retraction conditions following the return of the tide. The adaptive benefits of tissue retraction, the authors write, "include increased albedo, leading to a reduction in absorbed solar energy of 10%, ... and possible avoidance of photochemical damage or photoinhibition at high solar irradiance."

Nakamura and van Woesik (2001) evaluated the bleaching of large and small coral colonies along the

western coast of Okinawa, Japan during the summers of 1998 and 2001, arguing small coral colonies should survive thermal and light stress more readily than large coral colonies based on mass transfer theory, which suggests rates of passive diffusion are more rapid for small colonies than for large colonies. Bena and van Woesik (2004) offer still another reason why large coral colonies may suffer more than small colonies during environmental conditions conducive to bleaching: Small Acropora recruits "contain high concentrations of fluorescent proteins (Papina et al., 2002), which have photoprotective properties (Salih et al., 2000)," and "a high concentration of photoprotective pigments in early life, when planulae are near the surface and as newly settled recruits, may facilitate survival during this phase as well as during stress events involving both high irradiance and thermal anomalies (van Woesik, 2000)."

In addition to the adaptive phenomena described above, Earth appears to possess a natural "heat vent" over the tropics that suppresses the intensity of temperature and/or solar radiation to which corals are exposed whenever dangerously high water temperatures are approached. According to Hoegh-Guldberg (1999), 29.2°C is the threshold water temperature above which significant bleaching can be expected to occur in many tropical corals. As Sud et al. (1999) have demonstrated, deep atmospheric convection is typically initiated whenever sea surface temperatures (SSTs) reach a value of about 28°C, so that an upper SST on the order of 30°C is rarely exceeded. As SSTs reach 28-29°C, the cloud-base air mass is charged with sufficient moist static energy for the clouds to reach the upper troposphere. At this point, the billowing cloud cover reduces the amount of solar radiation received at the surface of the sea, while cool and dry downdrafts produced by the moist convection tend to promote ocean surface cooling by increasing sensible and latent heat fluxes at the air-sea interface that cause temperatures there to decline. This "thermostat-like control," as Sud et al. describe it, tends "to ventilate the tropical ocean efficiently and help contain the SST between 28-30°C," which is essentially a fluctuating temperature band of ±1°C centered on the bleaching threshold temperature of 29.2°C identified by Hoegh-Guldberg.

Other intriguing observations indicate a natural phenomenon of this nature. Satheesh and Ramanathan (2000), for example, determined polluted air from south and southeast Asia absorbs enough solar radiation over the northern Indian Ocean during the dry monsoon season to heat the atmosphere there by $1-3^{\circ}$ C per day at solar noon, thereby greatly reducing

the intensity of solar radiation received at the surface of the sea. Ackerman *et al.* (2000), however, calculated this atmospheric heating would decrease cloud-layer relative humidity and reduce boundarylayer mixing, thereby leading to a 25 to 50% drop in daytime cloud cover relative to that of an aerosol-free atmosphere, which could negate the surface cooling effect suggested by Satheesh and Ramanathan. In a test of this hypothesis based on data obtained from the Extended Edited Cloud Report Archive, Norris (2001) determined daytime low-level ocean cloud cover (which tends to cool the water surface) not only did not decrease from the 1950s to 1990s, it increased, in both the Northern and Southern Hemispheres and at essentially all hours of the day.

Norris remarks, "the observed all-hours increase in low-level cloud cover over the time period when soot aerosol has presumably greatly increased argues against a dominant effect of soot solar absorption contributing to cloud 'burn-off." He says "other processes must be compensating," one of which could be the phenomenon Sud *et al* described.

Another process is the "adaptive infrared iris" phenomenon Lindzen *et al.* (2001) described. Working with upper-level cloudiness data from the Japanese Geostationary Meteorological Satellite and SST data from the National Centers for Environmental Prediction, the atmospheric scientists found a strong inverse relationship between upper-level cloud area and the mean SST of cloudy regions, such that the area of cirrus cloud coverage (which tends to warm the planet) normalized by a measure of the area of cumulus coverage (which tends to cool the planet) decreased about 22 percent for each 1°C increase in the SST of the cloudy regions.

"Essentially," the scientists write, "the cloudymoist region appears to act as an infrared adaptive iris that opens up and closes down the regions free of upper-level clouds, which more effectively permit infrared cooling, in such a manner as to resist changes in tropical surface temperatures." So powerful is this phenomenon, Lindzen *et al.* say they are confident it could "more than cancel all the positive feedbacks in the more sensitive current climate models" routinely used to predict the climatic consequences of projected increases in atmospheric CO₂ concentration.

Is there any real-world evidence the natural thermostat discovered by Sud *et al.* and Lindzen *et al.* has been instrumental in preventing coral bleaching? Mumby *et al.* (2001) examined long-term meteorological records from the vicinity of the Society Islands, which provide what they call "the first empirical evidence that local patterns of cloud

cover may influence the susceptibility of reefs to mass bleaching and subsequent coral mortality during periods of anomalously high SST." Regarding the great El Niño of 1998, Mumby and his colleagues determined SSTs in the Society Islands sector of French Polynesia were above the 29.2°C bleaching threshold for a longer period of time (two months) than in all prior bleaching years of the historical record. Mass coral bleaching, which was extensive in certain other areas, was found to be "extremely mild in the Society Islands" and "patchy at a scale of 100s of km."

What provided the coral relief from extreme sun and heat? As Mumby and his associates write, "exceptionally high cloud cover significantly reduced the number of sun hours during the summer of 1998," much as one would have expected Earth's natural thermostat to have done in the face of such anomalously high SSTs. The marine scientists also note extensive spotty patterns of cloud cover, besides saving most of the coral they studied, "may partly account for spatial patchiness in bleaching intensity and/or bleaching-induced mortality in other areas."

Although the natural thermostat cannot protect all of Earth's corals from life-threatening bleaching during all periods of anomalously high SSTs, it apparently protects enough of them enough of the time to ensure sufficiently large numbers of corals survive and grow, since living reefs have persisted over the eons in spite of the continuing recurrence of ever-present environmental threats. That may be how it has always been, although a host of unprecedented anthropogenic forces of site-specific origin might be weakening the abilities of some species to tolerate the thermal and solar stresses they have successfully weathered in the past.

Smith *et al.* (2005) note "photoinhibition of photosynthesis and photodamage to photosystem II of the zooxanthellae, with the consequent increase in the production of damaging reactive oxygen species (ROS), have been implicated as the cause of thermal bleaching (Brown, 1997; Fitt *et al.*, 2001; Lesser, 2004; Tchernov *et al.*, 2004)." They also report the "thermal bleaching of many corals is ultimately the result of the destruction of photosynthetic pigments by ROS," and the production by the zooxanthellae of one particular ROS, hydrogen peroxide, "may be a signal that triggers a response in the host cell to eject the zooxanthellae or shed the host cell from the coral."

These facts resonate with other findings presented in this volume (see Section 7.3, Health Effects of CO_2) and suggest the ongoing rise in the air's CO_2 content may ultimately provide the solution to the worldwide problem of heat-induced coral bleaching. This concept originates from research conducted in the terrestrial realm, which reveals, Ren *et al.* (2001) write, "elevated CO_2 can enhance the capacity of plants to resist stress-induced oxidative damage."

In the case of ozone pollution, the primary problems occur in the leaf mesophyll, where ozone dissolves into the wet surfaces of exposed cell walls. There, reactions of ozone with water and solutes in the apoplasm lead to the formation of several ROS, including hydrogen peroxide (H_2O_2), hydroperoxide, superoxide, hydroxyl radicals, and singlet oxygen (Foyer *et al.*, 1994; Kangasjarvi *et al.*, 1994; Wohlgemuth *et al.*, 2002), all of which promote oxygen toxicity (Podila *et al.*, 2001).

In a free-air CO₂ enrichment (FACE) study of this phenomenon in aspen and paper birch seedlings exposed to ambient air, ozone-enriched air, CO₂enriched air, or air enriched with both ozone and CO₂, Oksanen *et al.* (2003) found H₂O₂ accumulation occurred only "in ozone-exposed leaves and not in the presence of elevated CO₂," adding "CO₂ enrichment appears to alleviate chloroplastic oxidative stress." Similarly, in a study of mature holm and white oak trees that had been growing near natural CO₂ springs in central Italy for 30 to 50 years, Schwanz and Polle (1998) found they exhibited significant reductions in their amounts of lipid peroxidation.

Yu et al. (2004) sought to ascertain whether the ROS-fighting properties of elevated CO₂ might also operate in the aquatic realm. They grew the marine microalgae Platymonas subcordiformis in the laboratory at ambient levels of atmospheric CO₂ and UV-B radiation flux density, and at elevated levels of 5,000 ppm CO₂ and/or UV-B radiation characteristic of what would result from a 25% stratospheric ozone depletion under clear sky conditions in summer. They found the elevated UV-B treatment significantly decreased microalgal dry weight and photosynthetic rate, whereas the elevated CO2 treatment enhanced dry weight and photosynthetic rate. They also report elevated UV-B significantly increased the production of the toxic superoxide anion and hydrogen peroxide, as well as malonyldialdehyde, which is an end product of lipid peroxidation, whereas elevated CO₂ did just the opposite. In the treatment consisting of both elevated UV-B and elevated CO₂, the concentrations of these three substances were lower than those observed in the elevated UV-B and ambient CO₂ treatment.

Yu *et al.* say their results suggest "CO₂ enrichment could reduce oxidative stress of reactive

oxygen species to *P. subcordiformis*, and reduce the lipid peroxidation damage of UV-B to *P. subcordiformis*." They note, "CO₂ enrichment showed a protective effect against the oxidative damage of UV-B-induced stress," and, therefore, elevated CO₂ can enhance "the capacity of stress resistance." They conclude, "algae grown under high CO₂ would better overcome the adverse impact of environmental stress factors that act via generation of activated oxygen species."

Smith et al. (2005) write, "thermal bleaching of many corals is ultimately the result of the destruction of photosynthetic pigments by ROS," and as Oksanen et al. (2003) observe, "CO2 enrichment appears to alleviate chloroplastic oxidative stress." It is thus clear some as-yet-undefined level of atmospheric CO₂ enrichment could completely counter coral thermal bleaching. In addition, since the presence of hydrogen peroxide, as Smith et al. (2005) write, "may be a signal that triggers a response in the host cell to eject the zooxanthellae or shed the host cell from the coral," and as Yu et al. (2004) write, "CO₂ enrichment could reduce ... lipid peroxidation damage," it readily follows some degree of atmospheric CO₂ enrichment should cause host cells not to eject their zooxanthellae.

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6.1.2.3 Resilience of Corals

The studies reviewed in this section examine observational evidence for the resilience of corals in responding to stress events that routinely occur in nature. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings.

- Corals have been around for a very long time, experiencing climatic conditions that have changed dramatically, from conditions both warmer and colder than the present.
- Many researchers have documented rapid recoveries of corals following recent mass bleaching/mortality events, and such recoveries have occurred on time scales previously assumed to be nearly impossible.
- A growing body of research indicates coral resilience is the rule, not the exception, and these findings are at odds with IPCC's projections of future coral demise.

As illustrated in the preceding section (6.1.2.2 Temperature-Related Responses to Stresses). numerous studies attest to the ability of corals to adapt and evolve in response to temperature-related stresses. Nevertheless, there have been many recorded instances where the severity of coral bleaching from temperature-related stresses was great enough to cause mass mortality of corals, and these occurrences have led IPCC to conclude corals are among the most vulnerable species of marine life, saying it "is very likely that coral reef ecosystems will not survive changes in sea temperature beyond an additional increase of 1°C." (p. 35 of Chapter 30. The Ocean, Working Group II, IPCC Fifth Assessment Report, dated March 28, 2013).

Corals, however, have been around for a very long time, experiencing climatic conditions that have changed dramatically, from conditions both warmer and colder than the present, suggesting they are much more resilient than IPCC claims.

The earliest coral reefs date to the Palaeozoic Era, more than 450 million years ago (Hill, 1956). The scleractinian corals, the major builders of the reefs of today (Achituv and Dubinsky, 1990), appeared in the mid-Triassic some 240 million years later (Hill, 1956), when Earth was considerably warmer than it is today (Chadwick-Furman, 1996). Although reefbuilding ceased for a time after the extinctions at the end of the Triassic, the Scleractinia came back during the Jurassic (Newell, 1971; Veron, 1995) and continued to exhibit great robustness throughout the Cretaceous, even when temperatures were as much as $8-15^{\circ}$ C higher (Chadwick-Furman, 1996; Veizer *et al.*, 1999), and atmospheric CO₂ concentrations two to seven times higher (Berner and Kothavala, 2001), than they are today.

At the end of the Cretaceous, 70% of the genera and one-third of the families of scleractinian corals disappeared (Veron, 1995) in the greatest biospheric extinction event in geological history, which may have been caused by a large asteroid impact (Alvarez et al., 1980; 1984). They developed again, however, throughout the Cenozoic, particularly during the Oligocene and Miocene (Chadwick-Furman, 1996). Throughout the past two million years of the Pleistocene, they survived at least 17 glacialinterglacial cycles of dramatic climate change and sea-level fluctuation, successfully adapting, over and over again, to these enormous environmental challenges (Pandolfi, 1999). According to Benzie (1999), this evidence suggests "coral reef communities are relatively resilient, have survived previous global climate change, and appear likely to survive future changes."

Such resilience helps explain why many researchers have documented rapid recoveries of corals following recent mass bleaching/mortality events, on time scales previously assumed to be nearly impossible. As more research is conducted on this topic, it appears coral resilience is the rule, not the exception. These findings are vastly at odds with IPCC's projections of future coral demise.

An early example of such resilience was observed after the widespread bleaching of corals in the Indian and Pacific Oceans during the peak warmth of the 1998 El Niño, the deadly effects of which were described at the time as the most extensive ever seen. Many of the devastated corals were not expected to recover (Normile, 2000). But barely a year later many of the reefs were in fact recovering, with large amounts of new coral found in what had been made to look like "graveyards" by the prior year's marine heat wave. Normile quotes Terry Done of the Institute of Marine Science in Cape Ferguson as saying these real-world observations forced many people to admit coral reefs are indeed "more resilient than we had thought." Since that admission, many more studies have illustrated similar recoveries as scientists have investigated and tracked coral recoveries.

Kayanne *et al.* (2002) assessed coral cover within the reef flat of Shiraho Reef, Ishigaki Island (situated at the southernmost end of the Ryukyus Islands of Japan) just before, during, and six times after an unprecedented bleaching event that began in early July 1998 and ended in early October of that year. They note "massive *Porites* were susceptible to bleaching, but regained their algae after the bleaching and sustained their coverage." Branching *Porites, Montipora,* and *Acropora* corals experienced significant mortality of 41.1%, 55.4%, and 82.4%, respectively, and approximately two-thirds of the surviving corals were completely or partly bleached. Nevertheless, coverage of large patches of the branching *Montipora* coral, initially reduced by 66%, recovered to pre-bleaching levels after two years.

Kayanne *et al.* note "the recovery of corals to their pre-bleaching levels has been inferred to take from 10 to 30 years for damaged coral populations and from 5 to 10 years for bleached corals that do not die (Hoegh-Guldberg, 1999; Wilkinson *et al.*, 1999)." Shiraho Reef, they report, "is recovering at an unexpectedly fast rate." The authors conclude, "even susceptible species have a high potential to regain zooxanthellae after bleaching or to recover after mortality."

Adjeroud *et al.* (2005) initiated a monitoring program on 13 islands (eight atolls and five high volcanic islands) in four of the five archipelagoes of French Polynesia, to document the effects of natural perturbations on coral assemblages. For the period covered by their report (1992–2002), these reefs were subjected to three major coral bleaching events (1994, 1998, 2002) and three cyclones (1997), and before this period the sites had experienced an additional seven bleaching events and 15 cyclones as well as several *Acanthaster planci* outbreaks.

They found the impacts of the bleaching events varied among the different study locations. They observed three temporal trends: "(1) ten sites where coral cover decreased in relation to the occurrence of major disturbances; (2) nine sites where coral cover increased, despite the occurrence of disturbances affecting seven of them; and (3) a site where no significant variation in coral cover was found." They report, "an interannual survey of reef communities at Tiahura, Moorea, showed that the mortality of coral colonies following a bleaching event was decreasing with successive events, even if the latter have the same intensity (Adjeroud *et al.*, 2002)."

The seven French scientists say the "spatial and temporal variability of the impacts observed at several scales during the present and previous surveys may reflect an acclimation and/or adaptation of local populations," and "coral colonies and/or their endosymbiotic zooxanthellae may be phenotypically (acclimation) and possibly genotypically (adaptation) resistant to bleaching events," citing Rowan *et al.* (1997), Hoegh-Guldberg (1999), Kinzie *et al.* (2001), and Coles and Brown (2003) in support of this conclusion.

Pratchett et al. (2013) developed a history of variations in coral bleaching among four key genera of reef-building corals (Acropora, Montipora, Pocillopora, and Porites) in Moorea, focusing on four mass-bleaching events that occurred there in 1991, 1994, 2002, and 2007. They documented the history of the bleaching susceptibility of each of the four coral genera in each of the four events, finding "Acropora and Montipora consistently bleached in far greater proportions than Pocillopora and Porites." They also found "an apparent and sustained decline in the proportion of colonies that bleached during successive bleaching events, especially for Acropora and Montipora." In 2007, for example, only 77% of Acropora colonies bleached compared with 98% in 1991. They acknowledge "temporal variation in the proportion of coral colonies bleached may be attributable to differences in environmental conditions among years" but also state, "alternately, the sustained declines in bleaching incidence among highly susceptible corals may be indicative of acclimation or adaptation." Pratchett et al. suggest it may be "that gradual removal of highly susceptible genotypes (through selective mortality of individuals, populations, and/or species) is producing a coral assemblage that is more resistant to sustained and ongoing ocean warming," which further suggests "there is some capacity for adaptation, which will delay devastating effects of global climate change."

Golbuu et al. (2007) examined recovery rates of coral communities on the Palauan reef complex of Micronesia (7°30'N, 134°30'E) at two depths (3 and 10 m) at several sites (nine outer-reef wave-exposed sites, four on the east coast and five on the west coast; two patch reef sites; and two sheltered-bay sites) three, four, and seven years after the 1998 El Niño-Southern Oscillation (ENSO)-induced bleaching event. The nine researchers report, "coral populations recovered rapidly on the reefs of Palau," but "recovery trajectories changed over time and were habitat and depth-dependent," noting "seven years after the bleaching event, some reefs supported >30%coral cover, and some habitats supported >40% coral cover." They observe "recovery within the bays at 3 m was mostly a consequence of growth of remnant (surviving) coral colonies, while recovery on the exposed slopes was mostly likely a consequence of both remnant regrowth and sexual recruitment events at 10 m, and more a consequence of recruitment at 3 m."

Guzman and Cortes (2007) studied coral reefs of the eastern Pacific Ocean that "suffered unprecedented mass mortality at a regional scale as a consequence of the anomalous sea warming during the 1982–1983 El Niño." At Cocos Island (5°32'N, 87°04'W), they found in a survey of three representative reefs, which they conducted in 1987, the remaining live coral cover was only 3% what it had been before the great El Niño four years earlier (Guzman and Cortes, 1992). Based on this finding and the similar observations of other scientists at other reefs, they predicted "the recovery of the reefs' framework would take centuries, and recovery of live coral cover, decades."

In 2002, nearly 20 years after the disastrous coralkilling warming, they returned to see how accurate their prediction had been, quantifying "the live coral cover and species composition of five reefs, including the three previously assessed in 1987." The two researchers report overall mean live coral cover increased nearly fivefold, from 2.99% in 1987 to 14.87% in 2002, at the three sites studied during both periods, and the mean live coral cover of all five sites studied in 2002 was 22.7%. They found "most new recruits and adults belonged to the main reef building species from pre–1982 ENSO, *Porites lobata*, suggesting that a disturbance as outstanding as El Niño was not sufficient to change the role or composition of the dominant species."

The 1998 El Niño-induced bleaching episode severely affected most Indian Ocean reefs, with the Maldives suffering 90% coral mortality in their central atolls. Before this mass mortality, Lasagna *et al.* (2008) write, "hard coral cover was generally between 30 and 60%, often reaching 100% in shallow water." One year later, they report, "coral cover had decreased to less than 8%, and reefs were dominated by algae."

In April 2006, Lasagna *et al.* "re-examined the status of the Maldivian reefs, focusing on their benthic composition to evaluate the possible change in dominance from hard corals to non-constructional organisms such as soft corals, algae or sponges," which have been predicted to replace hard corals after major bleaching episodes. The seven Italian scientists report, "eight years after the 1998 coral mass mortality, hard coral cover varied from 12% to 37%," and "cover of soft corals, algae and sponges was comparatively low (approximately 7% on average)." They say "a recent inventory of coral species showed

that their number is larger than that known before 1998 (Pichon and Benzoni, 2007)."

McClanahan et al. (2009) 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." The Kenyan, Swedish, Tanzanian, and U.S. researchers report 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."

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

Scopelitis *et al.* (2009) sought to determine the responses of corals of Saint-Leu Reef on la Reunion (a mountainous volcanic island of the Mascarene Archipelago in the Southwest Indian Ocean) to major devastating events that occurred there over the prior 35 years (between 1973 and 2007), including a category 5 cyclone (Firinga, of 29 January 1989). These events "caused 99% coral cover loss (Naim *et al.*, 1997)." A severe coral bleaching event in March 2002 followed on the heels of cyclone Dina of January 2002, and other bleaching episodes occurred in 1983, March–April 1987, and February 2003.

Scopelitis *et al.* studied vertical images of the reef provided by five aerial photographs taken in 1973, 1978, 1989, 1997, and 2003, along with two Quickbird satellite images taken in 2002 and 2006, as well as periodic quantitative *in situ* observations of parts of the reef-top that could be used to document ecological and substratum characteristics that produce the color and texture observable in the photos and satellite images. From these observations they constructed a history of changes in the reef's coral community over a period of 35 years (1973–2007). "Despite the multiple disturbance events," the six scientists write, "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, especially since "in the wake of cyclone Firinga, Saint-Leu Reef phase-shifted and became algaedominated for a period of five years," and even more impressive given that no corals had survived an unnamed cyclone of 27 January 1948. Such findings, the Australian and French researchers write, indicate "a high degree of coral resilience at the site, led by rapid recovery of compact branching corals."

According to Crabbe (2009), "coral reefs throughout the world are under severe challenges from a variety of environmental factors including overfishing, destructive fishing practices, coral bleaching, ocean acidification, sea-level rise, algal blooms, agricultural run-off, coastal and resort development, marine pollution, increasing coral diseases, invasive species, and hurricane/cyclone damage."

Crabbe employed a number of tools to analyze the resilience of the fringing reefs around Discovery Bay, Jamaica, documenting the responses of their populations "to a number of environmental stressors, in particular hurricanes and the mass bleaching event of 2005," which he describes as "by far the major acute influence on the reef sites." The UK researcher reports "there was a reduction in numbers of colonies in the smallest size class for all the species at all the sites in 2006, after the mass bleaching of 2005, with subsequent increases for all species at all sites in 2007 and 2008." At Dairy Bull Reef, he notes, "live coral cover increased from $13 \pm 5\%$ in 2006 to $20 \pm 9\%$ in 2007 and 31 \pm 7% in 2008," and "live Acropora species increased from $2 \pm 2\%$ in 2006 to $10 \pm 4\%$ in $2007 \text{ and } 22 \pm 7\% \text{ in } 2008."$

The UK researcher concludes his results "indicate good levels of coral resilience on the fringing reefs around Discovery Bay in Jamaica," even after having "suffered from long term human-induced chronic stressors, such as overfishing and land development," along with "die-off of the long-spined sea urchin" and "coral disease." Crabbe states he and a colleague "found a variety of clades of zooxanthellae, including clade C, in corals at Dairy Bull Reef (Crabbe and Carlin, 2007)," and "the potential for symbiont shuffling, as we have found in 111 colonies of *Acropora* species from the Ningaloo Reef, Australia (Crabbe and Carlin, 2009), may be a factor in their recovery," citing Stat *et al.* (2008).

In early 2006, mass bleaching of corals on

inshore reefs of the Keppel Islands in the southern Great Barrier Reef (GBR) caused high coral mortality, with severe bleaching affecting 77-95% of coral colonies (Weeks et al., 2008; Jones et al., 2008). This event, Diaz-Pulido et al. (2009) write, was followed by "an extraordinary bloom of the brown Lobophora variegata," seaweed which was "unprecedented in magnitude on the GBR" and "exacerbated coral mortality by overgrowing stressed coral tissue." After the natural seasonal decline in L. variegata, which in some places had increased its cover by 200-300% by August 2006, "the cover of branching Acropora corals at most sites showed an extremely rapid recovery," the Australian researchers write, "reaching pre-bleaching levels by December 2006-April 2007 ca 12-14 months after the onset of bleaching."

"Unexpectedly," as they describe it, "this rapid reversal did not involve reestablishment of corals by recruitment of coral larvae, as often assumed, but several ecological mechanisms depended on previously underestimated." Most interesting in this regard was "the 'phoenix effect' in which apparently dead coral branches regenerate live tissue (Krupp et al., 1993; Jokiel et al., 1993; Riegl and Piller, 2001)." This "remnant surviving coral tissue," Diaz-Pulido et al. continue, "rapidly expanded upwards along the dead coral branches and actively overgrew L. variegata, as well as a range of other algal types, including filamentous algal turfs, fleshy seaweeds and crustose coralline algae," resulting in "a 'seaweed sandwich' with algae engulfed between new and old layers of [coral] skeleton."

Noting reefs of the Keppel Islands "have shown rapid recovery of coral dominance, despite repeated coral bleaching events (1998, 2002, and 2006), severe flood plumes (e.g. 1991, 2008), and dense algal overgrowth," Diaz-Pulido *et al.* conclude these and other reefs that are "able to rapidly recover abundant corals may serve as key refugia, or sources of larvae for reef recovery at broader scales," and the phenomena they document in their research "may well be critical to the overall resilience and persistence of coral reef ecosystems globally."

Bruno *et al.* (2009) recognized additional resilience of corals against algal growth that often ensues after a bleaching event, noting one of the great concerns of marine scientists is "coral reefs are moving toward or are locked into a seaweeddominated state." Bruno *et al.* "analyzed 3,581 quantitative surveys of 1,851 reefs performed between 1996 and 2006 to determine the frequency, geographical extent, and degree of macroalgal dominance of coral reefs and of coral to macroalgal phase shifts around the world."

The five marine researchers found "the replacement of corals by macroalgae as the dominant benthic functional group is less common and less geographically extensive than assumed," noting "only 4% of reefs were dominated by macroalgae (i.e., >50% cover)." Across the Indo-Pacific, where regional averages of macroalgal cover were 9–12%, they found "macroalgae only dominated 1% of the surveyed reefs." In addition, "between 1996 and 2006, phase shift severity decreased in the Caribbean, did not change in the Florida Keys and Indo-Pacific, and increased slightly on the Great Barrier Reef."

Bruno *et al.* state "coral reef ecosystems appear to be more resistant to macroalgal blooms than assumed," and "the mismatch between descriptions of reef degradation in the literature and patterns in nature was caused by the generalization of a relatively small number of examples." They conclude their analysis suggests "the macroalgae problem has been exaggerated," and "overall," there has been "no general recent trend (i.e., post–1995) toward macroalgal dominance." They write, "macroalgal cover may currently be close to the historical baseline across most of the world."

Zapata et al. (2010) developed an extended history from data they obtained over the period 1998-2004 from 20 permanent transects at two sites on one of the largest and best developed coral reefs in the Colombian Pacific (La Azufrada reef on Gorgona Island), plus data obtained there even earlier by others. The four Colombian researchers report comparisons with previous studies showed the reef at La Azufrada returned to "pre-disturbance (1979) levels of coral cover within a 10-year period after the 1982-83 El Niño, which caused 85% mortality," and subsequently, "the effects of the 1997-98 El Niño, indicated by the difference in overall live coral cover between 1998 and 1999, were minor (<6% reduction)." They report "despite recurrent natural disturbances, live coral cover in 2004 was as high as that existing before 1982 at La Azufrada." Zapata et al. conclude "the recent history of La Azufrada reef since coral reef studies began at Gorgona Island three decades ago (Prahl et al., 1979; Glynn et al., 1982) suggests a remarkable ability of this reef to recover from past perturbations," which are of the type (extreme El Niño-driven temperature increases leading to coral bleaching) IPCC claims should be especially deadly and from which coral recovery should not be expected.

According to van Woesik et al. (2011), "over the

past three decades, thermal stress events have damaged corals globally," but few studies "have tracked the recovery process or assessed whether winners in the short term are also winners in the long term." They repeatedly evaluated (1997, 1999, 2000, 2001, 2004, 2007, 2010) a coral assemblage on the southeastern reef of Sesoko Island at the Tropical Biosphere Research Center of the University of the Ryukyus, Okinawa, Japan (26°38'N, 127°52'E), which experienced significant thermal stress events in 1998 and 2001.

The four researchers report, "by 2007, species richness had recovered to ~13 species per m^2 , which was similar to species richness in 1997," and "hard coral cover increased from 3% in 2001 to 47% in 2010." They also found "species composition had undergone change," as "some species were thermally tolerant and increased in relative abundance through time," some "increased in relative abundance through the thermal stress and remained constant thereafter," and some "were neither winners nor losers through time."

Van Woesik *et al.* conclude the ecosystem they studied was "able to absorb the thermal stressors without undergoing change to a less desirable state," citing the similar findings of Holling (1973) and Scheffer and Carpenter (2003). They note "Acropora populations had fully recovered seven years after an extreme thermal-stress event in Palau (Golbuu *et al.*, 2007)," and in the Arabian Gulf, "Riegl and Purkis (2009) showed that Acropora assemblages could recover from thermal-stress cycles occurring every fifteen years."

Marimuthu et al. (2013) investigated the recovery of the corals in the Andaman and Nicobar Islands in the eastern part of the Bay of Bengal following a significant warming event in summer 2010. At the time, sea surface temperatures (SSTs) rose to about 34°C, resulting in the bleaching of 74 to 77% of the corals surrounding Havelock Island and Port Blair Bay, respectively. Marimuthu et al. utilized prebleaching population data obtained by the line intercept transect (LIT) method of English et al. (1997) in July 2010, along with post-bleaching data they collected in January 2011 for the most severely affected corals, which included Acropora cerealis, A. humilis, Montipora sp., Favia pallida, Diploastrea sp., Goniopora sp., Fungia concinna, Gardineroseries sp., Porites sp., Favites abdita, and Lobophyllia robusta. They found "the observed post bleaching recovery [January 2011] of coral cover was 21.1% at Port Blair Bay and 13.29% at Havelock Island," and "once the sea water temperature resumed back to the normal condition, most of the corals where found recovered."

Gilmour et al. (2013) note, "coral reef recovery from major disturbance is hypothesized to depend on the arrival of propagules from nearby undisturbed reefs," and, therefore, "reefs isolated by distance or current patterns are thought to be highly vulnerable to catastrophic disturbance." In a test of this hypothesis. Gilmour et al. set out to "document the recovery of coral assemblages at Australia's largest oceanic reef system, where changes in assemblage structure and key demographic parameters were quantified for 16 years, through a regime of disturbances beginning with a catastrophic mass bleaching event in 1998." The authors focused on "the Scott system of reefs, which is surrounded by oceanic waters on the edge of Western Australia's continental shelf" and is "more than 250 km from the mainland and other reefs in the region, and more than 1000 km from a major center of urbanization."

The five Australian researchers report finding "for 6 years, recruitment rates were <6% of those prior to the disturbance," and "on the basis of these rates of change," they say "recovery was projected to take decades." Within just 12 years, "coral cover, recruitment, generic diversity, and community structure were again similar to the pre-bleaching years." The coral recovery "may have been even faster if not for a series of more moderate disturbances, including two cyclones, an outbreak of disease, and a second bleaching."

Gilmour et al. say their results demonstrate "even corals with a negligible supply of larvae from outside can recover relatively quickly from disturbances in the absence of chronic human pressures." They suggest "addressing local pressures, such as pollution and overfishing, is as important to the recovery of coral reefs as the establishment of networks of marine protected areas." They conclude, "managing local pressures to promote resilience will be critical to preventing the global degradation of coral reefs," which is true of several other damaging phenomena, many of which have particular application to Australia's Great Barrier Reef. These include rising nutrient levels caused by runoff from agricultural activity on land; outbreaks of the coral-devouring crown-of-thorns starfish; the barbed hooks and scything nets used in fishing; tourists and the developers who build resorts and marinas for them; increased sediment levels; the nets of prawn trawlers stirring up the growing load of sediments; the 6-10 tons of "bycatch" for each ton of prawns netted that are caught and die, which dramatically changes the

composition of reef life; sea life depleted to the point of exhaustion by over-fishing; huge catamarans and dive boats that take thousands of visitors to the Barrier Reef each day and dump their sewage in the sea on the way home; the live reef-fish trade; fishermen using dynamite and cyanide; coral diseases; and pollution.

Mondal *et al.* (2013) studied the fringing reefs off Little Andaman Island at the juncture of the Bay of Bengal and the Andaman Sea. A number of such reefs were essentially destroyed when a 2004 tsunami swept across them with devastating consequences. Five years later in 2009, however, 34 species of scleractinian corals had reappeared (Sawall *et al.*, 2010). But the next year brought a massive bleaching event caused by a dramatic increase in sea surface temperatures above their normal average ranges (Mondal and Raghunathan, 2011), after which Mondal *et al.* (2013) found "the bleached corals were transformed mostly into dead ones."

In February 2012 the three Indian researchers dove to depths of up to 35 meters to identify and record what species of scleractinian corals they encountered at three locations around Little Andaman Island. They employed the line intercept transect method (Bradbury et al., 1886) with a series of 20meter transects randomly placed at intervals of 10 meters, with three replicates of the procedure carried out at depths of 5, 10, 15, 20, 25, 30, and 35 meters. They discovered 124 species of youthful scleractinian corals, 90 more than the 34 species detected by Sawall et al. in 2009. Mondal et al. report the minimum value of the Shannon-Weaver Diversity Index was 5.09, which they state "is above the optimum hypothetical value," whereas the minimum value of Simpson's Density Index was 0.94, which they report "is very near to the maximum value which is most advantageous."

In light of these observations and because "bleaching was the only physiological process which happened in between 2009 and 2012," Mondal *et al.* conclude "bleaching is a prime regulator for the settlement of new recruitment of scleractinian corals which leads to diversified reef area," further noting "the adaptive features of bleaching can be seen as a mechanism that enables the exchange of symbionts in a better fit of the holobiont to a changed environment," citing Graham *et al.* (2011).

According to Miranda *et al.* (2013), sub-lethal bleaching effects "occur when corals do not experience mortality after bleaching, but rather undergo a temporary loss of zooxanthellae and/or of their photosynthetic pigments, with later recovery." This

implies, they write, "corals have an adaptive capacity or resistance to seasonal changes in environmental conditions," as suggested by Buddemeir and Fautin (1993), Hennige *et al.* (2010), and Hughes *et al.* (2011).

The three Brazilian researchers note "thermal anomalies on the Brazilian coast have been monitored by NOAA satellite imaging since 1998." They also observe, "there have been many reports of bleaching events occurring in association with ocean warming events," but "only Dutra et al. (2000) reported observations of the reefs after the occurrence of the beaching phenomenon." They studied the effects of bleaching in the corals of Caramuanas reefcomprised of three main flat reef banks (13°07'S, 38°43'W; 13°07'S, 38°44'W; 13°08'S, 38°44'W)by comparing them during and immediately after the thermal anomalies related to the ENSO event of 2010 in terms of "frequency and severity of bleaching, live coral cover, number of colonies, class size, disease occurrence and mortality rate," based on samples taken at 12 fixed transects in three reef locations.

Miranda *et al.* found, "after this bleaching event, neither the rate of mortality nor the number of colonies with disease increased; the size class structure of the most abundant species did not vary; and the number of live colonies and live coral cover also remained the same." They report, "the reef showed certain resilience to the perturbations caused by the 2010 ENSO event." In further support of their findings, they write, "the sub-lethal effects of bleaching in Brazilian corals have been observed previously," noting, "in 1998, the northern littoral of Bahia experienced a bleaching event that affected up to 60% of the coral community, which after one year have completely recovered," as reported by Dutra *et al.* (2000).

Miranda et al. point out, "the Brazilian zooxanthellate coral fauna is characterized by endemic species, with some reminiscent of a Tertiary coral fauna that may be adapted to these inhospitable environment conditions," citing Leao et al. (2003). They cite as some examples various species of the genus Mussismilia, as these species had "the lowest percent of bleached colonies," adding, "those that bleached completely recovered during this investigation." With respect to potential policy implications of their findings, the Brazilian biologists suggest "eliminating or reducing anthropogenic effects on this reef may increase its resistance and resilience to bleaching, allowing its maintenance," so "the Caramuanas reef could then act as a reserve of species and genes for this geographic region."

Earth's corals likely will be able to cope with any further increases in water temperatures, anthropogenic or natural. Corals have survived such warmth and worse many times in the past, including the Medieval Warm Period, Roman Warm Period, and Holocene Optimum, as well as numerous times during prior interglacial periods. There is no reason to think they cannot do so again if the need arises.

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6.1.2.4 Sea-level Rise

The studies reviewed in this section examine the threat potentially large increases in sea level may pose to corals. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- The warming-induced sea-level rise predicted for the coming century—which could be greatly exaggerated if predictions of CO₂-induced global warming are wrong—falls well within the range of typical coral vertical extension rates and can be less than half the rate of certain branching corals.
- Most coral reefs are known to have responded successfully to the sea-level rises that occurred between 14,000 and 6,000 years ago, which were more than twice as rapid as what is being predicted for the coming century.
- Earth's oceans have undergone, and their coral reefs survived, at least 17 major cycles of sea-level rise and fall during the Pleistocene, the most recent low phase of which ended 18,000 years ago with a global sea level some 120–135 meters below where it is today.
- Even if reef vertical growth rates could not keep up with rising sea levels, that would not spell their doom, as "propagules of the species could keep pace and settle at suitable depths each generation."
- Rising sea levels likely would benefit many coral reefs. Over the past 6,000 years, relatively stable sea levels have limited upward reef growth, resulting in the development of extensive reef flats. Rising sea levels likely would release them from this vertical constraint.

Some researchers claim CO₂-induced global warming will melt large portions of planetary ice, thereby raising sea levels at a rate faster than corals can adjust to, while reducing the amount of life-sustaining light that reaches coral algal symbionts. Such concerns are overblown and unlikely to occur, as discussed in the studies reviewed below.

The approximate 30- to 60-cm warming-induced sea-level rise that is predicted for the coming century-which could turn out to be greatly exaggerated if predictions of CO2-induced global warming are wrong-falls well within the range (2 to 6 mm per year) of typical coral vertical extension rates, which exhibited a modal value of 7 to 8 mm per vear during the Holocene and can be more than double that value in certain branching corals (Hopley and Kinsey, 1988; Done, 1999). Moreover, most coral reefs are known to have responded successfully to the sea-level rises that occurred between 14,000 and 6,000 years ago, which were accompanied by large changes in "CO2 concentrations, ... rainfall, cloud cover, storms and currents" (Wilkinson, 1996), and which were more than twice as rapid as what is being predicted for the coming century (Digerfeldt and Hendry, 1987).

Earth's oceans have undergone, and their coral reefs have survived (Chadwick-Furman, 1996), at least 17 major cycles of sea-level rise and fall during the Pleistocene, the most recent low phase of which ended 18,000 years ago with a global sea level some 120–135 meters below where it is now (Grigg and Epp, 1989). And most coral reefs handle increases in sea level, even rapid increases, much better than decreases (White *et al.*, 1998).

Even if reef vertical growth rates could not keep up with rising sea levels, that would not spell their doom. One of the important characteristics of essentially all reef cnidarians is their ability to produce free-swimming planulae, spores, or dispersive larval stages. Kinzie (1999) notes, "no matter how quickly sea level might rise, propagules of the species could keep pace and settle at suitable depths each generation," thereby creating what he calls jump-up reefs that "might well contain most of the species present in the original community." Done (1999) notes "coral communities have a history of tracking their preferred environmental niche which may suggest that as an entity, they will be predisposed to 'adapt' to prospective changes in environment over the next century," citing precedents that clearly demonstrate "coral communities have historically had a good capacity to track their re-distributed preferred physical niches."

As Kinzie and Buddemeier (1996) recount, coral reefs have survived many periods of "massive environmental changes" throughout the geologic record. Reefs are survivors, they state, "because they

do not simply tolerate environmental changes" but "exhibit an impressive array of acclimations" that allow them to deal with a variety of challenges to their continued existence in any given area. It is highly unlikely anticipated increases in sea level would spell the doom of Earth's corals.

Rising sea levels may actually have a positive effect on coral reefs (Roberts, 1993). Over the past 6,000 years, relatively stable sea levels have limited upward reef growth, resulting in the development of extensive reef flats. As Buddemeier and Smith (1988) and Wilkinson (1996) have noted, the sea-level rises predicted to result from CO₂-induced global warming should be beneficial, permitting increased growth in these growth-restricted areas. As Chadwick-Furman (1996) noted, "many coral reefs have already reached their upward limit of growth at present sea level (Buddemeier, 1992), and may be released from this vertical constraint by a rise in sea level." She also notes rising sea levels may allow more water to circulate between segregated lagoons and outer reef slopes, which could "increase the exchange of coral propagules between reef habitats and lead to higher coral diversity in inner reef areas." She, too, concludes "coral reefs are likely to survive predicted rates of global change."

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6.1.3 Crustaceans

The studies reviewed in this section examine the impact of rising temperatures on crustacean species. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- The larval form of the kelp crab is capable of adapting to both higher and lower temperatures than those at which it may have lived for long periods in the past.
- At higher temperatures, red king crab (*Paralithodes camtschaticus*) experienced "accelerated growth" and a "positive, indirect effect on survival," as "larger size associated with high temperature could provide for earlier refuge in size from the typical fish and invertebrate predators."
- A modest warming would prove advantageous to hymenosomatid crabs, increasing larval growth and survival rates, as well as fecundity.

- European green crabs (*Carcinus maenas*) on the west coast of North America have demonstrated phenotypic thermal tolerance and adaptation.
- *Palaemonetes varians*, a shallow-water brackish shrimp, "shows genuine acclimation capacities" due to the plasticity inherent in the organism's critical thermal limit and heat shock response to temperature.
- Some Branchiopod crustaceans display "substantial physiological plasticity or important adaptive variation," which enables them "to better cope with environmental change."
- "Copepod diversity, especially in extra-tropical regions, is likely to increase with climate change as their large-scale distributions respond to climate warming," because of a "strong positive correlation between diversity and temperature."

Storch et al. (2009) note, "temperature is often invoked as the main determinant of distribution ranges and boundaries for marine and terrestrial species," and the larval stages of many marine species "are more vulnerable to thermal and osmotic stresses than adults." They explored the rigidity of this temperature determinant of livable range for the Chilean kelp crab (Taliepus dentatus) in its most temperature-sensitive larval state. They studied stage zoea I larvae of two populations of the crab-one from Southern Chile (SC, 43°54'S) and one from Central Chile (CC, 33°29'S)—measuring "temperature-dependent activity, oxygen consumption, cardiac performance, body mass and the carbon and nitrogen composition in order to (1) examine thermal effects from organismal to cellular levels, and (2) compare the thermal tolerance of larvae from two environmental temperature regimes."

The six researchers report, "the thermal tolerance window of zoea from SC was found to be shifted to lower temperatures when compared with those from CC"; that is, the thermal tolerance window of zoea from CC was found to be shifted to higher temperatures when compared with those from SC. The Chilean and German scientists conclude "the small but clear shift between thermal tolerance windows between populations suggests an optimization of reaction norms and local adaptation in larvae of *T. dentatus*," noting "this differentiation allows the species to cover a wider range of distribution than when restricted to one and the same thermal window for all populations," which suggests the larval form of the kelp crab is capable of adapting to both higher and lower temperatures than those at which it may have lived for long periods in the past.

Stoner *et al.* (2010) write, "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." They investigated 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." The authors reared RKC in "four temperature treatments ranging from 1.5 to 12°C for a period of 60 days, both individually and in low-density populations," measuring various physiological processes and properties throughout this period.

The three researchers report "temperature had no significant effect on survival of RKC," and "there was no consistent difference in survival between individually cultured crabs and those in populations." Growth, they found, "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, "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, "growth increased as an exponential function of temperature, with slightly higher growth rates observed in populations than for isolated individuals." They found "no evidence that culturing RKC juveniles at elevated temperatures led to a decrease in condition or nutritional status."

Stoner *et al.* conclude the "accelerated growth" they observed in the RKC raised at the highest temperature might have a "positive, indirect effect on survival," as "larger size associated with high temperature could provide for earlier refuge in size from the typical fish and invertebrate predators on RKC."

Van den Brink *et al.* (2012) note "hymenosomatid crabs of the genus *Halicarcinus* have a reproductive strategy involving a terminal, pubertal moult where reproduction begins only when growth has ceased." This strategy, they explain, "allows females to maximize their reproductive output during a comparatively short (approximately six month) adult life span by producing broods continuously and successively, without the need for the female to suspend reproduction for moulting," citing Van den Brink and McLay (2009, 2010). Van den Brink *et al.* investigated the effect of temperature on brood development for "three intertidal hymenosomatid crabs: *Halicarcinus cookii, H. varius* and *H. innominatus*," which they collected from intertidal habitats around the Kaikoura Peninsula of New Zealand.

The results yielded three main findings. First, "if temperatures rise 2°C as predicted, each of the three species could produce one extra brood per female lifetime," which the authors say "would result in the production of over 1000 extra larvae per female resulting in a 10-15% increase in fecundity" that could "result in a single female producing 10-50 extra surviving offspring per lifetime." Second, "an increase in temperature is also likely to increase larval growth rates ... resulting in shorter development times," which "may also increase survival rates to final instars and eventually adults, thus potentially increasing the size of the population." Third, "the current six month peak breeding season in the three Halicarcinus species may increase as temperatures rise," which "may allow the three Halicarcinus crabs more time to carry eggs and therefore produce even more offspring per lifetime." These findings indicate a modest warming would prove extremely beneficial to hymenosomatid crabs.

Kelley et al. (2011) note, "measuring variation in physiological traits over broad spatial and temporal scales in an effort to investigate the ecological impacts of these traits (Chown et al., 2004)" can "aid in predicting how species or communities will respond to climate change," citing Baker et al. (2004), Harley et al. (2006), Hassol (2004), Helmuth et al. (2002, 2005), Kennedy et al. (2002), Parmesan (2006), Parmesan and Yohe (2003), Portner et al. (2001), and Stillman (2003). Employing this approach in their study of the European green crab (Carcinus maenas), Kelley et al. measured the upper lethal thermal thresholds of two populations of the invasive species living at the southern and northern limits of its current range on the west coast of North America-Sea Drift Lagoon. Stinson Beach California (CA: 37°54'27.82"N), and Pipestem Inlet, Vancouver Island, British Columbia (BC; 49°02.3'N). The two sites are separated by 1,200 km of coastline-where "ambient sea surface temperature in the northern part of the North American west coast range is 5 to 10°C lower, depending on the time of year, than near the southern range limit." The species' expansion from its initial introduction at the south end of its range to its current northern end occurred over a period of about 20 years.

The three U.S. scientists determined the warmadapted southern CA group of crabs had the highest level of organismal thermotolerance and the greatest degree of heat shock protein 70 (Hsp70) production. They also found carapace widths of male and female *C. maenas* individuals from CA were significantly smaller than those in BC. Kelley *et al.* say these findings "provide evidence that the northeastern Pacific population of *C. maenas* has incurred a shift in thermal tolerance compared to its southern counterpart," and "thermal adaptation at the level of the phenotype is a likely cause due to the short timescale of the invasion and the genetic connectivity of the two populations."

The authors state that over just two decades "it is possible that a large, northern cold-water phenotype may have already arisen," which further suggests the reverse of this phenomenon also could have occurred over the same length of time if the driving force for phenotypic change had arisen due to the crabs migrating from a cooler to a warmer environment, or, by further inference, that it could have occurred during a period of equivalent climatic warming in the same physical setting without any relocation. This is yet another example of a species demonstrating a capacity to cope with projected global warming, without the need to migrate.

Ravaux et al. (2012) point out "all organisms possess some capacity to modify their behavioral, physiological or morphological characteristics in response to changes in environmental temperature" via a phenomenon they characterize as thermal acclimation, citing Angilletta (2009). This special case of phenotypic plasticity would be of great significance to all organisms in a warming world. Ravaux et al. studied Palaemonetes varians, a shallow-water brackish shrimp native to Western Europe, assessing both cold- and warm-acclimated specimens collected from the Bay of Mont Saint-Michel (France), the plasticity of a common index of thermal tolerance, the critical thermal maximum (CT_{max}), and the plasticity of a widespread and conserved molecular response to stress, known simply as heat shock response (HSR).

The seven scientists determined *P. varians* "shows genuine acclimation capacities" due to the plasticity inherent in the organism's thermal limit (CT_{max}) and its heat shock response (*hsp*70 induction temperature). Ravaux *et al.* conclude *P. varians* "is readily able to expand its thermal range since it can shift its thermal maximum to higher temperatures and also mobilize the HSR over a wide range of temperatures above those experienced in nature." They state the shrimp "is potentially capable of expanding its upper thermal range," which suggests it may not have to migrate toward cooler regions in a potentially warming world of the future.

Pinceel et al. (2013) studied the ability of large

branchiopod crustaceans to phenotypically adapt, constructing "a molecular phylogeny based on a data set which includes about 85% of the *Branchinella* species currently known to science, as well as a number of recently discovered lineages." They discovered "substantial physiological plasticity or important adaptive variation present in some species, potentially enabling them to better cope with environmental change."

Letessier et al. (2011) modeled the influence of a suite of physical, chemical, and biological variables on euphausiid species abundance. Euphausiids are small, pelagic, shrimplike crustaceans of the order Euphausiacea; the authors say they constitute "an important component of the pelagic realm," where they "graze directly on phytoplankton and provide a food source for a range of predators including birds, seals, baleen whales and many commercially important fish species," citing Verity et al. (2002). The authors used a generalized additive model running environmental changes based on IPCC A1B climate scenario to make predictions of future species abundance changes in the Pacific and Atlantic Oceans, which they sub-divided into cells having east-to-west lengths of 300 km and north-to-south lengths of 200 km.

Letessier et al. found "the main drivers of species abundance, in order of decreasing importance, were sea surface temperature (SST, explaining 29.53% of species variability), salinity (20.29%), longitude (-15.01%, species abundance decreased from West to East), distance to coast (10.99%) and dissolved silicate concentration (9.03%)." The three UK researchers say their results suggest "the present broad patterns apparent in species abundance (low in high latitudes, high in intermediate latitudes and intermediate in the tropics) will become less pronounced in a warming ocean," and eventually, "species abundance will be enhanced within intermediate-to-high latitudes (30°N to 60°N and 30°S to 60°S) and diminished in the tropics (20°N to 20°S)." These changes, they write, are "consistent with changes already observed to be occurring in terrestrial systems in Europe and America," citing Rosenzweig et al. (2008), and with "already-observed changes in zooplankton assemblages in the North Atlantic (i.e., communities shifting north)," as reported by Beaugrand et al. (2002), Beaugrand and Ibanez (2004), and Richardson and Schoeman (2004). Considered in their entirety, such shifts in euphausiid species abundance may be viewed as positive developments, especially in light of the three scientists' finding that both the Atlantic and Pacific

Oceans "will on average see an increase in species abundance per cell."

Rombouts *et al.* (2009) studied marine copepods—small ocean crustaceans that form a key trophic link between phytoplankton and fish. Some are planktonic and drift in sea water, but more are benthic and live on the ocean floor. Rombouts *et al.* developed the first global description of geographical variation in the diversity of marine copepods in relation to 10 environmental variables.

They found "ocean temperature was the most important explanatory factor among all environmental variables tested, accounting for 54 percent of the variation in diversity." They report "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, they write, "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 conclude, "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 has typically been found on land for birds, butterflies, and several other terrestrial lifeforms, as their ranges expand and overlap in response to global warming. With more territory thus available to them, their foothold on the planet becomes increasingly strong, fortifying them against forces (many of them humaninduced) that might otherwise lead to their extinction.

Tremblay *et al.* (2011) compared time series of ice cover, wind forcing, and satellite-based assessments of photosynthetic carbon production in the Canadian Beaufort Shelf for the years 2002–2008 with corresponding *in situ* measurements of salinity, nutrients, new production, biological stocks, and biogenic fluxes obtained during overwintering surveys of copepods in 2003–2004 and 2007–2008. The 15 researchers report that in 2007–2008, in areas where ice was no longer present, due to enhanced seasonal warming, there was significant wind-induced upwelling of growth-promoting nitrates, which were brought up from deep and dark waters into the euphotic zone, where photosynthesis occurs. As a result of this fertilization effect, the herbivorous

copepod *Calanus glacialis*—which they say is "the key link between diatom production and apex consumers on Arctic shelves," citing Soreide *et al.* (2010)—experienced a total abundance "3 to 33 times higher than in 2003 during mid-fall and 1.6 to 13 fold higher than in 2004 during early summer." On the region's central shelf, the scientists observed "sedimentary chlorophyll *a* was over 20-fold higher than at any station not influenced by upwelling," and "benthic carbon demand was among the highest ever observed in the Arctic ocean," citing Clough *et al.* (2005). They report the "repeated instances of ice ablation and upwelling during fall 2007 and summer 2008 multiplied the production of ice algae, phytoplankton, zooplankton and benthos by 2 to 6 fold."

Tremblay *et al.* conclude the phenomena they observed are "likely to prevail with the increasingly deep and frequent seaward retreat of the central ice pack and the greater incidence of upwelling-favorable winds," as described in detail by Yang (2009), and "new production is also bound to rise as winds gain in intensity and upwelling draws deeper into the nutrient-rich, upper Pacific halocline."

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6.1.4 Fish

The studies reviewed in this section examine the impact of rising temperatures on marine fish species. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Primary production increases expected to result from future greenhouse gas emissions and their IPCC-projected impacts on climate "will provide opportunities to recover overfished fisheries, increase profitability of fisheries and conserve threatened biodiversity" around Australia.
- The population of one-year-old chum salmon in the Okhotsk Sea "was less during the period from the 1940s to the mid–1970s compared to the period from the mid–1980s to the present." This result "was directly affected by warmer sea

surface temperatures associated with global warming."

- There has been a "rapid microevolution for earlier migration timing in" pink salmon in Alaska, which has allowed both the odd- and even-year groups of salmon "to remain resilient to environmental change."
- Despite having low critical thermal maximum temperatures, a geographically diverse group of 11 species of Antarctic fishes "maintained the capacity to increase their heat tolerance through warm acclimation."
- "Adult seahorses show great resilience to heat stress and are not expected to go through any physiological impairment and behavioral change with the projected near-future warming."
- "Tropical marine fishes inhabiting fringing nursery environments may have the upper thermal tolerance necessary to endure substantial increases in sea temperatures."
- Developmental plasticity in fish "may allow adaptation to changing environmental conditions to have delayed effects," and "this may attenuate some of the more severe predictions about organisms' responses to global warming and eutrophication."

Brown et al. (2010) noted "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 Cury et al. (2008). They 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. They fed those results into a suite of models for calculating primary production of lower trophic levels (phytoplankton, macroalgae, seagrass, and benthic microalgae), and they used the results of those calculations 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 under 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." They note the calculated responses "are robust to the ecosystem type and the complexity of the model used." Brown *et al.* conclude the primary production increases suggested by their work to result from 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."

Drinkwater (2006) reviewed the status of marine ecosystems of the northern North Atlantic in the early twentieth century during a regime shift, which he defined as "a persistent radical shift in typical levels of abundance or productivity of multiple important components of the marine biological community structure, occurring at multiple trophic levels and on a geographical scale that is at least regional in extent." Drinkwater reports, "in the 1920s and 1930s, there was a dramatic warming of the air and ocean temperatures in the northern North Atlantic and the high Arctic, with the largest changes occurring north of 60°N," and this warming "led to reduced ice cover in the Arctic and subarctic regions and higher sea temperatures," as well as northward shifts of multiple marine ecosystems.

The early twentieth century warming of North Atlantic waters "contributed to higher primary and secondary production," Drinkwater notes, and "with the reduced extent of ice-covered waters, more open water allow[ed] for higher production than in the colder periods." As a result, cod "spread approximately 1200 km northward along West Greenland," and "migration of 'warmer water' species also changed with earlier arrivals and later departures." Drinkwater notes, "new spawning sites were observed farther north for several species or stocks while for others the relative contribution from northern spawning sites increased." Also, "some southern species of fish that were unknown in northern areas prior to the warming event became occasional, and in some cases, frequent visitors."

Seo *et al.* (2011) note, "Pacific salmon (*Oncorhynchus* spp.) play an important role as both keystone species in North Pacific ecosystems and as an ecosystem service that provides human food resources for countries of the North Pacific rim," citing Kaeriyama (2008), and they observe the

Hokkaido chum salmon (*O. keta*) experiences a period of critical mortality "characterized by sizedependent mortality and size-selective predation, immediately after seaward migration," citing Healey (1982), Kaeriyama (1986), Kaeriyama and Ueda (1998), and Kaeriyama *et al.* (2007). To determine the effect of global warming on this critical mortality period in the life of Hokkaido chum salmon, Seo *et al.* used multiple regression and path analysis to examine the effects of regional and larger spatial scales of climatic/oceanic conditions on the growth, survival, and population dynamics of the species.

The three researchers from the Faculty of Fisheries Sciences at Japan's Hokkaido University determined growth of one-year-old chum salmon in the Okhotsk Sea "was less during the period from the 1940s to the mid–1970s compared to the period from the mid–1980s to the present," and this result "was directly affected by warmer sea surface temperatures associated with global warming." They add, "the increased growth at age one led directly to higher survival rates and indirectly to larger population sizes."

Bentley and Burgner (2011) studied juvenile sockeye salmon (*Oncorhynchus nerka*) in an Alaskan watershed that had experienced a 1.9° C increase in summer water temperature over the prior 46 years. They hypothesized the warming of the region "would have resulted in a corresponding increase in fish metabolism, and thus potential consumption rates, that would increase infestation rates of the tapeworm *Triaenophorus crassus*." They tested their hypothesis by comparing infestation rate data for *T. crassus* collected between 1948 and 1960 with similar data obtained in 2008 and 2009 from the Wood River system of Bristol Bay, Alaska.

The two U.S. researchers from the University of Washington's School of Aquatic and Fisherv Sciences say in "comparing the average summer air temperature to the parasite prevalence of juvenile sockeve salmon, we found no significant relationship over the fifteen years of collected data." They also report in "evaluating the influence of average summer air temperature on the parasite infestation rates of juvenile sockeye salmon, we again found no significant relationship for either parasite abundance or parasite intensity," and "when we compared the 13 years of historic parasite prevalence to equivalent data collected in 2008 and 2009, we did not find a statistically significant positive long-term trend in the data." Bentley and Burgner write, "the parasite abundance of examined sockeve salmon smolts also did not exhibit a statistically significant long-term

trend using the eight years of historic data and the two years of contemporary data." They report, "evaluating the relationship between time and parasite intensity produced similar results as the other five comparisons, with there not being a statistically significant positive relationship." Bentley and Burgner conclude their data demonstrate "the complex effects of warming have not summed to generate a measurable change in the infestation rates of juvenile sockeye salmon in the Wood River system."

Kovach et al. (2012) studied salmon in Auke Creek, a small lake-outlet stream near Juneau, Alaska, where there have been complete daily counts of all adult pink salmon migrating into the creek since 1971. They used "phenotypic data on migration timing, archived genetic samples and data from a marker locus, the allele frequencies of which were experimentally altered more than 30 years ago, to determine whether change in migration timing in a population of pink salmon has a genetic basis (i.e., microevolution)." The three researchers determined both even- and odd-year adult pink salmon that spawn in the warming Alaskan stream are migrating into fresh water nearly two weeks earlier than their predecessors did 40 years ago. They also found experimental data "support the hypothesis that there has been directional selection for earlier migration timing, resulting in a substantial decrease in the latemigrating phenotype (from more than 30% to less than 10% of the total abundance)." They also report, "from 1983 to 2011, there was a significant decrease—over threefold—in the frequency of a genetic marker for late-migration timing, but there were minimal changes in allele frequencies at other natural loci "

Kovach *et al.* say "these results demonstrate that there has been rapid microevolution for earlier migration timing in this population," and this has allowed both the odd- and even-year groups of salmon "to remain resilient to environmental change," as also was demonstrated by Kinnison and Hairston (2007). They note, "population abundance in 2011 was the second highest on record," further indicating the salmon of Auke Creek are "persisting through rapid temperature warming."

Aurelio *et al.* (2013) examined "the effect of environmental warming on the metabolic and behavioral ecology of a temperate seahorse, *Hippocampus guttulatus.*" They compared routine metabolic rates, thermal sensitivity, ventilation rates, food intake, and behavioral patterns at the average spring temperature (18°C), the average summer temperature (26°C), the temperature that seahorses often experience during summer heat wave events (28°C), and the temperature of a near-future warming (+2°C) scenario (= 30° C) in Portugal's Sado estuary.

The 10 scientists state "both newborn juveniles and adults showed significant increases in metabolic rates with rising temperatures," with newborn juveniles being "more impacted by future warming via metabolic depression." In addition, "in adult stages, ventilation rates also increased significantly with environmental warming, but food intake remained unchanged." They report, "the frequency of swimming, foraging, swinging, and inactivity did not significantly change between the different thermal scenarios." Aurelio et al. conclude "adult seahorses show great resilience to heat stress and are not expected to go through any physiological impairment and behavioral change with the projected near-future warming," but juveniles in their early life stages "display greater thermal sensitivity and may face greater metabolic challenges."

Bilyk and DeVries (2011) note "most animals do not have a static heat tolerance; rather it changes in response to their recent thermal history through acclimation." They continue, "given the long residence of Antarctic fishes in constant freezing seawater, this plasticity had long been thought either lost or marginal (Brett, 1970)." They say "understanding the heat tolerance of Antarctic fishes and its plasticity is critical for understanding the threat to this cold adapted fauna," especially "given the future predicted increases in water temperatures in the southern Ocean from global climate change."

Bilyk and DeVries employed the critical thermal maximum (CTMax) methodology—the temperature at which an animal loses the ability to escape from constant rapid warming (Paladino *et al.* 1980)—"to survey heat tolerance in a geographically diverse group of eleven species of Antarctic fishes acclimatized to the cold water temperatures of their natural habitats." They also used this methodology on eight of the species "following warm acclimation to 4°C, which when compared to their environmental CTMaxs provided a measure of the plasticity of their heat tolerance," as these fish "had been caught or held at temperatures below -0.9°C."

The researchers found "when acclimatized to their natural freezing water temperatures, environmental CTMaxs ranged from 11.95 to 16.17°C," and when the eight further-studied species were warmacclimated to 4°C, "all showed a significant increase over their environmental CTMaxs, with several showing plasticity comparable in magnitude to some far more eurythermal fishes." Bilyk and DeVries write, "despite their low CTMaxs, all the Antarctic species maintained the capacity to increase their heat tolerance through warm acclimation," and when this capacity was quantified, it showed "a surprising level of thermal plasticity at low temperatures," which they say was surprising "given the presumed loss of selection for thermal flexibility that has long been assumed in this fauna."

Eme *et al.* (2011) write, "temperate fishes have been considered especially vulnerable to changing climate conditions," and "increasing water temperatures may also threaten shallow-water marine fishes inhabiting nursery environments, like tropical mangroves and seagrass beds." To evaluate these hypotheses, the authors "used critical thermal methodology to quantify critical thermal maxima (CTmaxima) of juvenile squaretail mullet (*Liza vaigiensis*) and juvenile crescent terapon (*Terapon jarbua*) captured from shallow seagrass nursery areas around Hoga Island, southeast Sulawesi, Indonesia."

The three U.S. researchers report groups of mullet acclimated to a constant temperature of 37°C, as well as temperature cycles of 35-39°C or 37-41°C, all displayed statistically similar mean CTmaxima of 44.7, 44.4, and 44.8°C, respectively. They found terapon acclimated to a constant temperature of 37°C or a temperature cycle of 37-40°C both displayed mean CTmaxima of 43.8°C. Eme et al. conclude "terapon and mullet demonstrate exceptional tolerance to high temperatures," and "it seems likely that shallow-water sea surface temperatures would have to be much higher to adversely affect these and other shallow water marine fishes (Eme and Bennett, 2009)," as these "exceptionally high CTmaxima afford mullet and terapon a significant measure of protection against changing habitat conditions." The scientists write, "despite diverse independent origins across taxa, fishes may share a common suite of physiological adaptations allowing them to survive periodic exposure to high environmental temperature (Hochachka and Somero, 2002; Somero, 2010)," and "exceptional thermal tolerance may be common throughout the biodiverse shallow waters of the Indo-Pacific." They conclude, "tropical marine fishes inhabiting fringing nursery environments may have the upper thermal tolerance necessary to endure substantial increases in sea temperatures."

In a controlled laboratory experiment, Donelson *et al.* (2012) reared the offspring from eight wildcaught damselfish (*Ancanthochromis polyacanthus*) for two generations, "in present day (+0.0°C) and predicted future increased water temperatures (+1.5°C and +3.0°C) to test their capacity for metabolic acclimation to ocean warming." After three months, the authors assessed the responses in resting metabolic rate (RMR) relative to maximum metabolic rate (MMR) for each individual. They used this "metabolic performance" measure to characterize changes in the ability of each fish to perform aerobic activities (which would include functions such as behavior, growth, and reproduction) at its summer average water temperature ($+0.0^{\circ}$ C) and above ($+1.5^{\circ}$ C and $+3.0^{\circ}$ C).

The experiment revealed second-generation offspring had superior metabolic performance at all temperatures when their parents had been reared to maturity at a temperature of +1.5°C or +3.0°C. In addition, one pair of damselfish (i.e., one particular genetic lineage) contributed many more secondgeneration offspring that did well at +3.0°C than did the other wild parents: 75% of all fish that reproduced at +3.0°C were the offspring of wild pair #41. In contrast, wild pair #41 contributed 57% of offspring reproducing at +1.5°C and only 44% of those reproducing at +0.0°C. Thus, in addition to acclimation occurring within two generations, there was rapid selection of genotypes (and associated phenotypes) tolerant of higher temperatures. Donelson et al. conclude "this study provides evidence that, contrary to some expectations, a tropical marine species has the capacity for acclimation and adaptation to temperature increases over timescales much shorter than the rate of anthropogenic climate change," and "the discovery that advantageous offspring phenotypes are produced within two generations could indicate that some tropical marine species are more capable of coping with global warming than has been suggested."

Grenchik *et al.* (2013) note "tropical ectotherms are predicted to be especially sensitive to global warming because they may possess a narrow thermal tolerance range as a result of having evolved in a relatively stable thermal environment." They say having a narrow thermal tolerance range would mean "tropical species tend to live close to their thermal optimum," so "even relatively small increases in temperature could lead to declines in individual performance," because "as water temperature increases, so does the cost of maintaining basic cell function (resting metabolic rate, RMR; Bret, 1971)."

Grenchik *et al.* reared newly settled juveniles of the tropical damselfish *Pomacentrus moluccensis* for four months in four temperature treatments: currentday summer average (28.5°C) and up to 3°C above the average (29.5, 30.5, and 31.5°C). The three Australian researchers found the RMRs of fish reared at 29.5 and 31.5°C were "significantly higher than the control group reared at 28.5°C," and "fish that developed in 30.5 and 31.5°C exhibited an enhanced ability to deal with acute temperature increases." They conclude, "this study shows that there is capacity for thermal acclimation during development, with individuals reared from an early age at some temperatures able to modify their physiology to maintain RMRs at near present-day levels," and this developmental thermal acclimation "may assist coral reef fish to cope with increases in water temperature without a substantial loss to performance."

Simpson *et al.* (2011) write, "marine ecosystems in the northeast Atlantic have warmed particularly rapidly, with mean sea temperatures in the North Sea and Celtic-Biscay Shelf regions increasing between 1982 and 2006 by 1.31°C and 0.72°C, respectively," four times faster than the global average. They considered these regions and timeframe to be ideal for determining how real-world fish respond to realworld warming. The researchers "assessed the full impacts of warming on the commercially important European continental shelf fish assemblage using a data-driven Eulerian (grid-based) approach that accommodates spatial heterogeneity in ecological and environmental conditions."

They analyzed "local associations of species abundance and community diversity with climatic variables, assessing trends in 172 cells from records of >100 million individuals sampled over 1.2 million km^2 from 1980–2008." They contrasted this work with the climate envelope approach, which relies on macro-ecological analyses of the effects of climate change on marine fish assemblages that do not account for "constraints on distributional shifts due to population dependence on essential habitat, such as favored substrates, appropriate predator and prey fields, and close proximity to nursery grounds, all of which are often unknown and difficult to quantify."

The seven scientists say they discovered "responses to warming in 72% of common species, with three times more species increasing in abundance than declining." These trends were "reflected in international commercial landings," where landings of nine species identified as declining in warm conditions fell by half during the period of their study, whereas landings of 27 species identified as increasing in warm conditions rose by 2.5 times. They write, this "profound reorganization of the relative abundance of species in local communities occurred despite decadal stability in the presence-absence of species," such as would have been suggested by the climate envelope approach on a larger spatial scale. Simpson *et al.* conclude their "finding of stability in presence-absence of species over decadal periods, but significant temperature-driven responses in local species abundance and assemblage composition, suggests that climate envelope models based on species presence-absence alone will not predict the most ecologically and economically significant effects of climate change."

Lloyd et al. (2012) write, "at a broad geographical scale, species richness and diversity decrease as latitude increases both north and south of the equator," and in marine systems this distribution pattern "has been linked most consistently to variation in sea temperature," primarily via studies conducted in north-temperate seas, such as those of Fisher et al. (2008) and Hiddink and Hofstede (2008). Noting there is a paucity of such studies from the Southern Hemisphere, Lloyd et al. analyzed measurements of sea surface temperature and spear-fishing records pertaining to 84 species of marine fish personally harvested by one of their team. This analysis was performed for each day of diving over the years 1989-2007, during which time interval there was a 0.47°C increase in mean sea surface temperature, which rose from an average of 23.36°C for the period 1989–1996 to an average of 23.83°C for 2002–2007.

The five Australian researchers report over the specified time interval, "the proportion of the catch made up by temperate species, in terms of both the number and mass of fish, consistently decreased, whereas the proportion of the catch made up by tropical species consistently increased between the two time periods," and "the contribution of broadly distributed species to the overall catch remained approximately the same." In addition, "average species richness and diversity increased 33 and 15%, respectively, between the two time periods." These findings, the authors write, "are broadly consistent with a predicted poleward shift in species ranges and a predicted increase in species richness and diversity with increasing sea temperature," confirming "largescale climate change causing a widening of the tropical belt and subsequent ocean warming is having a profound impact on marine species abundance patterns and community composition at a local scale in the sub-tropics."

Capelin (*Mallotus villosus*) are small, short-lived forage fish that are the primary prey of many top predators in northern marine ecosystems. They typically spawn in one of two specific habitats with divergent temperature regimes: beach (warm, variable) and deep water (demersal: cool, stable). In recent years there has been some concern about how capelin may respond to projected global warming.

In 2009 and 2010, Davoren (2012) investigated "the influence of temperature on spawning habitat selection in coastal Newfoundland by quantifying habitat-specific temperature, population-level habitat use, and individual-level movements of male capelin via acoustic telemetry." The Canadian researcher reports "capelin spawned only at beaches in 2009. when temperatures were significantly colder and frequently fell below suitable ranges at demersal sites, whereas demersal sites were predominantly used under opposing conditions in 2010." She remarks "males detected in both habitats primarily dispersed from the initial habitat when temperatures routinely fell outside of suitable ranges," noting "this movement often involved traveling long distances (11.0-32.7 km) against currents, suggesting energetic costs."

Davoren writes, "overall, temperature appeared to be an important environmental cue for habitat selection by capelin," and she concludes, "the flexible use of spawning habitats under divergent temperature conditions suggests that capelin have a high capacity to respond to and possibly tolerate predicted oceanclimate change."

Zambonino-Infante et al. (2013) note rising temperatures typically cause "a monotonic decrease in dissolved oxygen concentration in numerous coastal and estuarine ecosystems around the world, resulting in the increased frequency, intensity and length of hypoxia episodes in shallow areas," with a primary consequence of these phenomena being the progressive widening of the gap between the availability of dissolved oxygen in the coastal water and the metabolic demand of various marine animals. Zambonino-Infante *et al.* studied the common sole (Solea solea), which inhabits shallow marine areas highly exposed to environmental changes, to see "whether temperature and trophic conditions experienced during the larval stage had delayed effects on life-history traits and resistance to hypoxia at the juvenile state," thereby examining "the combined effect of global warming and hypoxia in coastal waters, which are potential stressors to many estuarine and coastal marine fishes."

Their analysis showed "warmer larval temperature had a delayed positive effect on body mass and resistance to hypoxia at the juvenile stage," which "suggests a lower oxygen demand of individuals that had experienced elevated temperatures during larval stages." Zambonino-Infante *et al.* say "this study clearly demonstrates that environmental conditions experienced during early developmental

stages are important in controlling environmental adaptation performance at later life stages." They state "sole that had experienced elevated temperatures during their early-life exhibited higher body masses and tolerance to hypoxia, probably through long-term programming of metabolic pathways," noting "such a cohort effect on growth performance and hypoxia tolerance could have major implications for population dynamics." They conclude, "developmental plasticity in animals may allow adaptation to changing environmental conditions to have delayed effects," and "this may attenuate some of the more severe predictions about organisms' responses to global warming and eutrophication."

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6.1.5 Other Marine Species

In studying the impact of rising temperature on other marine species, researchers have made some important findings that challenge the projections of IPCC on this matter. As listed in the bullet points below and discussed further in the body of this section, such findings include:

- Single environmental metrics, such as air temperature, are not sufficient for making projections of the impacts of climate change.
- Caution should be applied when interpreting results from laboratory-based studies, which are often incapable of mimicking conditions in the real world and often yield results quite different from those observed in nature.
- Warmer temperatures capable of reducing sea ice density and cover reduce the risk of narwhal mortality.
- Intertidal marine species along Australia's east coast have easily withstood a significant climatic warming of ~1.5°C over the past 60 years without having to migrate poleward.
- Thermal heterogeneity within marine habitats must be fully understood in order to properly interpret and ascribe patterns of biogeographic response to climate change.
- Offspring of female turtles grew larger and survived better at hotter incubation. The increased heat tolerance appears to be genetically based.

Helmuth et al. (2011) note "virtually every physiological process is affected by the temperature of an organism's body, and ... with the advent of new molecular and biochemical techniques for studying organismal responses to thermal stress ... there has been a renewed interest in the effects of temperature extremes on the ecology and physiology of organisms given the observed and forecasted impacts of global climate change." Using a simple heat budget model that was ground-truthed with approximately five years of in situ temperature data obtained by biomimetic sensors, Helmuth et al. (2011) "explored the sensitivity of aerial (low tide) mussel body temperature at three tidal elevations to changes in air temperature, solar radiation, wind speed, wave height, and the timing of low tide at a site in central California USA (Bodega Bay)."

The six U.S. scientists found "while increases in air temperature and solar radiation can significantly alter the risk of exposure to stressful conditions, especially at upper intertidal elevations, patterns of risk can be substantially reduced by convective cooling such that even moderate increases in mean wind speed (\sim 1 m/sec) can theoretically counteract the effects of substantial (2.5°C) increases in air temperature." They also found "shifts in the timing of low tide (+1 hour), such as occur [when] moving to different locations along the coast of California, can have very large impacts on sensitivity to increases in air temperature," noting, "depending on the timing of low tide, at some sites increases in air temperature will primarily affect animals in the upper intertidal zone, while at other sites animals will be affected across all tidal elevations." In addition, "body temperatures are not always elevated even when low tide air temperatures are extreme," due to "the combined effects of convective cooling and wave splash."

Helmuth *et al.* say their findings suggest the timing and magnitude of organismal warming "will be highly variable at coastal sites, and can be driven to a large extent by local oceanographic and meteorological processes." They "strongly caution against the use of single environmental metrics such as air temperature" for "making projections of the impacts of climate change." Moreover, caution should be applied in interpreting the findings of laboratory-based studies, which often do not mimic conditions in the real world and therefore can yield results and implications quite different from those observed in the real world.

Byrne et al. (2011) studied the thermotolerance of the planktonic life phase of sea urchin Heliocidaris erythrogramma along the southeast coast of Australia, where sea surface temperatures (SSTs) have risen by 2.3°C over the past 60 years. They employed experimental treatments ranging from 18 to 26°C, with the latter value representing a 3 to 4°C increase above recent ambient SSTs. They found "development success across all stages (gastrula, 24 h; larva, 72 h; juvenile, 120 h) decreased with increasing temperature," and they acknowledge "significant deleterious effects were evident at +3 to 4°C." They also report, "larvae that developed through the early bottleneck of normal development at 26°C metamorphosed successfully," and there was a 25% decrease in planktonic larval duration (PLD) of the larvae in the highest of the temperature treatments. In parallel studies of progeny derived from the northern and southern parts of the coastline, they found "northern embryos had significantly higher thermotolerance."

The five researchers say ocean warming may be advantageous to *H. erythrogramma* larvae "through early settlement and reduction of the vulnerable planktonic period." They also state the higher thermotolerance of the species' northern embryos "provides the possibility that *H. erythrogramma* populations might keep up with a warming world through poleward migration of thermotolerant propagules, facilitated by the strong southward flow of the East Australian Current." They conclude "due to its extensive latitudinal distribution, its potential developmental thermotolerance and independence of its lecithotrophic larvae from exogenous food and the need to make a functional skeleton, *H. erythrogramma* may be particularly robust to ocean change."

Laidre and Heide-Jorgensen (2005) used a combination of long-term satellite tracking data, climate data, and remotely sensed sea ice concentrations to detect localized habitat trends of the narwhal (Monodon monoceros) in Baffin Bay between Greenland and Canada-which is home to the largest numbers of the world's narwhals-to study the species' vulnerability to ongoing and projected climate change. The two researchers write, "since 1970, the climate in West Greenland has cooled, reflected in both oceanographic and biological conditions (Hanna and Cappelen, 2003)," with the result "Baffin Bay and Davis Strait display strong significant increasing trends in ice concentrations and extent, as high as 7.5% per decade between 1979 and 1996, with comparable increases detected back to 1953 (Parkinson et al., 1999; Deser et al., 2000; Parkinson, 2000a,b; Parkinson and Cavalieri, 2002; Stern and Heide-Jorgensen, 2003)."

Laidre and Heide-Jorgensen report, "cetacean occurrence is generally negatively correlated with dense or complete ice cover due to the need to breathe at the surface," and "lacking the ability to break holes in the ice," narwhals are vulnerable to reductions in open water availability, as has been demonstrated by ice entrapment events "where hundreds of narwhals died during rapid sea ice formation caused by sudden cold periods (Siegstad and Heide-Jorgensen, 1994; Heide-Jorgensen et al., 2002)." These events are becoming more likely as temperatures continue to decline and sea ice cover and variability increase; the researchers found the latter two trends to be "highly significant at or above the 95% confidence level." They conclude, "with the evidence of changes in sea ice conditions that could impact foraging, prey availability, and of utmost importance, access to the surface to breathe, it is unclear how narwhal subpopulations will fare in light of changes in the high Arctic." Clearly, warmer temperatures capable of reducing sea ice cover would benefit narwhals, making them less vulnerable to death from the cold.

Poloczanska *et al.* (2011) resurveyed a historical census of rocky-shore marine fauna that had been conducted in the 1940s and 1950s, to ascertain whether there had been subsequent latitudinal

changes in the distribution and abundance of intertidal marine species consistent with global climate change along Australia's east coast, which, as they demonstrate, "has undergone rapid warming, with increases in temperature of ~1.5°C over the past 60 years." Their survey was conducted at 22 rocky-shore sites located between 23 and 35°S latitude, stretching across 1,500 km of coastline.

Of the 37 species the authors encountered that had distributional data available from both time periods, "only six species showed poleward shifts consistent with predictions of global climate change." Four others moved in the opposite direction "inconsistent with expectations under climate change," and the rest "showed no significant changes in range edges." The seven scientists state a combination of wave exposure, local currents, and the presence of factor influencing primary biogeographic distributions along the subtropical east coast of Australia."

The contemporaneous study of Seabra et al. (2011) supports this conclusion, describing how intertidal marine species can easily withstand significant climatic warming without having to migrate poleward. They examined the relative magnitudes of local-scale versus large-scale latitudinal patterns of the intertidal body temperatures of robolimpets (Lima and Wethey, 2009): autonomous temperature sensor/ loggers mimicking the visual aspect and temperature trajectories of real limpets. These temperatures were measured at 30-minute intervals for recurring periods of 170 days at 13 exposed or moderately exposed rocky shores along 1,500 km of the Atlantic coast of the Iberian Peninsula, where they were attached to steep rocky surfaces—both north-facing (typically shaded) and south-facing (sun-exposed)-at three tidal heights covering the entire vertical range inhabited by real-life limpets.

The "most relevant finding" of the study, the four researchers write, was "sunny versus shaded differences were consistently larger than the variability associated with [a] the seasons, [b] shore-specific characteristics (topography, orientation, wave exposure, etc.) and [c] shore level." Seabra *et al.* say these findings emphasize the importance of analyzing temperature variability at scales relevant to the organisms being studied, "since the usage of sea surface temperature (SST) derived from remotely sensed data to model the distribution of intertidal species may be missing key environmental features," especially since their results "clearly show that other factors than SST play a much stronger role in determining the body temperatures of these organisms." They also suggest "the observed temperature variability may explain the weak correlations found in many studies modeling the distribution of intertidal species using SST data (e.g. Lima *et al.*, 2007b), which negatively impacts attempts of forecasting distributional changes in response to predicted climate warming."

Seabra *et al.* further state "habitat heterogeneity as determined by surface orientation and, to a lesser extent, height on the shore may provide thermal refugia allowing species to occupy habitats apparently inhospitable when considering only average temperatures," and "this may be important for understanding range shifts contrary to global warming predictions (e.g. Lima *et al.*, 2007a, 2009; Hilbish *et al.*, 2010)." Thus, they emphasize again "thermal heterogeneity within habitats must be fully understood in order to interpret patterns of biogeographic response to climate change."

Webster *et al.* (2011) note sponges comprise a major component of coral reef macrofauna and play key ecological roles, including providing habitat for other invertebrates and complex microbial symbioses, citing Bell (2008). Concerned that projected increases in air and sea surface temperatures of up to 4° C by 2100, as suggested in IPCC (2007) report, will have a direct and significant impact on sponges and their holobionts, Webster *et al.* "assessed the effect of elevated seawater temperature on bacterial communities in larvae of the Great Barrier Reef sponge, *Rhopaloeides odorabile*," in a series of laboratory experiments to "compare the thermal thresholds for the different life history phases of this model sponge species."

Although R. odorabile adults were previously observed to experience significant negative repercussions above 32°C, the four researchers found their larvae exhibited "a markedly higher thermal tolerance," with no adverse effects detected at temperatures up to 36°C, and their microbial communities "were conserved at temperatures up to 34°C." The Australian scientists state, "we demonstrated that sponge larvae maintain highly stable symbioses at seawater temperatures exceeding those that are predicted under current climate change scenarios." Given the likelihood both the sponge and its holobionts would experience considerable adaptive evolution between now and the end of the twenty-first century, it is safe to say predicted global warming would have little or no impact on their survival and normal functioning.

Weber et al. (2012) note, "temperature has a

profound effect on hatching success, embryonic development and sex in marine turtles," and these effects have logically led to "growing concerns regarding the impacts of climate warming on their reproductive success." Weber et al. tested for "local adaptation in an island-nesting population of green (Chelonia mydas) where incubation turtles temperatures vary dramatically among closely adjacent nesting beaches," one with pale sand (Long Beach, LB) and one with dark sand (Northeast Bay, NEB) that was consistently 2–3°C warmer than the pale sand beach only 6 km away. They employed "a combination of in situ and common-garden approaches to compare survival (as a measure of fitness), developmental rates and size at hatching for offspring of LB and NEB females at different incubation temperatures, while simultaneously accounting for egg-mediated maternal effects."

The six scientists report the offspring of female turtles nesting on the naturally hot (black sand) beach "survived better and grew larger at hot incubation temperatures" compared with the offspring of females nesting on the cooler (pale sand) beach. These differences, they write, were caused by "shallower thermal reaction norms in the hot beach population, rather than shifts in thermal optima, and could not be explained by egg-mediated maternal effects." They conclude "the results of the common-garden experiment suggest that the increased heat-tolerance of NEB turtles has a genetic basis."

Weber *et al.* also say their results suggest "marine turtle nesting behavior can drive adaptive differentiation at remarkably fine spatial scales," and "previous studies may have underestimated the extent of adaptive structuring in marine turtle populations that may significantly affect their capacity to respond to environmental change." They conclude, whereas "global warming is predicted to have multiple deleterious effects on the reproductive success of marine turtles, including the loss of nesting beaches to rising sea levels, increasingly feminized populations and reduced hatching success," their results suggest "in at least one of these respects, marine turtles have the capacity to adapt to warmer temperatures."

Doonan *et al.* (2012) write, *"Katharina tunicata*, commonly known as the Black Katy Chiton, is an abundant intertidal grazer with a limited pelagic larval stage of approximately six days (Paine, 1992)," which is distributed along the Pacific coast of North America from Alaska's Aleutian Islands to southern California, where it is "an important regulator of intertidal ecosystems." They say the species "has recently suffered declines in localized parts of its
range as a result of exploitation by humans and sea otters." Noting it is also "under threat from the effects of climate change," they sought to determine "whether local-scale barriers to gene flow could potentially compromise the dispersal capacity of the species in the face of climate change." They "used nuclear single-nucleotide polymorphisms and mitochrondrial DNA sequencing to elucidate fine-scale patterns of genetic variation between populations of the Black Katy Chiton separated by 15–150 km in southwest Vancouver Island."

The four UK researchers from Queen's University in Belfast report, "both the nuclear and mitochondrial data sets revealed no genetic differentiation between the populations studied," and "an isolation-with-migration analysis indicated extensive local-scale gene flow, suggesting an absence of barriers to dispersal." They write, "population demographic analysis also revealed long-term population stability through previous periods of climate change associated with the Pleistocene glaciations," and at the Pleistocene-Holocene transition of approximately ten thousand years ago, as discussed by Fields et al. (1993). Doonan et al. conclude, "taken together, the current evidence of high dispersal and a lack of biogeographic barriers to gene flow, coupled with the signature of long-term population stability through previous periods of climate change, suggest that this dispersal potential may act as a lifeline for K. tunicata as their southerly habitats rapidly warm, and a poleward migration is required for survival," citing Graham et al. (2010).

In an ecosystem-level study, Stuart-Smith *et al.* (2010) state, "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." They undertook "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, they write, "has experienced relatively rapid warming during the last century as a consequence of a strengthening of the warm East Australian Current (Ridgway, 2007)," which manifested "an increase in sea surface temperature of 2.28 \pm 0.35°C per century for the period 1944–2002 (Ridgway, 2007), which is considerably more rapid than the global mean of 0.6 \pm 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 the global mean, making this region a prime location to examine the impacts of rising temperature on marine species in the real world.

Contrary to their expectations, the four researchers discovered "Tasmanian shallow rocky reef communities have been relative stable over the past decade," despite 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 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."

Poloczanska *et al.* (2013) "investigated the peerreviewed literature that addresses the question of whether or not climate change impacts marine ecological phenomena, and found 208 studies of 857 species and assemblages." From these reports they extracted "1,735 observations of the following types of response: distribution, phenology, abundance, community change, calcification and demography," for which "either regional or global climate change was considered as a driver."

The 20 researchers report, "from this database, 81–83% of all observations for distribution, phenology, community composition, abundance, demography and calcification across taxa and ocean basins were consistent with the expected impacts of climate change." They add, "of the species responding to climate change, rates of distribution shifts were, on average, consistent with those required to track ocean surface temperature changes." The findings of this massive review of the relevant scientific literature indicate Earth's marine life is well-equipped to deal with predicted changes in the global ocean environment and are, in fact, already doing so.

Linares *et al.* (2013) note, "several studies have provided evidence that thermal stress affects the growth, survival and physiology of tropical and temperate macro-invertebrate species," but "few studies have focused on sub-tidal temperate species and the potential differential thermal tolerances of populations dwelling under contrasting temperature conditions." Linares *et al.* assessed "the role that environmental history plays in the response of the temperate gorgonian *Eunicella singularis* to thermal stress," comparing populations dwelling in the coldest and warmest areas of the NW Mediterranean Sea.

The four researchers report, "*E. singularis* populations from both areas exhibited a high resistance to thermal stress," but "populations from warmer areas had an increased tolerance to thermal stress," such that "the upper thermal limits found for cold and warm populations were 28 and 29°C, respectively." Linares *et al.* conclude by noting their results "agree with results for other Mediterranean anthozoans (Rodolfo-Metalpa *et al.* 2006; Torrents *et al.*, 2008) and tropical corals (Middlebrook *et al.*, 2008), demonstrating thereby that shallow populations) have a higher tolerance to thermal stress than deep populations."

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6.2 Freshwater Warming

The vast majority of studies examining the potential effects of CO_2 -induced global warming on aquatic life are focused on marine life, but some scientists have conducted research on the impacts of elevated temperature on freshwater species. The following bulleted key findings indicate the cautious optimism this research suggests, and the findings are discussed in greater detail thereafter.

- Increases in water temperature at Lake Zurich from 1977 to 2008 have resulted in an increase in the number of phytoplankton species and phytoplankton families.
- Annual bass growth is positively and significantly correlated with annual temperature metrics, revealing above-average growth during the warmest and driest years.
- Golden perch growth rates likely will increase in

southerly Australian populations due to warmer temperatures and a lengthening of the growing season.

- Over the past two decades, when IPCC claims Earth warmed at a rate and to a degree unprecedented over the past millennium, the majority of French fish—plus some newcomers to the country's streams and rivers—thrived under warmer water conditions, increasing in both species numbers (diversity) and population size.
- Many predictions of the impact of climate change on aquatic life assume a species-specific response to changing environments, yet substantial differences in thermal plasticity have been observed between populations within species, enabling some populations to cope effectively with changes in the environment that other populations cannot tolerate. The probability of climate-induced species extinctions is much lower than what is often projected.
- Three species of freshwater mussels can adjust their individual critical thermal maximum (the upper temperature at which the onset of behavioral incapacitation occurs) upwards in response to periodic heat waves or significantly warmer years.

In contrast to IPCC-based projections, modest warming has been shown to be highly beneficial to some freshwater species.

Pomati et al. (2012) explain that among human impacts on aquatic biodiversity, eutrophication has caused a number of undesirable environmental effects worldwide, including "a general reduction in species richness (Smith and Schindler, 2009) and a loss of ecosystem resilience against further degradation (Folke et al., 2004)." They indicate "lake restoration programs in many regions started at the peak of the eutrophication period (late 1970s, early 1980s)," but the resulting reduction in nutrient loading "coincided with rising temperature from climate warming," citing Van Donk et al. (2003) and Jeppesen et al. (2005), so we currently have "limited understanding of how combined climate change and reduction in nutrients affect species richness, ecosystem functioning or resilience."

Pomati *et al.* analyzed physical and biological parameters in Lake Zurich on the Swiss Plateau just north of the Swiss Alps at depths of 0, 1, 2.5, 5, 7.5, 10, 12.5, 15, 20, 30, 40, 80, 120, and 135 meters that had been collected monthly over a number of decades

by the Zurich Water Supply Company, focusing on data from 1977 to 2008. The five scientists discovered increases in water temperature (0.24°C/decade at the lake surface; 0.13°C/decade near the lake bottom) and spatial (depth) heterogeneity were the best predictors of phytoplankton richness, as the number of phytoplankton species increased from about 40 to 100 and the number of phytoplankton families increased from approximately 25 to 45. They note phytoplankton richness and spatial heterogeneity had the strongest effects on zooplankton richness.

The researchers write, "our analysis highlights that climate warming and re-oligotrophication may favor an increase in spatial (depth) heterogeneity in the water column of deep lakes, enhancing the potential for phytoplankton species co-existence and an increase in plankton richness." They conclude, "although our study focuses on a single lake, the responses we have documented may be common at least throughout lakes within the European peri-alpine climatic region," citing Buergi and Stadelmann (2002), Buergi *et al.* (2003), and Anneville *et al.* (2005).

Morrongiello et al. (2011) analyzed the yearly growth increments laid down in the otolithsaragonite (CaCO₃) structures in fish that are used for acoustic perception and balance, also known as earstones-of populations of a native fish species (the golden perch) living in two artificial impoundments (Lakes Mokoan and Eppalock) near their southerly distribution limits in central Victoria, Australia. Over a 15-year period that both predated and encompassed a significant supra-seasonal drought, the authors determined "fish growth declined as water levels in the lakes dropped during the drought," but "this effect was offset by increased growth in warmer years." It was in fact more than offset; based on the relationships they found in their data, future projections of mean annual growth of two-year-old golden perch in Lakes Mokoan and Eppalock in the year 2070, respectively, increase by 14.9% and 17.2% under low CO_2 emission and 56.5% and 58.6% under high CO_2 emission scenarios compared with 1990 CO₂ levels. The Australian scientists conclude, "despite climatic models predicting significant declines in future water availability, fish growth may increase due to a disproportionate lengthening of the growing season." They forecast "golden perch growth rates in southerly [Australian] populations may increase as warmer conditions associated with climate change will lengthen the growing season and make these high [southern] latitude habitats more favorable."

Rypel (2009) applied tree-ring techniques to the

otoliths of 397 largemouth bass (Micropterus salmoides Lacepede) to explore potential relationships between annual bass growth and various climate metrics in the southeastern USA, as manifest in six rivers and seven reservoirs in Georgia, Alabama, and Mississippi sampled during the summers and autumns of 2005–2008. 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 "aboveaverage during the warmest, driest years, and belowaverage 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."

These findings indicate the warming and drying that are predicted by models to occur in many places will benefit largemouth bass because an increase in temperature generally "stimulates metabolism, and enhances growth rates of fishes," Rypel writes, citing Beitinger and Fitzpatrick (1979) and Brander (1995).

Poulet et al. (2011) write, "over the past 200 years, owing to the industrial and agricultural revolutions, various new and intense pressures have been applied to freshwater ecosystems resulting in the decline of many species both in range and number (Maitland, 1995)." Of these additional threats, they highlight five: overexploitation, water pollution, flow modification, destruction or degradation of habitat, and invasion by exotic species, citing Dudgeon et al. (2006). Poulet et al. used the extensive electrofishing database of the French National Agency for Water and Aquatic Environment to evaluate time trends of 48 freshwater fish taxa at 590 sites across France over the period 1990-2009, to assess the recent and ongoing net impact of these modern threats to the fish of France.

The three French researchers found "species richness increased steadily from the beginning of the monitoring period," and "the number of species displaying a significant increase in spatial distribution or abundance was greater than those showing a significant decrease." They write, "these results are in agreement with recent findings which describe an increase in the number of species and density of fish communities in large French rivers over the past 25 years," citing Daufresne and Boet (2007). They add, "predictions about the future distribution of 30 common fish species in French streams in 2008, suggested increases in local species richness and in occurrences of the majority of species (Buisson *et al.*,

2008)," and they note "both studies described population growth of warm and cool water species in response to global warming."

Over the past two decades, when IPCC claims Earth warmed at a rate and to a degree unprecedented over the past millennium or two, the majority of French fish, plus some newcomers to the country's streams and rivers, thrived under warmer water conditions, increasing in both species numbers (diversity) and population size.

While not all aquatic species may respond in such a positive manner, there is little reason to accept IPCC's model-based projections of widespread future species decline (and possible extinctions) in response to CO_2 -induced global warming. A growing body of evidence demonstrates the ability of aquatic life to adapt and evolve to overcome challenges imposed by rising water temperatures.

Seebacher *et al.* (2012) note "within-individual plasticity (acclimation) counteracts potentially negative physiological effects resulting from environmental changes and thereby maintains fitness across a broad range of environments." They write, "the capacity for the acclimation of individuals may therefore determine the persistence of populations in variable environments."

They "determined phylogenetic relationships by Amplified Fragment Length Polymorphism (AFLP) analysis of six populations of mosquitofish (Gambusia holbrooki) from coastal and mountain environments and compared their capacity for thermal acclimation." The six scientists demonstrated mosquitofish populations "are divided into distinct genetic lineages and that populations within lineages have distinct genetic identities." They report, "there were significant differences in the capacity for acclimation between traits (swimming performance, citrate synthase and lactate dehydrogenase activities). between lineages, and between populations within lineages," demonstrating "there can be substantial variation in thermal plasticity between populations within species." They conclude "similar responses are likely to be found in other species that comprise structured populations."

Noting "many predictions of the impact of climate change on biodiversity assume a species-specific response to changing environments," Seebacher *et al.* argue, "this resolution can be too coarse and ... analysis of the impacts of climate change and other environmental variability should be resolved to a population level," because their findings suggest some populations of a species may be able to cope with a change of climate with which others cannot,

thereby preventing the otherwise-inevitable climateinduced extinction of the species.

Gailbraith et al. (2012) studied thermal adaptation of three species of freshwater mussels (Alasmidonta varicosa, Elliptio complanata, and Strophitus undulatus) that had been acclimatized to a water temperature of either 15 or 25°C. The temperature of the water in which the mussels were immersed was gradually raised at a rate of 0.35°C per minute, until the researchers observed the onset of extreme gaping, a periodic valve movement resulting in the rapid opening and closing of the mussels' shells that indicates their impending demise. The authors thus studied the mussels' critical thermal maximum (CTM), defined as the upper (warm) temperature at which the onset of behavioral incapacitation (usually loss of equilibrium) occurs-in the words of Gailbraith et al. quoting Hutchison (1961)—"the animal loses its ability to escape from conditions that will promptly lead to its death." Although it sounds like a fixed, immutable value for a given species, the CTM has been proven to be a function of temperature itself.

The three U.S. researchers report, "responses varied by species, but mussels acclimated to 25°C generally had a higher CTM than mussels acclimated to 15°C." For one of the three species (*E. complanata*), they observed the effects of acclimation and another variable (aeration) were interactive, leading them to conclude "combinations of environmental stressors may influence thermal tolerance" and "such responses vary among species." They note results similar to theirs "are well documented for other freshwater organisms, particularly for fish (Becker and Genoway, 1979; Elliott, 1981) but also for the zebra mussel, *Dreissena polymorpha* (McMahon and Ussery, 1995; Lutterschmidt and Hutchison, 1997)."

Although multiple factors may thus come into play in determining an animal's current CTM, it is evident from the results of Galbraith *et al.* that some degree of warming above that species-specific value can at times lead to a longer-term increase in the species' CTM. In the case of global warming, the evidence suggests species may adjust their individual CTMs upward in response to periodic heat waves or significantly warmer years.

Crozier *et al.* (2011) note "environmental change can shift the phenotype of an organism through either evolutionary or non-genetic processes," but "despite abundant evidence of phenotypic change in response to recent climate change, we typically lack sufficient genetic data to identify the role of evolution." They studied the potential role of rapid evolution by investigating the drivers of a long-term trend toward earlier upstream migration date in adult sockeye salmon (Oncorhynchus nerka Walbaum) that currently migrate up the Columbia River 10.3 days earlier than they did in the 1940s. Noting water temperature records in the lower river showed a rise of 2.6°C in mean July temperature since 1949, the researchers "developed a functional model relating survival during upstream migration to temperature on the basis of the results of recent studies that tracked individual fish through the migration," after which they "hindcast this function over the historical record to estimate the putative selection differential over the time series." Thereafter, they "assembled a set of possible environmental drivers of interannual variation in migration timing from the literature" and used "a state-space modeling framework to combine selection and these environmental variables as covariates to explain mean population migration date in a formal time-series analysis," employing "modelselection techniques to determine which factors best predicted annual migration timing."

The three researchers from the Northwest Fisheries Science Center in Seattle, Washington (USA) determined "an evolutionary response to thermal selection was capable of explaining up to two-thirds of the phenotypic trend" they observed, and "adaptive plastic responses to June river flow explain most of the remainder." Crozier et al. note the amount of evolutionary change they calculated to have taken place "is typical of numerous studies of contemporary evolution," citing Hendry and Kinnison (1999) and Kingsolver et al. (2001). They suggest evolutionary change "will play an important role in protecting species from extinction during ongoing climate change, as demonstrated in recent simulations of evolution in Fraser River sockeye salmon," citing Reed et al. (2011). They conclude. "directional environmental changes are very likely to induce more rapid evolution in the future."

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6.3 Ocean "Acidification"

6.3.1 Introduction

As the air's CO_2 content rises in response to increasing anthropogenic CO_2 emissions, more CO_2 dissolves in the surface waters of the world's oceans. Theoretical reasoning, some of it reviewed in Section

6.3.1.2 below, suggests the pH values—a negative or inverse measure of the acidity of water—of the planet's oceanic waters should be gradually decreasing.

By some estimates, the globe's seawater has declined by about 0.1 pH unit relative to what it was in preindustrial times, and model calculations imply there could be an additional drop somewhere in the neighborhood of 0.3 to 0.7 pH by the year 2300. IPCC and others refer to this small potential change in oceanic pH and its presumed impacts on aquatic life as "ocean acidification." That term, however, is misleading and deceptive. The world's oceans are currently basic (or alkaline), with an average pH of around 8.1, and there is no chance future anthropogenic CO₂ emissions will ever cause the oceans to become acidic

(pH less than 7). The general public, not scientifically trained, naturally interprets the phrase literally and assumes rising atmospheric CO_2 is turning the world's oceans, lakes, and streams into a dangerous acid that is harming (or will harm) marine life.

IPCC characterizes the projected pH reduction as a cause for great concern, because it has been postulated to harm calcifying marine life such as corals, not only by reducing the calcifying rates of marine organisms but also by impeding the responses of other growth and developmental parameters of these organisms. The ocean chemistry aspect of this ocean acidification hypothesis is rather straightforward, but it is not as solid as model projections make it out to be. Some researchers, including Pieter

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Tans, senior scientist at the National Oceanic and Atmospheric Administration (NOAA) Earth System Research Laboratory in Boulder, Colorado (USA), have published papers suggesting the drop in oceanic pH will not be nearly as great as IPCC and others predict. Figures 6.3.1.1 and 6.3.1.2 illustrate Tans' analysis.

The first of the two figures depicts much of the past and projected history of fossil-fuel carbon utilization, together with historical and projected atmospheric CO₂ concentrations to the year 2500, as calculated by Tans (2009). As the figure shows, the air's CO₂ concentration is expected to peak well before 2100 and at only 500 ppm, as compared to the 800 ppm predicted in one of IPCC's scenarios. It is



Figure 6.3.1.1. Past and projected trends of fossil-fuel carbon utilization and the atmosphere's CO₂ concentration. Adapted from Tans (2009).

also worth noting that by the year 2500, the air's CO_2 concentration should actually drop back to about what it is today.

When these emission estimates are calculated for their expected reductions of oceanic pH, as shown in Figure 6.3.1.2, the projected pH change at 2100 is far below what IPCC estimates. The pH projections from Tans' data also suggest a recovery to values near those of today by the year 2500, a striking contradiction of IPCC's estimates. (Tans' research is described in more detail in the next section.)

The increase of CO_2 in the air should lead to additional weathering of terrestrial carbonates and dissolution of marine carbonates, which would increase delivery of Ca^{2+} and CO_3^{2-} to the oceans and largely compensate for the CO_2 -induced decrease in



Figure 6.3.1.2. Past and projected trends of oceanic pH based on fossil-fuel carbon utilization estimates from Tans (2009) and IPCC's A2 scenario.

oceanic calcium carbonate saturation, further suggesting IPCC's projections of ocean acidification may be exaggerated. In addition, as with all phenomena involving living organisms, the introduction of life into the ocean acidification picture greatly complicates things, as several interrelated biological phenomena must be considered; when they are, it becomes much more difficult to draw such sweeping negative conclusions as IPCC does.

As the research reviewed in the subsections below demonstrates, the rising CO_2 content of Earth's atmosphere may be a beneficial phenomenon with many positive consequences for the oceans as well as other aspects of the environment (Idso, 2009).

Before proceeding into those specifics, however, we provide a brief discussion of changes in oceanic pH, followed by some additional considerations of ocean chemistry.

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6.3.1.1 Assessing and Projecting Changes in Oceanic pH

Based on four theoretical constructs-a geochemical model, an ocean general-circulation model, an IPCC CO₂ emissions scenario for the twenty-first century, and a projected logistic function for the burning of Earth's post-twenty-first century fossil-fuel reserves -Caldeira and Wickett (2003) calculated the atmospheric CO₂ concentration could approach 2,000 ppm around the year 2300, leading to a surface seawater pH reduction of 0.7 unit, a change they describe as being much more rapid and considerably greater "than any experienced in the past 300 million years." This long time interval makes the phenomenon sound truly catastrophic, especially as IPCC claims this "ocean acidification" phenomenon will impede the process of calcification in corals and other marine life. In judging the plausibility of this scenario, it is important first to know whether the acidification phenomenon is really severe and unprecedented.

In a special issue of Oceanography published in December 2009, Feely et al. (2009) review what is known about the current pH status of the world's oceans and what can likely be expected by the end of the current century. The three researchers write, "estimates based on the Intergovernmental Panel on Climate Change business-as-usual emission scenarios suggest that atmospheric CO₂ 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 preindustrial value of about 8.2 to about 7.8 in IPCC A2 scenario by the end of this century." They warn, as a result, "the skeletal growth rates of calcium-secreting organisms will be reduced" and conclude, "if anthropogenic CO₂ emissions are not dramatically reduced in the coming decades, there is the potential for direct and profound impacts on our living marine ecosystems."

In the same issue of *Oceanography*, Tans (2009) presents a much different take on the subject. He begins by noting the anthropogenic component of the air's CO_2 concentration "depends primarily on the total amount emitted, not on the rate of emissions,"

and "unfortunately, 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 CO₂."

"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 gigatons of carbon (GtC), and 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.

The past and projected history of fossil-fuel carbon utilization, together with historical and projected atmospheric CO₂ concentrations out to the year 2500, as calculated by Tans, is presented in Figure 6.3.1.1 above. According to the data presented there, Tans shows the air's CO₂ concentration peaking well before 2100 at only 500 ppm, as compared to the 800 ppm Feely *et al.* take from IPCC. By the year 2500, the air's CO₂ concentration drops back to about what it is today, according to Tans' analysis.

Based on his more modest projections of future atmospheric CO₂ concentrations, Tans finds the projected pH reduction of ocean waters in the year 2100 to be only one-half of the 0.4 value calculated by Feely et al., with a recovery to a reduction of slightly more than 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.). Graphical data presented by Pelejero et al. (2010) depict 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 years 1984 to 2007 (Bates, 2007), further demonstrating large pH variations are occurring in some ocean basins as a result of seasonal seawater 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). 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). These natural and recurring pH declines (0.50 and 0.54) are greater than the 0.3 to 0.4 decline IPCC expects to occur between now and the end of the century, and much greater than Tans' estimate of about 0.2.

Hofmann *et al.* (2011) state "natural variability in pH is seldom considered when effects of ocean acidification are considered," and they suggest this omission is disturbing because "natural variability may occur at rates much higher than the rate at which carbon dioxide is decreasing ocean pH," which is about 0.0017 pH unit per year, according to Dore *et al.* (2009) and Byrne *et al.* (2010). They contend "ambient fluctuation in pH may have a large impact on the development of resilience in marine populations," noting "heterogeneity in the environment with regard to pH and pCO₂ exposure may result in populations that are acclimatized to variable pH or extremes in pH."

Hofmann *et al.* recorded continuous highresolution time series of upper-ocean patterns of pH variability with autonomous sensors deployed at 15 locations from 40.7303°N to 77.8000°S latitude and from 0 to 166.6712°E longitude and 0 to 162.1218°W longitude, over a variety of ecosystems ranging from polar to tropical, open ocean to coastal, and kelp forest to coral reef. The 18 researchers report their measurements revealed "a continuum of month-long pH variability with standard deviations from 0.004 to 0.277 and ranges spanning 0.024 to 1.430 pH units." This variability was "highly site-dependent, with characteristic diel, semi-diurnal, and stochastic patterns of varying amplitudes."

Hofmann et al. write, "these biome-specific pH signatures disclose current levels of exposure to both high and low dissolved CO₂, often demonstrating that resident organisms are already experiencing pH regimes that are not predicted until 2100." These facts suggest the current real-world heterogeneity of the world's oceans with regard to pH and pCO₂ exposure may already have "result[ed] in populations that are acclimatized to variable pH or extremes in pH," such as those that have been predicted to be the new norm in 2100. Lower ocean pH levels may therefore not mature in the way projected by IPCC, a conclusion Loaiciga (2006) shares, having written years earlier, "on a global scale and over the time scales considered (hundreds of years), there would not be accentuated changes in either seawater salinity or acidity from the rising concentration of atmospheric CO₂."

Marine photosynthesis may also reduce CO_2 induced lowering of ocean pH levels lower ocean pH levels, as it tends to increase surface seawater pH, countering the tendency for pH to decline as the air's CO_2 content rises, as demonstrated by Lindholm and Nummelin (1999). This phenomenon has been found to dramatically increase the pH of marine bays, lagoons, and tidal pools (Gnaiger *et al.*, 1978; Santhanam, 1994; Macedo *et al.*, 2001; Hansen, 2002) and significantly enhance the surface water pH of areas as large as the North Sea (Brussaard *et al.*, 1996).

Middelboe and Hansen (2007) studied a waveexposed boulder reef in Aalsgaarde on the northern coast of Zealand. Denmark. plus a sheltered shallowwater area in Kildebakkerne in the Roskilde Fjord, Denmark. As one would expect if photosynthesis tends to increase surface-water pH, the two researchers found "daytime pH was significantly higher in spring, summer and autumn than in winter at both study sites," often reaching values of 9 or more during peak summer growth periods vs. 8 or less in winter. They also found "diurnal measurements at the most exposed site showed significantly higher pH during the day than during the night," sometimes reaching values greater than 9 during daylight hours but typically dipping below 8 at night, and "diurnal variations were largest in the shallow water and decreased with increasing water depth."

In addition to their own findings, Middelboe and Hansen cite Pearson *et al.* (1998), who found pH averaged about 9 during the summer in populations of *Fucus vesiculosus* in the Baltic Sea; Menendez *et al.* (2001), who found maximum pH was 9 to 9.5 in dense floating macroalgae in a brackish coastal lagoon in the Ebro River Delta; and Bjork *et al.* (2004), who found pH values as high as 9.8 to 10.1 in isolated rock pools in Sweden. Noting "pH in the sea is usually considered to be stable at around 8 to 8.2," the two Danish researchers conclude "pH is higher in natural shallow-water habitats than previously thought."

Liu *et al.* (2009) note, "the history of ocean pH variation during the current interglacial (Holocene) remains largely unknown," and it "would provide critical insights on the possible impact of acidification on marine ecosystems." Working with 18 samples of fossil and modern *Porites* corals recovered from the South China Sea, the nine researchers employed ¹⁴C dating using the liquid scintillation counting method, along with positive thermal ionization mass spectrometry to generate high-precision δ^{11} B (boron) data, from which they reconstructed the paleo-pH record of the past 7,000 years, as depicted in Figure 6.3.1.1.2.

As the figure illustrates, there is nothing unusual, unnatural, or unprecedented about the two most recent pH values. They are not the lowest of the record, nor is the rate of decline that led to them the greatest of the record. This strongly indicates these recent values have little to do with the nearly 40%



Figure 6.3.1.1.2. Reconstructed pH history of the South China Sea. Created from Table 1 of Liu *et al.* (2009).

increase in the air's CO_2 concentration that occurred over the course of the Industrial Revolution. As for the prior portion of the record, Liu *et al.* note there is also "no correlation between the atmospheric CO_2 concentration record from Antarctica ice cores and $\delta^{11}B$ -reconstructed paleo-pH over the mid-late Holocene up to the Industrial Revolution."

Further insight comes from the earlier work of Pelejero *et al.* (2005), who developed a more refined history of seawater pH spanning the period 1708–1988 (depicted in Figure 6.3.1.1.3), based on δ^{11} B data obtained from a massive *Porites* coral from Flinders Reef in the western Coral Sea of the southwestern Pacific. These researchers also found "no notable trend toward lower δ^{11} B values." They discovered "the dominant feature of the coral δ^{11} B record is a clear interdecadal oscillation of pH, with δ^{11} B values ranging between 23 and 25 per mil (7.9 and 8.2 pH units)," which they say "is synchronous with the Interdecadal Pacific Oscillation."



Figure 6.3.1.1.3. Reconstructed pH history of Flinders Reef of the Western Coral Sea of the Southwestern Pacific. Adapted from Pelejero *et al.* (2005).

Pelejero *et al.* also compared their results with coral extension and calcification rates obtained by Lough and Barnes (1997) over the same 1708–1988 time period. As best as can be determined from their graphical representations of these two coral growth parameters, extension rates over the last 50 years of this period were about 12% greater than they were over the first 50 years, and calcification rates were approximately 13% greater over the last 50 years.

Wei *et al.* (2009) derived the pH history of Arlington Reef (off the north-east coast of Australia). Their data show a 10-year pH minimum centered at about 1935 (which obviously was not CO_2 -induced) and a shorter, more variable minimum at the end of the record (which also was not CO_2 -induced). Apart from these two non- CO_2 -related exceptions, the majority of the data once again fall within a band that exhibits no long-term trend.

Numerous scientific studies have demonstrated atmospheric CO_2 enrichment stimulates pH-boosting photosynthesis in marine micro- and macro-algae (see Sections 6.3.2 and 6.5.1). This phenomenon suggests anything else that enhances marine photosynthesis— such as nutrient delivery to the waters of the world's coastal zones (i.e., eutrophication)—may do so as well, as Borges and Gypens (2010) have found.

Employing 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), the two researchers investigated "the decadal changes of seawater carbonate chemistry variables related to the increase of atmospheric CO₂ and of nutrient delivery in the highly eutrophied Belgian coastal zone over the period 1951-1998." They write, "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 "faster than those related solely to ocean acidification." They add, "the response of carbonate chemistry to changes of nutrient delivery to the coastal zone is stronger than ocean acidification."

Given its failure to account for the full spectrum of important phenomena that affect ocean acidification, IPCC's current assessment of potential impacts on aquatic life should be considered far more uncertain and much less extreme than IPCC claims it to be.

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6.3.1.2 Some Thoughts on Ocean Chemistry

Contributed by Tom V. Segalstad Associate Professor of Geochemistry (Resource- and Environmental Geology) University of Oslo, Norway

The "acidification" of the ocean—or rather its potential progression toward less alkaline conditions—is postulated to result in serious consequences to marine life, including the dissolution of lime shells of various marine organisms. However, the foundation of the ocean acidification scare is disputed and challenged in the scientific literature as indicated in the multiple peer-reviewed studies referenced throughout Sections 6.3–6.5. The present section approaches and critiques the hypothesis from a geochemical perspective.

Water (H_2O) in the ocean is about one pH unit alkaline. Water protolyses as:

 $H_2O \leftrightarrow H^+ + OH^-[1]$

The ordinary hydrogen atom (H) has one proton and one electron. When the hydrogen's electron is lost to the hydoxyl (OH⁻), the remaining H⁺ is just a proton. This dissociation of water is called protolysis: the formation of a proton from water.

The concentration of such protons in water determines its acidity or alkalinity. A high concentration is typical of acids, while a dominance of hydroxyl is typical of alkalies. Water is considered neutral (neither alkaline or acidic) when concentrations of H^+ and OH^- are equal. In thermodynamics the concentration is commonly expressed as activity—a thermodynamic concentration, denoted "a".

pH ("power of hydrogen") is a measure of the acidity of water, defined as the negative logarithm to the activity of H^+ (a_{H^+}):

 $pH \equiv -\log a_{H^+} [2]$

The protolysis constant for the chemical reaction for water protolysis, equation [1], has a value of $\sim 10^{-14}$ at 25°C. At this temperature, the pH has a range up to 14 units, with a value of 14 representing the most alkaline waters, a value of 7 indicating neutral water, and values below 7 for acidic waters. The protolysis constant varies with temperature (and somewhat by pressure), so the value for neutral water changes with changing temperatures. Dissolved gases and solids also can change the pH of water.

6.3.1.2.1 The Assertion of Ocean Acidification

Oceanic pH varies naturally with latitude and ocean depth across Earth. Hence, no single value exists to define oceanic pH. For instance, the pH of surface waters in the western Pacific Ocean varies from around 7.8 to 8.5 between 60°N and 60°S. Although significant pH variations can occur both above and below this range, ocean water is generally characterized as alkaline. And because pH units of measure fall on a logarithmic scale (each pH unit change requires an order of magnitude change in the activity of H^+), large additions of gases and/or dissolved solids into water are needed to induce significant changes in pH.

Some researchers assert ocean waters have become less alkaline (by about 0.1 pH unit) since preindustrial times (e.g., Caldeira and Wickett, 2003). Ocean waters are projected to experience a further pH decline of 0.1-0.2 unit during the next decennia, and a reduction of 0.5-0.7 by the year 2100, caused by anthropogenic CO₂ (NIVA, 2008).

In its first assessment report, published in 1990, IPCC claimed anthropogenic CO₂ has a long lifetime in the atmosphere, of between 50 and 200 years. This long lifetime, according to IPCC, accounts for the modern rise in atmospheric CO₂, which they assert is caused by anthropogenic CO₂ emissions accumulating in the air year after year. Solomon et al. (2009) suggest an even longer residence time for anthropogenic CO_2 in the atmosphere, estimating it may be more than 1,000 years, where the CO₂ content flattens out asymptotically towards infinity in their model. Other researchers have provided contrasting findings. Many scientific papers, for example, contend the atmospheric CO₂ lifetime (halflife) is much shorter, at around five years (Bolin and Eriksson, 1959), that a similar lifetime is found for oceanic CO₂, and that natural processes play a far more significant role influencing the atmospheric content of CO₂ than previously thought (e.g., Segalstad, 1992; 1996; 1998; 2008; 2009; Starr, 1993; Rohde, 2000).

It is important to note the dissolution of CO_2 in water is governed by Henry's Law, evidenced by the fact there is approximately 50 times more CO_2 dissolved in the ocean than in the atmosphere at present. It is this vast mass of dissolved CO_2 in the ocean that holds the regulating power—not the relatively small amount of CO_2 contained in the air. Furthermore, the chemical reaction speeds involved in the dissolution of CO_2 are high, as is the ocean circulation speed in the upper parts of the ocean.

The ocean acidification hypothesis also ignores the presence of vast amounts of dissolved calcium in the ocean: the upper 200 m of ocean water contains enough dissolved calcium to bind all anthropogenic CO_2 as precipitated calcium carbonate (in the ocean) without affecting the ocean's pH (Jaworowski et al., 1992a; Segalstad, 1996; 1998). The ocean acidification hypothesis also ignores or downplays other oceanic buffers (pH stabilizing reactions), the thermodynamic stability of solid calcium carbonate in ocean water, and photosynthesis by marine biological systems. Many assertions of ocean acidification are based on a methodology that has been called into serious question. For example, the Norwegian Institute for Water Research (NIVA, 2008) built its assertions of ocean acidification on a paper by Haugan and Drange (1996), who derived their claims from the work of Spivack et al. (1993). This latter group of authors presented a proxy history of the ocean's pH over the past 21 million years that used boron isotopes in foraminifera from only five dated boron isotope analyses. This methodology was challenged by Lemarchand et al. (2000), who found the boron isotopes in foraminifera represent changes in the marine boron isotope budget rather than changes in the ocean's pH. Claims that the oceans are presently "acidifying," if based on boron isotope measurements, are highly questionable, if not altogether invalid.

6.3.1.2.2 The Geochemistry of CO₂

Depending on physical conditions, CO_2 can both rapidly dissolve and de-gas in water. This is succinctly demonstrated in the making of carbonated sodas canned by breweries and the degassing of the dissolved CO_2 to the air with time upon opening the soda container.

The dissolved CO₂ first hydrolyzes with the water

into carbonic acid, H₂CO₃. Next, the carbonic acid protolyzes in two steps, first producing H⁺ and dissolved bicarbonate HCO_3^- , and next producing H^+ and dissolved carbonate $CO_3^{2^2}$. With the presence of vast amounts of dissolved calcium Ca^{2+} in the ocean, calcium combines with dissolved carbonate or bicarbonate (the dominating dissolved carbon species in the ocean) to form solid calcium carbonate. In simple terms, this process explains how and why some marine organisms form solid calcium carbonate shells. And it further explains how and why the chemical sedimentation of precipitated calcium carbonate can occur to make limestone (or dolomite) on the ocean floor.

Budyko et al. (1987) has pointed out periods of maximum carbonate precipitation (as limestone and dolomite) tend to occur at times of intense volcanism (releasing vast amounts of CO₂ from Earth's interior). These periods also tend to correspond with periods of higher atmospheric CO₂, highlighting a geochemical path of CO₂ that initiates from Earth's interior, degasses from volcanoes to the atmosphere, dissolves into the oceans, and precipitates solid marine carbonate rocks on the ocean floor. The chemical reactions for these processes are illustrated below, where (g) = gas, (aq) = aqueous (dissolved in water), and (s) = solid. The protolysis of the water must be added to the system because the ocean water is alkaline, dominated by hydroxyl OH⁻. By adding all the partial reactions in this system, the total net reaction for the marine precipitation of solid calcium carbonate from the air's CO₂ and dissolved calcium in ocean water can be obtained:

| $CO_2(g) \leftrightarrow CO_2(aq)$ | dissolution [3] |
|---|--------------------|
| $CO_2 (aq) + H_2O \leftrightarrow H_2CO_3 (aq)$ | hydrolysis [4] |
| $H_2CO_3 (aq) \leftrightarrow H^+ + HCO_3^- (aq)$ | 1st protolysis [5 |
| $\text{HCO}_3^-(\text{aq}) \leftrightarrow \text{H}^+ + \text{CO}_3^{-2-}(\text{aq})$ | 2nd protolysis [|
| $Ca^{2+}(aq) + CO_3^{2-}(aq) \leftrightarrow CaCO_3(s)$ | precipitation [7] |
| $2 \text{ H}^+ + 2 \text{ OH}^- \leftrightarrow 2 \text{ H}_2\text{O}$ | protolysis [1] |
| $CO_2(g) + Ca^{2+}(aq) + 2 OH^- \leftrightarrow CaCO_3(s) + H_2O$ | total net reaction |
| | |

The Law of Mass Action ensures when all these chemical reactions have been accounted for in the total net reaction (and when increasing the amount of a gas, CO_2 , in the air), calcium carbonate (solid) will be stabilized in the ocean, because the chemical reaction will be forced in the direction from left to right. This result is the opposite of what is commonly asserted (that solid calcium carbonate would be dissolved by the increasing amount of CO_2 in the air).

A simple example of this equation is seen in the

oft-demonstrated school chemistry experiment of blowing one's exhaled breath (CO₂ gas) through a straw into a reaction tube with dissolved calcium hydroxide Ca(OH)₂ in water. Solid calcium carbonate precipitates out into the solution within seconds, providing a good visual of what happens in the ocean when gaseous CO₂ dissolves in the ocean, where there is an ample supply of dissolved calcium and hydroxyl.

6.3.1.2.3 pH Stabilizing Reactions in the Ocean

A "buffer" can be defined as a reaction system that modifies or controls the magnitude of an intensive (mass independent) thermodynamic variable, such as pressure, temperature, concentration, pH (acidity), etc. The ocean's carbonate system acts as a pH buffer through the presence of a weak acid (H₂CO₃ and its protolysis products) and a salt of the acid $(CaCO_3)$. The pH of the water can be calculated as:

$$pH \approx [\log K + a(CO_2,g) + a(Ca^{2+},aq)] / -2$$
 [9]

where K is the chemical equilibrium constant, and a the activity (thermodynamic concentration). At the ocean surface the $a(Ca^{2+},aq)$ is much larger than the $a(CO_2,g)$. Therefore the alkalinity is the determining factor for the pH, and not the activity (or the fugacity or the partial pressure) of atmospheric CO₂ (Charlson and Emerson, 2000).

In his book on geochemical thermodynamic calculations, Bethke (1996) shows that in a system

| dissolution [3] |
|------------------------|
| hydrolysis [4] |
| 1st protolysis [5] |
| 2nd protolysis [6] |
| precipitation [7] |
| protolysis [1] |
| total net reaction [8] |

with only water and CO_2 , without mineral buffers more present, than а doubling of the amount of CO_2 in the air above the water surface will lead to a pH decrease of less than 0.4 pH unit. He further demonstrates this is within

the natural variation, and thus nothing to worry about.

The ocean is not chemically uniform. Colder water will have a naturally lower pH, because the protolysis constant for water changes with temperature. An upwelling ocean current with colder water, or movement of water from higher latitudes, may lead to a somewhat lower pH within the natural variation-without an anthropogenic influence.

It is also important to note when solid calcium carbonate is brought into the system, a change in the amount of CO₂ gas alone cannot change the pH, because of the buffer action of the calcium carbonate. Thermodynamic calculations on an ocean water

composition in equilibrium with calcium carbonate at 25°C show the pH would have to be

lowered by 2 units in order to dissolve the calcium carbonate at this temperature. This means the H^+ concentration would have to be increased by 2



Figure 6.3.1.2.1. A phase diagram for the system CO_2 — H_2O — $CaCO_3$ at 25°C and water composition of average sea water. The blue stability fields show the stability of different aqueous species for given pH and log activity of bicarbonate. The green star indicates the sea water position, within the CaCO₃ stability field. The diagram was constructed using the program package "The Geochemist's Workbench," by Craig Bethke.

logarithm units, i.e. 100 times (see Figure 6.3.1.2.1).

When adding more CO_2 (g), more bicarbonate will be produced. Yet as the phase diagram illustrates (Figure 6.3.1.2.1), such a CO_2 addition will only stabilize CaCO₃ even more—the star in the figure (denoting the sea water composition) would move upward. Furthermore, the star would have to be moved out of the CaCO₃ (s) stability field in order for calcium carbonate (calcite) to be dissolved. This is impossible to do by adding CO_2 (g) when calcium carbonate is present (Segalstad, 2008). Hence, the pH of ocean water appears to be well buffered with respect to adding more CO_2 to the atmosphere. At 0°C the pH would have to be lowered 1.5 pH units for solid calcium carbonate (calcite) to be dissolved.

The carbonate buffer is not the only pH buffer

acting in the ocean. The ocean has a set of other mineral-buffer-reactions, such as the buffer:

$$CaAl_2Si_2O_8(s) + 2H^+ + H_2O \leftrightarrow Al_2Si_2O_5(OH)_4(s) + Ca^{2+}(aq)$$
[10]

This anorthite feldspar \leftrightarrow kaolinite buffer has a buffering capacity 1,000 times larger than the ocean's carbonate buffer (Stumm and Morgan, 1970). There are also clay mineral buffers, plus a calcium silicate \leftrightarrow calcium carbonate CO₂ buffer (MacIntyre, 1970; Krauskopf, 1979) [for simplicity]:

$$CaSiO_3(s) + CO_2(g) \leftrightarrow CaCO_3(s) + SiO_2(s)$$
 [11]

All these buffers act as a "security net" under the $CO_2(g) \leftrightarrow CaCO_3(s)$ buffer. Together they constitute an almost infinite buffer capacity (Stumm and Morgan, 1970; Segalstad and Jaworowski, 1991).

The last two buffers mentioned are slower than the $CO_2(g) \leftrightarrow CaCO_3(s)$ buffer at low temperatures. But their reactions are fast at the hot mid-ocean ridges, where temperatures can reach several hundred degrees C. There is no shortage of dissolved calcium in the ocean water, because this element is constantly being added from weathered surface rocks to the ocean by rivers, and by water-rock interactions at hot mid-ocean ridges.

Rainwater has a pH of about 5.7 (Krauskopf, 1979), because of the acidity caused by dissolution and protolysis of atmospheric CO₂. All the acidic rain supplied to the ocean water through the millennia have not changed the ocean's pH of near 8, which also supports the notion of strong pH buffering in ocean water (Pytkowicz, 1972).

6.3.1.2.4 Carbon Isotopes and Mass Balance Calculations

Stable ¹³C/¹²C isotope ratios, expressed as δ^{13} C vs. PDB, provide the only way to determine unequivocally the fraction of anthropogenic CO₂ in the atmosphere. The natural atmospheric CO₂ reservoir has δ^{13} C \approx -7‰ when in isotopic equilibrium with marine HCO₃⁻ (aq) and CaCO₃ (s). CO₂ gas from burning of fossil-fuel and biogenic materials has δ^{13} C \approx -26‰ (Ohmoto and Rye, 1979; Deines, 1980).

IPCC identifies 280 ppmv (ppm by volume) as the preindustrial CO_2 value, but that may be arbitrarily influenced by the selection of low-value CO_2 data from ice cores (where measured values up to 7,400 ppmv were omitted), as well as from the mismatching of contemporary measurements with different ages (Jaworowski *et al.*, 1992a; 1992b). IPCC claims the rise in CO_2 to 353 ppmv in 1990, and 379 ppmv in 2005, is due only to anthropogenic CO_2 (IPCC, 1990; 2007).

The δ^{13} C value reported for atmospheric CO₂ was -7.489‰ in December 1978, decreasing 10 years later to -7.807‰ in December 1988 (Keeling *et al.*, 1989). If the resultant decrease were solely the product of mixing natural CO₂ with CO₂ produced from the burning of fossil fuels or plants (~79% / ~21% CO₂ mix; lifetime 50–200 years; IPCC, 1990), the current atmospheric CO₂ δ^{13} C value should be -11, much lower than reported (Segalstad, 1992; 2008).

The December 1988 atmospheric CO₂ composition has been computed for its 748 Gt C (Gt = 10^{15} g) total mass and δ^{13} C value of -7.807‰ for three components: (1) natural fraction remaining from the preindustrial atmosphere, (2) cumulative fraction remaining from all annual fossil-fuel CO₂ emissions, and (3) carbon isotope mass-balanced natural fraction. The masses of component (1) and (2) were computed for different atmospheric lifetimes of CO₂ (Segalstad, 1992).

The result fits a lifetime of about five years, in agreement with ¹⁴C studies (see Sundquist, 1985; Segalstad, 1998; 2009; for further references). The mass of all past fossil-fuel and biogenic emissions remaining in the current atmosphere was -30 Gt C or less; i.e. a maximum of around 4% of the total, corresponding to an atmospheric concentration of approximately 14 ppmv. The implication of the five-year lifetime is that approximately 135 Gt C (18%) of the atmospheric CO₂ is dynamically exchanged each year (Segalstad, 1992; 1996; 1998; 2008).

The above calculations also demonstrate that over this 10-year period (1978–1988), at least 96% of the atmospheric CO_2 is attributed to non-fossil-fuel sources, and this percentage has not likely varied much in the years since. Hence, it is clear marine degassing and juvenile degassing from sources such as volcanoes must be much more important for the atmospheric CO_2 budget than the burning of fossilfuels and biogenic materials. IPCC has failed to recognize this conclusion.

6.3.1.2.5 Can Anthropogenic Carbon Double the Atmospheric CO₂ Content?

Many models suggest there is enough fossil carbon on

Earth that, if burned, would raise the atmospheric CO_2 concentration to two or more times its preindustrial value. There are reasons to conclude such an increase may never occur.

The equilibrium partition coefficient for the CO_2 distribution between the atmosphere and ocean is approximately 1:50 (Revelle and Suess, 1957; Skirrow, 1975), given by Henry's Law and the Henry's Law Constant. This partition coefficient can be used to set an upper limit for how much the CO_2 concentration will rise in the atmosphere if all available fossil carbon fuel (coal, petroleum, gas) were burned.

To permanently double the current level of CO_2 in the atmosphere under chemical equilibrium conditions, the atmosphere would have to be supplied with approximately 51 times the present amount of CO₂ if equilibrium should be attained, in order to keep the partition coefficient (air:sea = 1:50) constant according to Henry's Law. At the double amount of CO_2 in the air, the new ratio would have to be 2:100. In other words, an increase of one unit CO₂ in air leads to an increase of 50 units CO₂ in the sea; thus a total of 51 units has to be supplied. All available fossil fuel carbon amounts to 11 times the amount of carbon in today's atmospheric CO₂ (Jaworowski et al., 1992a). Therefore, mankind does not have enough fossil fuel to double the current level of atmospheric CO₂ under equilibrium conditions, all other factors held constant.

If the total fossil fuel reservoir of 7,200 Gt C were burned during the next 300 years, only the dissolved organics (carbon pool of about 1,000 Gt C) would consume all manmade CO_2 by their photosynthesis, because this period covers 6 to 15 turnovers of the upper-ocean pool of dissolved organic carbon, based on radiocarbon (¹⁴C) studies. However, the vast oceanic dissolved inorganic carbon reservoir of 38,000 Gt C indicates the sea is a much more powerful sink for atmospheric CO_2 . Hence, it is unlikely a permanent doubling of the amount of atmospheric CO_2 is attainable by human activities. See Jaworowski *et al.* (1992a) for further details and references.

6.3.1.2.6 Conclusion

Brian Mason (1966) wrote in his textbook, *Geochemistry* (3rd edition), "The ocean may thereby act as a self-balancing mechanism in which most of the elements have reached an equilibrium concentration." That statement remains valid, as seen through a considerable constancy of sedimentation and pH over many past hundreds of millions of years. The circulation of CO_2 among the atmosphere, ocean, and biosphere is a fast exchange, with an average measured lifetime (half-life) for one atmospheric CO_2 molecule of about five years (Bolin and Eriksson, 1959; Segalstad, 1992; 1996; 1998; 2008; 2009; Starr, 1993; Rohde, 2000).

According to Mason, "it is apparent that the oceans, by controlling the amount of atmospheric CO_2 , play a vital part in maintaining stable conditions suitable for organic life on the Earth." As the material above demonstrates, physical chemistry and thermodynamics provide strong reasons for questioning the validity of the so-called ocean "acidification" hypothesis, especially when considering the vast buffering capacity of the ocean's many buffering mechanisms.

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6.3.2 Effects on Marine Plants

6.3.2.1 Phytoplankton

6.3.2.1.1 Coccolithophores

Coccolithophores are single-celled algae and protists found throughout the surface euphotic zones of the world's oceans. They contain chlorophyll, conduct photosynthesis, and possess special plates or scales known as coccoliths, which they create through calcification. This section reviews the results of studies that address how they may be affected by a possible decline in ocean pH levels in a CO₂-enriched world of the future. Several of the findings challenge the alarming negative projections of IPCC, as noted in the bullet points below and further discussed in the main portion of the section.

- Shifts in dominance among species of coccolithophores or clones within a species have been found to occur as the air's CO₂ content rises, which may enable the species to function much as they do today—if not better—in a high-CO₂ world of the future.
- Contemporary evolution likely will help to maintain the functionality of microbial processes at the base of marine food webs in the face of projected lower pH levels.
- Various coccolithophore species appear able to track the environmental value of ocean pH in real time.
- There is evidence the coccolithophore *Calcidiscus leptoporus* has adjusted successfully to the 80 ppm CO₂ difference between preindustrial and the present, as well as the 180 ppm CO₂ difference between glacial times and the present.

Riebesell (2004) notes a doubling of present-day atmospheric CO_2 concentrations "is predicted to cause

a 20–40% reduction in biogenic calcification of the predominant calcifying organisms, the corals, coccolithophorids, and foraminifera." But he also notes "a moderate increase in CO_2 facilitates photosynthetic carbon fixation of some phytoplankton groups," including "the coccolithophorids *Emiliania huxleyi* and *Gephyrocapsa oceanica*." In what constitutes a major challenge to the model-based claim atmospheric CO_2 enrichment will harm such marine organisms, Riebesell suggests "CO₂-sensitive taxa, such as the calcifying coccolithophorids, should therefore benefit more from the present increase in atmospheric CO_2 compared to the non-calcifying diatoms."

Leonardos and Geider (2005) grew a noncalcifying strain (PML 92A) of the marine coccolithophorid Emiliania huxleyi (Lohmann) Hay & Mohler in chemostats-cyclostats aerated with air of either 360 or 2,000 ppm CO₂ under both high- and low-light conditions in seawater either replete with or deficient in nitrogen and/or phosphorus, while measuring a suite of physical and biochemical properties of the coccolithophorid populations and the media in which they lived. They found "increased atmospheric CO_2 concentration enhances CO_2 fixation into organic matter," but "only under certain conditions, namely high light [HL] and nutrient limitation." Under N-limited conditions, for example, they found particulate organic carbon (POC) "was greatest under HL and elevated CO₂ (by up to 46% relative to HL and ambient CO₂)." Their work also revealed "the increase in POC was a consequence of both an increase in cell density and an increase in the cell organic carbon content."

The two UK researchers state "enhanced CO_2 uptake by phytoplankton such as *E. huxleyi*, in response to elevated atmospheric CO_2 , could increase carbon storage in the nitrogen-limited regions of the oceans and thus act as a negative feedback on rising atmospheric CO_2 levels." According to their calculations, if the results obtained for *E. huxleyi* are indicative of the effects of CO_2 on primary production in other N-limited phytoplankton, changes of the magnitude they measured in *E. huxleyi* due to increased CO_2 could increase export production of the oligotrophic ocean by an amount equivalent to the estimated postindustrial increase in the terrestrial carbon sink.

Leonardos and Geider state their findings are "consistent with the response of primary productivity to manipulation of aqueous phase CO_2 in the oligotrophic North Atlantic (Hein and Sand-Jensen, 1996)," where increases in primary productivity "of

up to 100% were observed, although the average increase was 15% to 19%." They note "stimulation of carbon fixation by elevated CO_2 had already been documented for nutrient-limited lake phytoplankton (Urabe *et al.*, 2003)."

Working with two previously untested coccolithophores—*Calcidiscus leptoporus* and *Coccolithus pelagicus*—which they describe as two of the most productive marine calcifying species, Langer *et al.* (2006) conducted batch-culture experiments in which they observed a deterioration of coccolith production above as well as below present-day CO_2 concentrations in *C. leptoporus*, and a lack of a CO_2 sensitivity of calcification in *C. pelagicus* over an atmospheric CO_2 concentration range of 98–915 ppm. Both observations, they write, "refute the notion of a linear relationship of calcification with the carbonate ion concentration and carbonate saturation state," as various scientists proposed early on.

With respect to C. leptoporus, Langer et al. observed that at both higher and lower CO₂ concentrations than those of today, the proportion of coccoliths showing incomplete growth and malformation notably increased. To determine whether this takes place in the real world, the seven scientists studied coccolith morphologies in six sediment cores extracted along a range of latitudes in the Atlantic Ocean. They report changes in coccolith morphology similar to those "occurring in response to the abrupt CO₂ perturbations applied in our experimental treatments are not mirrored in the sedimentary record." This finding indicates, as they suggest, "in the natural environment C. leptoporus has adjusted to the 80 ppm CO₂ and 180 ppm CO₂ difference between present, preindustrial and glacial times, respectively."

The team of researchers from Germany and the United Kingdom write, "it is reasonable to assume that C. leptoporus has adapted its calcification mechanism to the change in carbonate chemistry having occurred since the last glacial maximum," suggesting as a possible explanation for this phenomenon "the population is genetically diverse, containing strains with diverse physiological and genetic traits, as already demonstrated for E. huxleyi (Brand, 1981, 1982, 1984; Conte et al., 1998; Medlin et al., 1996; Paasche, 2002; Stolte et al., 2000)." They also state this adaptive ability "is not likely to be confined to C. leptoporus but can be assumed to play a role in other coccolithophore species as well." Langer et al. conclude such populations "may be able to evolve so that the optimal CO_2 level for calcification of the species tracks the environmental

value." The authors conclude "genetic diversity, both between and within species, may allow calcifying organisms to prevail in a high CO₂ ocean."

Working with 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. They found a history of "changing particle volume since the late 20th century consistent with an increase in the mass of coccoliths produced by the larger coccolithophore species," leading them to conclude "in the real ocean the larger coccolithophore species increase their calcification in response to anthropogenic CO₂ release." The four researchers state this positive calcification response "could be attributed to an alleviation of CO₂ 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)."

Stoll (2009) addressed the speculative claims of scientists promoting the view "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 that are, by volume, the most important shell producers. She had a much more optimistic view of the subject, thanks in large part to the research findings of Langer *et al.* (2009).

The latter scientists-from France, Germany, Spain, and the Netherlands-grew four strains of the coccolithophore Emiliania huxleyi in dilute batch cultures of seawater with carbonate chemistries characteristic of those expected to prevail beneath an atmosphere with CO₂ concentrations ranging from approximately 200 to 1,200 ppm, while they measured particulate organic carbon content, particulate inorganic carbon content, and organic and inorganic carbon production. 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, other aspects of their earlier studies (Langer et al. 2006, 2007), and the diverse findings of others who had used different strains of the species, the five scientists conclude "the sensitivity of different strains of E. huxleyi to acidification differs substantially" and "likely has a genetic basis."

Stoll agrees with that assessment. She notes the work of those who foresaw disastrous consequences typically "precludes the kind of natural selection and adaptation that might occur over decades and centuries in the ocean." Langer *et al.* (2009) state "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 note far too often "the possibility of adaptation is not taken into account."

Stoll notes the great genetic diversity that exists in the real world, both among and within species, "is good insurance in a changing ocean." It can be interpreted as evidence coccolithophorids are well prepared for whatever the future may bring, for as Langer *et al.* (2006) state, "genetic diversity, both between and within species, may allow calcifying organisms to prevail in a high CO_2 ocean." That appears to be the consensus of most studies that have moved on from theoretical speculation to the intermediate crucible of laboratory experimentation and the final test of real-world observation.

Beaufort *et al.* (2011) note "culture experiments investigating the physiological response of coccolithophore calcification to increased CO_2 have yielded contradictory results between and even within species," citing Riebesell *et al.* (2000), Langer *et al.* (2006), Iglesias-Rodriguez *et al.* (2008), and Langer *et al.* (2009). They investigated 180 surface-water and 555 sediment-core samples encompassing a wide spectrum of present and past oceanic conditions, some stretching back in time as much as 40,000 years.

The 13 researchers report, "significant overall correlations of coccolith mass with pH and pCO_2 were recorded, but with notable regional variations, indicating that these parameters are not solely responsible for the observed trend." They also report some cultured strains of coccolithophores "are capable of maintaining calcification (degree and/or rate) over certain carbonate-chemistry ranges, a phenomenon that could contribute to localized within-sample deviations from the broad trend linking coccolith mass to carbonate chemistry." The results indicated changes in the relative abundance of taxa were "predominantly responsible for the decrease in coccolith mass with ocean acidification that was seen in modern samples."

Beaufort *et al.* also note, "in Patagonian-shelf and Chilean upwelling waters with low $CO_3^{2^-}$, in which the overall trend would predict low coccolith mass," they detected "an unexpectedly highly calcified *Emiliania huxleyi* morphotype," and "the relative abundance of this morphotype increased with decreasing pH along the Pacific transect towards Chile." Noting "coccolith morphotype is thought to be subject to genetic regulation (Langer *et al.*, 2009)," they state "this highly calcified *E. huxleyi* morphotype may be a genetic entity with an adaptation enabling it to calcify heavily in the relatively acidic upwelling waters."

The scientists conclude "the presence of highly calcified *E. huxleyi* in CO₂-rich modern waters demonstrates that prediction of future responses is unlikely to be straightforward," and "such complexity could account for the lack of an obvious overall direction in the response of coccolithophore calcification over a potentially analogous ocean acidification event about 55 million years ago at the Palaeocene-Eocene Thermal Maximum," citing Gibbs *et al.* (2006).

Fiorini et al. (2011) measured the growth rates of three coccolithophores (Emiliania huxleyi, Calcidiscus leptoporus, and Syracosphaera pulchra) in laboratory batch cultures in their haploid and diploid life stages, while they were growing in filtered seawater maintained in equilibrium with air containing either 400 or 760 ppm CO₂. For all three species, "the growth rate was consistently higher at elevated pCO₂," but "the response of other processes varied among species." Calcification rates of C. leptoporus and S. pulchra, for example, did not change at elevated pCO₂, whereas this important process was increased in the case of E. huxleyi. They also found these CO2-induced impacts were most pronounced in the haploid stage.

Fiorini et al. state these effects "must be taken into account when predicting the fate of coccolithophores in the future ocean." The European scientists write, "the phenotypic and physiological differences of the two life stages allow each species to use two different niches to exploit a wider range of ecological conditions (Cros et al., 2000), to limit the competition in the utilization of resources (food, light) inside the species and to rapidly escape negative selection pressures exerted on one stage such as grazing, parasitic attack, viral infections (Frada et al., 2008), or abrupt environmental changes (Noel et al., 2004)." In this way, they continue, "the survival of a species is ensured by one life stage when the environmental conditions do not favor the development of the other life stage (Houdan et al., 2005)."

Lohbeck *et al.* (2012) note the present understanding of the sensitivity of marine life to lower ocean pH levels has been based primarily on shortterm experiments that often depict negative effects. Suggesting phytoplanktonic species with short generation times "may be able to respond to environmental alterations through adaptive evolution," they studied "the ability of the world's single most important calcifying organism, the coccolithophore *Emiliania huxleyi*, to evolve in response to ocean acidification in two 500-generation selection experiments."

The three German researchers grew freshly isolated coccolithophore genotypes from Bergen, Norway, in batch cultures for more than 500 asexual generations at three different atmospheric CO₂ concentrations-ambient (400 ppm). medium (1,100 ppm), and high (2,200 ppm)—where the medium CO₂ treatment was chosen to represent the atmospheric CO₂ level projected for the beginning of the next century. They conducted a multi-clone experiment designed to provide existing genetic variation that "would be readily available to genotypic selection," plus a single-clone experiment initiated with one "haphazardly chosen genotype," where evolutionary adaptation would require new mutations.

Compared with populations kept at ambient CO_2 partial pressure, Lohbeck *et al.* found those selected at increased CO_2 levels "exhibited higher growth rates, in both the single- and multi-clone experiment, when tested under ocean acidification conditions." Calcification rates were somewhat lower under CO_2 enriched conditions in all cultures, but the research team state they were "up to 50% higher in adapted [medium and high CO_2] compared with non-adapted cultures." They conclude "contemporary evolution could help to maintain the functionality of microbial processes at the base of marine food webs in the face of global change."

The marine biologists say the swift adaptation processes they observed may "have the potential to affect food-web dynamics and biogeochemical cycles on timescales of a few years, thus surpassing predicted rates of ongoing global change including ocean acidification." They also note "a recent study reports surprisingly high coccolith mass in an *E. huxleyi* population off Chile in high-CO₂ waters (Beaufort *et al.*, 2011)." This observation, they write, indicates "across-population variation in calcification, in line with findings of rapid microevolution identified here."

Lohbeck *et al.* suggest "contemporary evolution could help to maintain the functionality of microbial processes at the base of marine food webs in the face of global change." Writing about this development in a *News & Views* item in the same issue of *Nature Geoscience*, Collins (2012) notes, "marine microbes, with their large population sizes and fast division rates, are certainly going to evolve over a timeframe of decades," and "we can expect that future coccolithophore populations will be shaped by a combination of species succession and adaptive evolution."

McCarthy et al. (2012) note diatoms are a type of algae, most of which are unicellular, that serve as primary producers in various marine food chains. They investigated how diatoms might respond to continued increases in the air's CO₂ content, since they are responsible for about 40% of current marine primary productivity (Field et al., 1998). The team of four Canadian researchers grew the coccolithophore Emiliania huxleyi and two strains of the diatom Thalassiosira pseudonana under low light in turbidostat photobioreactors bubbled with air containing either 390 ppm or 750 ppm CO₂, finding "increased CO₂ led to increased growth rates in all three strains" and "CO₂ thus had a fertilization effect on all species, enhancing growth rates 20%-40%." They observe, "total cellular protein did not change between ambient and 750 ppm CO₂ treatments," but "cellular RUBISCO content showed a 2- to 3-fold increase with [elevated] CO₂ in both E. huxleyi and in the coastal diatom strain."

McCarthy *et al.* note the CO₂ fertilization effect on the growth rates of *T. pseudonana* and *E. huxleyi* provides these species with increased competitive ability. They conclude their results suggest "there could be a net increase in capacity for primary productivity at 750 ppm CO₂, at least with regard to small diatoms and coccolithophores in coastal environments," where the two types of phytoplankton provide the bulk of current marine primary productivity.

Smith *et al.* (2012) write, "laboratory studies are unrealistic in many respects and, because of their typically short timescales, preclude the possibility of evolutionary adaptation to the imposed change, a key uncertainty in OA [ocean acidification] research," citing Gattuso and Buddemeier (2000), Langer *et al.* (2006), and Ridgwell *et al.* (2009). They decided "to complement laboratory experiments with observational studies of coccolithophores living in the natural habitats to which they are evolutionarily adapted."

Focusing on two morphotypes (over-calcified and normal) of the world's most abundant coccolithophore species (*Emiliania huxleyi*), Smith *et al.* assessed their numbers, along with seawater carbonate chemistry and other environmental variables, at monthly intervals between September 2008 and August 2009 along a 1,000 km route, including over deep oceanic waters in the Bay of Biscay. They found a pronounced seasonality in the morphotypes of *E. huxleyi.* "Surprisingly," they write, "the overcalcified morphotype was found to dominate the *E*. *huxleyi* population in winter," even though seawater pH and CaCO₃ saturation were lowest in winter. The heavily calcified form of *E*. *huxleyi* dominated dramatically, shifting from less than10% of the total *E*. *huxleyi* population in summer to more than 90% of the population in winter.

Smith *et al.* acknowledge their findings "do not suggest that the changing carbonate chemistry was necessarily responsible for this shift in morphotypes." But "if it was not, then the alternative is that carbonate chemistry is not the sole and overriding control over coccolithophore calcification." This, they write, should "seriously call into question" the contention "ocean acidification will lead to a replacement of heavily-calcified coccolithophores by lightly-calcified ones."

Jin *et al.* (2013) note, "as a key group of oceanic primary producers, coccolithophores play a crucial role in the global carbon cycle, not only in terms of photosynthesis but also by producing calcium carbonate in the form of extracellular plates." They note coccolithophores are "important in the sulfur cycle in terms of dimethyl-sulphide (DMS) production (Malin and Erst, 1997)," which leads to enhanced cloud formation and the reflectance back to space of increased amounts of incoming solar radiation, which tends to cool the planet.

The three researchers also note the particulate inorganic carbon (PIC) produced by coccolithophores in the surface ocean sinks to deep in the sea; this phenomenon, known as the carbonate pump, "is a critical part of the global carbon cycle and has a major feedback effect on global climate (Hutchins, 2011)." Jin *et al.* grew in a laboratory environment the coccolithophore *Gephyrocapsa oceanica* for approximately 670 generations in water in equilibrium with both ambient and CO₂-enriched (1,000 ppm) air, with the latter treatment reducing the water's pH to a value of 7.8.

Jin *et al.* found "high CO₂-selected cells showed increases in photosynthetic carbon fixation, growth rate, cellular particulate organic carbon (POC) or nitrogen (PON) production, and a decrease in the C:N elemental ratio, indicating a greater up-regulation of PON than of POC production under ocean acidification." They note these findings are "in good agreement with a recent study in which *E. huxleyi* positively adapted to increased CO₂ levels," citing Lohbeck *et al.* (2012). Jin *et al.* conclude their data indicate "the coccolithophorid could adapt to ocean acidification with enhanced assimilations of carbon and nitrogen." The experimental findings and real-world observations discussed above suggest coccolithophores are well-equipped to deal with whatever decline in ocean pH levels may be on the way.

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6.3.2.1.2 Cyanobacteria

Cyanobacteria—also known as blue-green algae, blue-green bacteria, or Cyanophyta (the smallest of which, less than two micrometers in diameter, are typically referred to as picocyanobacteria)—obtain their energy through photosynthesis and are thus important primary producers in many areas of the world's oceans, as well as significant components of the marine nitrogen cycle. This section briefly reviews studies that address how they may be affected by lower ocean pH levels in a CO₂-enriched world of the future, as noted in the bullet points below and further discussed in the main body of the section.

- Ocean acidification enhances the productivity of one of the world's most important diazotrophic (N-fixing) cyanobacteria (*Trichodesmium erythraeum*) in N-limited oligotrophic regions of the world's oceans, providing more essential nitrogen to support greater amounts of higher-order marine animal life.
- The same is true of the unicellular diazotrophic cyanobacterium *Crocosphaera*, recognized as being perhaps equally as important as *Tricho- desmium* to the global ocean's nitrogen cycle.
- Acidification-induced increases in photosynthesis and N₂ fixation by both types of cyanobacteria may stimulate productivity in N-limited oligotrophic regions and thus provide a negative feedback on rising atmospheric CO₂ levels.
- The potentially toxic cyanobacterium *Cylindro*spermopsis raciborskii becomes less profuse as atmospheric CO₂ concentrations rise.

Arguing cyanobacteria "should be one of the focus points regarding biological responses to the rise in atmospheric CO_2 concentration," Lu *et al.* (2006) studied physiological changes in phycocyanin (PC)rich and phycoerythrin (PE)-rich *Synechococcus* strains of picocyanobacteria under atmospheric CO_2 concentrations of 350, 600, and 800 ppm in batch cultures maintained in one-liter glass flasks under a 12-hour:12-hour light:dark regime for periods of 12 days, measuring physiological parameters related to the growth and well-being of the picocyanobacteria. They found the growth of the PE strain was unaffected by atmospheric CO_2 enrichment, but the PC strain grown at 800 ppm CO_2 experienced a 36.7% increase in growth compared to when it was grown at 350 ppm CO_2 .

The PC strain showed no significant change in carbohydrate content over the CO_2 range investigated, but the PE strain exhibited a CO_2 -induced increase of 37.4% at 800 ppm CO_2 . The PC strain exhibited a 36.4% increase in its RNA/DNA ratio between 350 and 800 ppm CO_2 , and this ratio, Lu *et al.* write, "provides a good estimate of metabolic activities and has been used extensively as a biochemical indicator of growth rate in a variety of marine organisms." In both *Synechococcus* strains, cellular pigment contents were generally greater in the CO_2 -enriched treatments than in the ambient-air controls. At day 12 in the PE strain, for example, they averaged more than 70% greater at 800 ppm CO_2 than at 350 ppm CO_2 .

These results clearly indicate both strains of the Synechococcus picocyanobacteria benefited greatly from the extra CO₂, albeit in different ways. In comparing the different responses of the two strains, Lu et al. conclude, "the PC strain would probably benefit more than the PE strain from future increases in atmospheric CO₂ concentration," but "differences in photosynthetic characteristics may allow the coexistence of the two picocyanobacterial strains through a subtle form of niche differentiation," citing Ernst et al. (2003) and Stomp et al. (2004). Consequently, there is reason to believe the continuing rise in atmospheric CO₂ content will lead to a significant increase in primary production and nutrient cycling throughout the world's oceans, driven by the positive impacts of "acidification" on these very tiny organisms.

Levitan *et al.* (2007) note, "among the principal players contributing to global aquatic primary production, the nitrogen (N)-fixing organisms (diazotrophs) are important providers of new N to the oligotrophic areas of the oceans." They cite several studies demonstrating "cyanobacterial (phototrophic) diazotrophs in particular fuel primary production and phytoplankton blooms which sustain oceanic foodwebs and major economies and impact global carbon (C) and N cycling." They examined how the ongoing rise in the air's CO₂ content might impact these relationships, exploring the response of the cyanobacterial diazotroph *Trichodesmium* to changes in the atmosphere's CO₂ concentration. They studied this particular diazotroph because it contributes more than 50% of total marine N fixation.

The eight Israeli and Czech researchers grew Trichodesmium IMS101 stock cultures in a YBCII medium (Chen et al., 1996) at 25°C and a 12-hour:12hour light/dark cycle (with the light portion of the cycle in the range of 80–100 μ mol photons m⁻² s⁻¹) in equilibrium with air of three CO₂ concentrations (250. 400, and 900 ppm, representing low, ambient, and high concentrations, respectively). They continuously bubbled air of the three CO₂ concentrations through the appropriate culture vessels throughout various experimental runs, each lasting a little over three weeks, while they periodically monitored a number of diazotrophic physiological processes and properties. They found Trichodesmium in the high CO₂ treatment "displayed enhanced N fixation, longer trichomes, higher growth rates and biomass yields." In the high CO₂ treatment there was "a three- to four-fold increase in N fixation and a doubling of growth rates and biomass," and the cultures in the low CO₂ treatment reached a stationary growth phase after only five days, "while both ambient and high CO₂ cultures exhibited exponential growth until day 15 before declining."

The researchers suggest "enhanced N fixation and growth in the high CO₂ cultures occurs due to reallocation of energy and resources from carbon concentrating mechanisms required under low and ambient CO2." They conclude, "in oceanic regions, where light and nutrients such as P and Fe are not limiting, we expect the projected concentrations of CO₂ to increase N fixation and growth of Trichodesmium," and "other diazotrophs may be similarly affected, thereby enhancing inputs of new N and increasing primary productivity in the oceans." They state in the final sentence of their paper, "Trichodesmium's dramatic response to elevated CO₂ may consolidate its dominance in subtropical and tropical regions and its role in C and N cycling, primarv fueling subsequent production, phytoplankton blooms, and sustaining oceanic foodwebs."

Fu *et al.* (2008) examined "the physiological responses of steady-state iron (Fe)-replete and Felimited cultures of the biogeochemically critical marine unicellular diazotrophic cyanobacterium *Crocosphaera* [*watsonii*] at glacial (190 ppm), current (380 ppm), and projected year 2100 (750 ppm) CO₂ levels." They employed semi-continuous culturing methods that used filtered, microwave-sterilized surface Sargasso seawater enriched with phosphate and trace nutrients. When the seawater was replete with iron, daily primary production at 750 ppm CO_2 was 21% greater than it was at 380 ppm, whereas at 190 ppm CO_2 it was 38% lower than at 380 ppm. When the seawater was iron-limited, daily primary production at 750 ppm CO_2 was 150% greater than it was at 380 ppm, and at 190 ppm CO_2 it was 22% lower than at 380 ppm. N₂ fixation rates varied little among the three CO_2 treatments when the seawater was iron-limited; but when the seawater was replete with iron, N₂ fixation at 750 ppm CO_2 was 60% greater than it was at 380 ppm, and at 190 ppm CO_2 it was 33% lower than at 380 ppm.

Fu *et al.* write, "several studies examining the marine diazotrophic cyanobacterium *Trichodesmium* have shown significant increases in N₂ fixation and photosynthesis in response to elevated CO₂ concentration (Hutchins *et al.*, 2007; Levitan *et al.*, 2007; Ramos *et al.*, 2007)," and their data "extend these findings to encompass the marine unicellular N₂-fixing cyanobacterium *Crocosphaera.*" This group, they add, "is now recognized as being perhaps equally as important as *Trichodesmium* to the ocean nitrogen cycle (Montoya *et al.*, 2004)." They conclude, "anthropogenic CO₂ enrichment could substantially increase global oceanic N₂ and CO₂ fixation."

Kranz et al. (2009) write, "marine phytoplankton contribute up to 50% of global primary production (Falkowski et al., 1998) and influence Earth's climate altering various biogeochemical bv cycles (Schlesinger, 2005)." They also note, among diazotrophic cvanobacteria (dinitrogen-fixers), Trichodesmium species contribute "about half of all marine N₂ fixation (Mahaffey et al., 2005)," supporting "a large fraction of biological productivity in tropical and subtropical areas and exerting, over long timescales, a significant influence on global carbon cycles by providing a major source of reactive N to the water column (Falkowski and Raven, 1997)."

Kranz *et al.* grew *Trichodesmium erythraeum* IMS101 in semi-continuous batch cultures through which they bubbled air with CO_2 concentrations of either 370 or 1,000 ppm. After the cultures were acclimated to their respective CO_2 concentrations for at least 14 days (covering more than five generations), the scientists measured the rates of particulate organic carbon (POC) and particulate organic nitrogen (PON) fixation, discovering "a strong increase in photosynthesis and N₂ fixation under elevated CO_2 levels," such that POC and PON production rates rose "by almost 40%."

The German scientists note other scientists have worked with the same *Trichodesmium* species:

"Barcelos e Ramos *et al.* (2007) and Levitan *et al.* (2007) observed stimulation in N₂ fixation by approximately 40% and even up to 400%, while Hutchins *et al.* (2007) obtained stimulation by up to 35%." Kranz *et al.* write, "the observed increase in photosynthesis and N₂ fixation could have potential biogeochemical implications, as it may stimulate productivity in N-limited oligotrophic regions and thus provide a negative feedback on rising atmospheric CO₂ levels."

Kranz *et al.* (2011) wrote, "marine phytoplankton are responsible for almost half of all photosynthetic carbon fixation on Earth and play a vital role in altering the CO₂ exchange between ocean and atmosphere," citing Maier-Reimer *et al.* (1996) and Gruber (2004). They point out a lack of nitrates often limits phytoplanktonic growth, and diazotrophic cyanobacteria that fix nitrogen, such as *Trichodesmium* species, thus play "a crucial role in many marine ecosystems by providing a new source of biologically available nitrogen." The scientists describe how atmospheric CO₂ enrichment helps enhance both parts of this important phenomenon.

The three researchers from the Alfred Wegener Institute for Polar and Marine Research in Bremerhaven, Germany report, "four recent studies tested the effect of different CO_2 concentrations on the growth, biomass production and elemental composition of *Trichodesmium* (Barcelos e Ramos *et al.*, 2007; Hutchins *et al.*, 2007; Kranz *et al.*, 2009; Levitan *et al.*, 2007)," and these studies "concordantly demonstrated higher growth and/or production rates under elevated p CO_2 , with a magnitude exceeding those CO_2 effects previously seen in other marine phytoplankton."

Focusing on particulate organic nitrogen (PON) production, they note *Trichodesmium* species are particularly effective in this regard: "the stimulation in N₂ fixation and/or PON production between present-day pCO₂ values (370–400 ppm) and those predicted for the year 2100 (750–1000 ppm) ranged between 35 and 240%." They state "data on CO₂ dependency of N₂ fixation rates from recent publications suggest that N₂ fixation by *Tricho-desmium* species might increase by more than 20 Tg N per year to about 100 Tg N per year until the end of this century," citing Hutchins *et al.* (2009).

These findings indicate the oceans are primed to do their part in preserving and protecting the biosphere, as they ramp up their productivity to sustain a greater population of aquatic organisms that may be tapped to supply additional food for the planet's burgeoning human population, and remove from the atmosphere and sequester in their sediments increasing amounts of carbon as anthropogenic CO_2 emissions continue to rise.

Garcia *et al.* (2011) emphasize N₂ fixation by marine diazotrophic cyanobacteria (such as various species of *Trichodesmium*) "contributes substantial new nitrogen to marine environments, including the North Atlantic, Pacific, and Indian Oceans (Carpenter *et al.*, 1993; Capone *et al.*, 1997, 2005; Karl *et al.*, 2002)." They further note phosphorus and iron have been identified as key factors that control N₂ fixation in those environments. They report other studies suggest the current low partial pressure of CO₂ in the atmosphere "may be another possible limiting factor for N₂ fixation and CO₂ fixation by *Trichodesmium*," citing Barcelos e Ramos *et al.* (2007), Hutchins *et al.* (2007), Levitan *et al.* (2007, 2010), and Kranz *et al.* (2009).

In a laboratory study designed to explore the limiting potential of low partial pressure of CO₂, Garcia et al. examined the effects of near-present-day (~380 ppm) and elevated (~750 ppm) atmospheric CO_2 concentrations on CO_2 and N_2 fixation by T. erythraeum isolates from the Pacific and Atlantic Oceans under a range of irradiance conditions. According to the seven scientists, "the positive effect of elevated CO₂ on gross N₂ fixation was large (~50% increase) under mid and/or low irradiances compared with that at high light (~20% increase)," noting data from Kranz et al. (2010) and Levitan et al. (2010) corroborated their findings. In the Kranz et al. study, they report, "under low light, gross N₂-fixation rates were 200% higher in a high-CO₂ treatment (900 ppm) compared with a low-CO₂ treatment (150 ppm), whereas under high light, gross N₂-fixation rates were only 112% higher under elevated CO2." In the case of CO₂ fixation, they found CO₂-fixation rates increased significantly "in response to high CO₂ under mid- and high irradiances only."

As the atmosphere's CO_2 concentration continues to rise, therefore, this phenomenon should boost the growth rates of marine diazotrophic cyanobacteria and enable them to make more nitrogen available to themselves and co-occurring species, which should significantly increase both the quantity and quality of the worldwide phytoplanktonic food base that ultimately supports all marine animal life.

Holland *et al.* (2012) studied the potentially toxic cyanobacterium *Cylindrospermopsis raciborskii*, originally described as a tropical-subtropical species but increasingly found in temperate regions. Noting "climate change is hypothesized to be a factor in this expansion," the five researchers state, "identifying

future risk from this, and other nuisance cyanobacteria, is paramount." Working with a strain of the cyanobacterium that was originally isolated from a lake near Brisbane (Australia), Holland *et al.* "used continuous (turbidostats) and batch cultures grown under two different light regimes, and adjusted the alkalinity of the media (with an associated change in pH, HCO₃⁻ and CO₂) to assess the effect of these parameters on the specific growth rate, inorganic carbon acquisition and photosynthetic parameters of *C. raciborskii.*"

Although there were insufficient data to confirm results obtained from the low-light experiments, the Australian researchers discovered "there was a positive linear relationship in the 'high' light turbidostats between the growth rate and pH," as the potentially toxic *C. raciborskii* grew more profusely when atmospheric CO₂ concentrations were low and water pH was high, leading Holland *et al.* to conclude high-CO₂/low-pH conditions may change the composition of marine communities "to favor species that are better adapted to these new growth conditions, such as Chrysophytes," which are known to produce "more than half of the food consumed by aquatic animals," citing Maberly *et al.* (2009).

Teira et al. (2012) "tested the direct effect of an elevated CO₂ concentration (1,000 ppm) on the biomass and metabolic rates (leucine incorporation, CO₂ fixation and respiration) of two isolates belonging to two relevant marine bacterial families, Rhodobacteraceae (strain MED165) and Flavobacteriaceae (strain MED217)," referring to the former as simply Roseobacter and the latter as Cytophaga. "Contrary to some expectations," they found "lowering pH did not negatively affect bacterial growth." Doing so in fact increased the growth efficiency of Cytophaga. The scientists note, "in both cases, the bacterial activity under high CO₂ would increase the buffering capacity of seawater," concluding the responses of the two marine bacterial families "would tend to increase the pH of seawater, acting as a negative feedback between elevated atmospheric CO_2 concentrations and ocean acidification."

Lomas *et al.* (2012) note, "marine cyanobacteria, both unicellular *Prochlorococcus* and *Synechococcus* and colonial *Trichodesmium* spp., play important roles in the ocean carbon cycle and the biological carbon pump, particularly in the subtropical and tropical gyres (e.g. Partensky *et al.*, 1999; Capone *et al.*, 2005)," adding, *Trichodesmium* "is thought to account for about half of the total N₂-fixation in the oceans," citing Barcelos e Ramos *et al.* (2007), Hutchins *et al.* (2007), Levitan *et al.* (2007), and Kranz *et al.* (2009, 2010).

Working on board the RV Atlantic Explorer between July 2009 and April 2010 at the Bermuda Atlantic Time-series Study (BATS) site in the subtropical North Atlantic Ocean about 86 km southeast of Bermuda, Lomas et al. examined the Cfixation responses of natural assemblages of cyanobacteria dominated by Synechococcus and Prochlorococcus and the N₂- and C-fixation responses of isolated Trichodesmium colonies to changes in pH/pCO₂ conditions between the time of the last glacial minimum (8.4/150 ppm) and projected year 2100 values (7.8/800 ppm). They found "whole community assemblages dominated by Prochlorococcus and Synechococcus, whether nutrient-replete or P-limited, did not show a clear response of Cfixation rates to changes in pH/pCO2." They observed "Fe- and P-replete colonies of Trichodesmium increased N₂-fixation rates at pH 7.8 by 54% over ambient pH/pCO₂ conditions, while N₂-fixation at pH 8.4 was 21% lower than at ambient pH/pCO₂." They found C-fixation rates of Trichodesmium "were on average 13% greater at low pH than at ambient pH and 37% greater than at high pH." They note "these results for natural populations of all three cyanobacteria concur with previous research and suggest that one important response to changes in ocean pH and pCO₂ might be an increase in N₂ and C fixation by Trichodesmium under nutrient-replete conditions."

Lomas *et al.* say their results for *Trichodesmium*, along with similar findings by several other marine scientists, suggest "ocean acidification would likely result in a positive feedback on the growth and physiology of natural populations, resulting in a positive change in their role in ocean carbon and nitrogen cycles."

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6.3.2.1.3 Diatoms

Diatoms are a type of algae, most of which are unicellular, although they also form colonies that take the shape of filaments or ribbons. A unique feature of diatom cells is that they are encased within a special cell wall made of silica that is called a frustule, which can assume a wide variety of forms but usually consists of two asymmetrical sides with a split between them. Functionally, diatoms serve as primary producers in various marine food chains, and thus it is important to know how they may respond to continued increases in the air's CO_2 content. This section reviews much of what scientists have learned about the subject over the past several years, as summarized in the following bullet points.

- The light-saturated photosynthetic rate of the widely distributed *Skeletonema costatum* diatom is increased by elevated CO₂'s stimulating of cell numbers, chlorophyll *a* content, the photosynthetic chemistry of photosystem II, and the efficiency of its light reaction.
- The growth-promoting effect of elevated atmospheric CO₂ on diatoms and coccolithophores

probably has been responsible for limiting the rise in atmospheric CO_2 since the dawn of the Industrial Revolution to approximately 90% of what it otherwise would have been.

- Because diatoms are responsible for about half of the world's primary marine production, their enhanced growth due to atmospheric CO₂ enrichment should provide a significant brake on the rate of rise of the air's CO₂ content and reduce its ability to cause global warming.
- As diatoms serve as primary producers in numerous marine food chains, the several trophic levels above them should benefit from lower ocean pH levels as the atmosphere's CO₂ content continues to rise.

Chen and Gao (2004) grew a strain (2042) of *Skeletonema costatum*—a unicellular marine diatom, widely distributed in coastal waters throughout the world, that constitutes a major component of natural assemblages of most marine phytoplankton—in filtered nutrient-enriched seawater maintained at 20°C under a 12-hour/12-hour light/dark cycle at a light intensity of 200 µmol m⁻² s⁻¹, while continuously aerating both cultures with air of either 350 or 1,000 ppm CO₂ as they measured physiological parameters of the diatom's photosynthetic activity.

The scientists report cell numbers of the diatom "increased steadily throughout the light period, and they were 1.6 and 2.1 times higher after the 12-hour light period for the alga grown at 350 and 1000 ppm CO₂, respectively." They also found chlorophyll a concentrations in the bulk of the two CO₂ cultures "increased 4.4- and 5.4-fold during the middle 8 hours of the light period for the alga grown at 350 and 1000 ppm CO₂, respectively," and "the contents of cellular chlorophyll a were higher for the alga grown at 1000 ppm CO₂ than that at 350 ppm CO₂." The initial slope of the light saturation curve of photosynthesis and the photochemical efficiency of photosystem II "increased with increasing CO₂, indicating that the efficiency of light-harvesting and energy conversion in photosynthesis were increased." The two scientists report "the light-saturated photosynthesis rate based on cell number, the chlorophyll a content, the photosynthetic chemistry of photosystem II and the efficiency of the light reaction all increased to various degrees with elevated CO₂."

Three years later, in a study conducted between 15 May and 9 June of 2005 at the Espegrend Marine Biological Station of the University of Bergen, on a fjord in southern Norway, Riebesell *et al.* (2007) maintained nine cylindrical mesocosms—which extended from the water surface to a depth of 9–10 meters—in equilibrium with air of either ambient CO₂ concentration (350 ppm), doubled CO₂ (700 ppm) or tripled CO₂ (1,050 ppm), while measuring several phytoplanktonic physiological parameters. They found "net community carbon consumption under increased CO₂ exceeded present rates by 27% (2 x CO₂) and 39% (3 x CO₂)," and continuous oxygen measurements in the mesocosms identified "enhanced net photosynthesis to be the source of the observed CO₂ effect."

Noting "the phytoplankton groups dominating in mesocosm studies-diatoms and coccothe lithophores-are also the main primary producers in high productivity areas and are the principal drivers of biologically induced carbon export to the deep sea," the 11 scientists say their findings "underscore the importance of biologically driven feedbacks in the ocean to global change." Noting "increased CO₂ has been shown to enhance fixation of free nitrogen, thereby relaxing nutrient limitation by nitrogen availability and increasing CO₂ uptake (Barcelos e Ramos et al., 2007)," Arrigo (2007) states in a News & Views discussion of Riebesell et al.'s paper "neither these, nor other possible non-steady-state biological feedbacks, are currently accounted for in models of global climate-a potentially serious omission, given that the biological pump is responsible for much of the vertical CO₂ gradient in the ocean." Arrigo reports the diatom and coccolithophore growth-promoting effect of CO₂ measured and described by Riebesell et al. probably has been responsible for limiting the rise in atmospheric CO₂ since the dawn of the Industrial Revolution to approximately 90% of what it otherwise would have been

Sobrino *et al.* (2008) grew cultures of *Thalassiosira pseudonana*, "a widely distributed diatom," exposing them to either photosynthetically active radiation (PAR: 400–700 nm) or PAR plus ultraviolet radiation (UVR: 280–400 nm) in 500-mL Teflon bottles maintained at 20°C, using a semicontinuous approach that employed daily dilutions with fresh growth medium (filtered seawater from the Gulf Stream that was enriched with f/2 nutrients) through which air of one of two atmospheric CO₂ concentrations (380 or 1,000 ppm) was continuously bubbled. They discovered exposure of the seawater medium to CO₂-enriched air increased the photosynthetic rate of the marine diatoms by approximately 45% in the presence of PAR and by about 60% in the

presence of both PAR and UVR, and it increased their growth rate by approximately 20% in both of the radiation environments. They note, "among the phytoplankton species inhabiting the [ocean's] surface layer, diatoms are responsible for almost 40% of the ocean primary productivity (Nelson *et al.*, 1995)."

Tortell et al. (2008) measured CO₂ uptake of in phytoplankton assemblages collected at situ 35 stations in the Ross Sea polynya during austral spring and summer, together with ¹⁴C uptake for a subset of 11 station samples, while they conducted CO₂ manipulation experiments with phytoplankton collected at three Ross Sea locations in the Southern Ocean via shipboard incubations using a semicontinuous batch-culture technique. The researchers report, "for the Phaeocystis-dominated springtime phytoplankton assemblages, there was a statistically significant increase in ${}^{14}C$ fixation between 100 and 380 ppm CO₂, but no further effects observed at 800 ppm CO2." In the case of the diatom-dominated summertime phytoplankton assemblages, the CO₂induced increase in both relative growth rate and primary productivity continued through 800 ppm, and it promoted "a shift towards larger chain-forming species." Noting the larger chain-forming species of diatoms "are prolific bloom formers with a very high capacity for organic carbon export to the sediments (Stickley et al., 2005)," Tortell et al. conclude "potential CO2-dependent productivity increases and algal species shifts could thus act to increase the efficiency of the biological pump, enhancing Southern Ocean CO₂ uptake and contributing to a negative feedback on increased atmospheric CO₂."

Wu *et al.* (2010) suggest increased CO_2 availability may benefit marine phytoplankton, because "the low affinity of their carboxylating enzyme (Rubisco) for CO_2 (Badger *et al.*, 1998) ... could lead to enhanced phytoplankton growth and photosynthetic carbon fixation" in a high- CO_2 world of the future, as had been suggested by the work of Riebesell *et al.* (1993) and Hein and Sand-Jensen (1997).

Wu *et al.* cultured the diatom *Phaeodactylum tricornutum*, which had been isolated from the South China Sea, for at least 20 generations in artificial seawater equilibrated with air of either 388 or 1,000 ppm CO₂, which resulted in water pH values of either 8.15 or 7.80, respectively, while they measured the diatom's photosynthetic carbon fixation, dark respiration, and growth rates. The three researchers found photosynthetic carbon fixation was enhanced by 12% under the high CO₂ and low pH conditions. Since dark respiration also was enhanced, the daily net photosynthetic production was stimulated by a lesser 5.8%, and this value "closely agreed with the observed increase in growth," which they had independently determined to have been enhanced by 5.2% under the high CO₂ and low pH conditions.

Wu *et al.* write, if "the roughly 5% increase in the growth of diatoms were taken into account based on the values obtained in this study, this would allow diatoms to rapidly accumulate more biomass (by about 34% in 6 days) and draw down available nitrogen and other nutrients, leading to a greater biological carbon flux to the deep sea." And because diatoms contribute "about half of the marine primary production," this phenomenon would provide a significant brake on the rate of rise of the atmosphere's CO₂ concentration and its ability to cause global warming.

Boelen *et al.* (2011) assessed the photophysiology of the Antarctic diatom *Chaetoceros brevis* in seawater equilibrated with ambient CO_2 air (380 ppm) and air of approximately twice-ambient CO_2 (750 ppm) and half-ambient CO_2 (190 ppm), under four irradiance regimes: two simulating deep and shallow vertical mixing, and two that mimicked limiting and saturating stable water column conditions.

The six scientists found no significant differences between the enhanced and reduced CO₂ levels with respect to "growth, pigment content and composition, photosynthesis, photoprotection and Rubisco activity." They conclude, "within the range tested, CO₂ does not significantly affect the photophysiological performance of C. brevis." Their results "agree with other studies on marine diatoms showing little or no effect of elevated CO₂ on growth (Burkhardt et al., 1999) or maximum rates of photosynthesis (Rost et al., 2003; Trimborn et al., 2009)," although they note in other studies "elevated CO₂ concentrations enhanced growth rates (e.g., Riebesell et al., 1993; Clark and Flynn, 2000)," and "a recent field study in the Southern Ocean (Tortell et al., 2008) showed an increase in phytoplankton productivity and the promotion of large chainforming *Chaetoceros* species under elevated CO₂."

Boelen *et al.* state, "under saturating and limiting, as well as under dynamic and constant irradiance conditions, the marine Antarctic diatom *C. brevis* has the ability to adjust its cellular physiology in response to changing CO_2 levels with minimal effects on growth and photosynthesis." Although this maintenance of the status quo could be considered a neutral response to elevated CO_2 , it also could be regarded as a positive finding, given that many people contend atmospheric CO_2 enrichment will be bad for almost all forms of oceanic life.

Crawfurd et al. (2011) note diatoms are very important for the productivity of the world's oceans, as they contribute about 45% of global marine primary production, citing Mann (1999); therefore it is essential to understand how diatoms and other marine phytoplankton will respond to the higher aqueous CO₂ and lower pH conditions that will prevail in ocean surface waters in the near future, as a result of the dissolution of anthropogenic CO₂ in them. They grew more than 100 generations of the diatom Thalassiosira pseudonana in seawater maintained in equilibrium with air of either current (ambient) CO₂ concentration or expected end-of-thecentury (twice-ambient) CO2 concentration (380 or 760 ppm)—which produced pH values of 8.1 and 7.8, respectively-for three months, after which they evaluated a number of the species' physical and physiological characteristics. The five UK researchers found "very few effects on T. pseudonana of longterm culture at different pCO₂ and pH." They report, "growth rates were identical in cultures supplied with 780 or 360 ppm CO₂," and "similar results have been reported for other diatom species," citing Tortell et al. (1997), Tortell (2000), Kim et al. (2006), and Shi et al. (2009). Crawfurd et al. conclude, "if all diatoms respond in a similar fashion to T. pseudonana, acidification of this magnitude in the future ocean may have little effect on diatom productivity."

McCarthy et al. (2012) grew two strains of the diatom Thalassiosira pseudonana under low light in turbidostat photobioreactors bubbled with air containing either 390 or 750 ppm CO₂. They found the increased concentration of CO₂ led to increased growth rates in both strains of 20%-40%. They also report total cellular protein did not change between the ambient and 750 ppm CO₂ treatments, but cellular rubisco content showed a two- to three-fold increase with elevated CO₂. McCarthy et al. state the CO₂ fertilization effect on the growth rate of T. pseudonana observed at low light and nutrient repletion imparts this species with increased competitive ability, concluding "there could be a net increase in capacity for primary productivity at 750 ppm CO₂, at least with regard to small diatoms in coastal environments."

Li *et al.* (2012) investigated the diatom *Phaeodactylum tricornutum* as a model organism, culturing its cells in both low CO₂ (390 ppm) and high CO₂ (1,000 ppm), as well as at low nitrogen (10 μ mol/L) and high nitrogen (110 μ mol/L) concentrations. They report, "no direct effects on growth

rate were found between the CO_2 treatments" and "no direct effects on pigmentation were found between the CO_2 treatments." They also note "no significant change in the [quantum] yield was found between the low and high CO_2 levels" and "increased dissolved CO_2 concentration did not affect the mean cell size and cell volume of *Phaeodactylum tricornutum*." Moreover, "under the nitrogen replete treatment the CO_2 concentration did not affect the C:N ratio, even though the cells at the high CO_2 level significantly increased their nitrogen content by 13%."

Real-world data suggest diatoms will continue to operate much as they have over prior millennia as the air's CO_2 content continues to rise, or they will be significantly stimulated to do everything they did before, only much better and on a larger scale. Given that diatoms serve as the primary producers in numerous marine food chains, the several trophic levels above them also should be at worst unharmed, and probably benefited by, lower ocean pH levels.

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6.3.2.1.4 Foraminifera

Foraminifera are amoeboid protists with reticulating pseudopods—fine strands of cytoplasm that subdivide into branches that merge to form a dynamic network. They are typically less than one mm in size (but can be much larger), and they produce an elaborate calcium carbonate shell called a test, which may have one or more chambers. According to Schiebel (2002), these widespread calcifying protozoa are responsible for 32–80% of the global deep-ocean flux of calcite. Therefore, it is important to determine how various forams, as they are often called, may be affected by likely future declines in ocean pH levels. This section describes some of what scientists have learned about this subject over the past several years, briefly summarized in the following bullet points.

- Some foraminiferal species will tolerate CO₂ values one to two orders of magnitude higher than those predicted for the next few centuries.
- Other forams will tolerate CO₂ values one to two orders of magnitude greater than those predicted to occur for the extreme case of burning all the fossil fuels in Earth's crust.

• Some forams not only survive but successfully reproduce in seawater maintained in equilibrium with air containing as much as 200,000 ppm of CO₂.

Lombard et al. (2010) cultured specimens of Orbulina universa collected by scuba divers off the coast of Catalina Island, California (USA) and Globigerinoides sacculifer obtained near Puerto Rico (USA) under high and low irradiances (335 and 35 μ mol photons m⁻² s⁻¹, respectively) in filtered seawater that had its pH and carbonate ion concentration (CO_3^{2-}) manipulated by adding NaOH or HCl to it. They measured the forams' initial and final size, survival time (days from collection to gametogenesis), and final shell weight for individuals that underwent gametogenesis and grew at least one chamber. They determined under the IS92a "business as usual" scenario as defined by IPCC and projected for the year 2100, the calcification rates of G. sacculifer and O. universa "could decline by 6-13% compared to recent rates." That is not a large decline, and the four researchers note, "the future increase in temperature [predicted by IPCC] could increase the production of calcite by foraminifera, counter-acting the negative impact of ocean acidification."

Kuroyanagi et al. (2009) cultured asexually produced individuals of Marginopora kudakajimensis-a large calcifying microorganism that contributes to organic and inorganic carbon production in coral reefs-under laboratory conditions for 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, with the lower values being created by addition 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 rose by 8.6%; its mean shell weight rose by a much smaller and insignificant 0.7%. As the seawater's pH declined to 7.7, the organism's mean maximum shell diameter fell by 12.1% and its mean shell weight fell by 49.3%. Kuroyanagi et al. conclude if oceanic pH remains within the range of 8.2 to 7.9, "large foraminifers should be able to maintain present calcification rates."

Bernhard *et al.* (2009) grew the marine foraminiferal protist *Allogromia laticollaris*—which they described as "a ubiquitous protistan constituent of marine microbial systems" and "an important link in the marine food web"—in a mixture of 32% seawater and Alga-Gro seawater medium in 20-ml glass culture tubes, examining its response to several super-high atmospheric CO₂ concentrations to which the tubes were exposed: 15,000, 30,000, 60,000, 90,000 and 200,000 ppm, values compared to the study's atmospheric control concentration of 375 ppm CO₂. The protist was "able to survive 10-14-day exposure to elevated CO₂ as high as 200,000 ppm." They write, "both ATP [adenosine triphosphate, an indicator of cellular energy] data and microscopic examination demonstrated that considerable populations of A. laticollaris survived exposure to all experimental treatments of elevated CO₂, even both replicates of the 200,000-ppm CO₂ experiments." They also found "at least three specimens reproduced during exposure to either 90,000 ppm or 200,000 ppm CO₂," whereas "such reproduction was observed only once in an atmospheric [375-ppm CO₂] treatment."

The four researchers state "A. laticollaris is an appropriate species to predict the response of shallow-water thecate foraminifera to predicted increases in atmospheric CO₂, given its isolation [i.e., acquisition] from a shallow-water semi-tropical setting." They say their results indicate "at least some foraminiferal species will tolerate CO₂ values that are one to two orders of magnitude higher than those predicted for the next few centuries." Indeed, their results indicate A. laticollaris will tolerate CO₂ values one to two orders of magnitude greater than those predicted to occur for the "extreme case" of burning all fossil fuels in Earth's crust.

But aren't all forams amazingly resilient creatures? In a study broaching this question, Cannariato et al. (1999) investigated the character, magnitude, and speed of biotic responses of benthic foraminifera to millennial-scale climatic oscillations, using data from an ocean sediment core in the Northeast Pacific that extended back in time some 60,000 years. A number of rapid climatic switches over the 60,000-year record were noted, representing periods of what the three researchers call "extreme environmental variability." They found no evidence of extinctions, and the benthic ecosystems appeared to be "both resilient and robust in response to rapid and often extreme environmental conditions." The scientists note faunal turnovers occurred within decades throughout the record "without extinction or speciation." They conclude, "broad segments of the biosphere are well adapted to rapid climate change," which suggests broad segments of the biosphere may be equally well adapted to lower ocean pH levels.

Hikami *et al.* (2011) measured foram net calcification rates of two algal symbiont-bearing, reef-dwelling forams (*Amphisorus kudakajimensis* and *Calcarina gaudichaudii*) in seawater maintained at five pCO_2 concentrations (245, 375, 588, 763, and 907 ppm). They also conducted a second culture experiment in seawater in which bicarbonate ion concentrations were varied, while keeping carbonate ion concentration constant.

In the first experiment, Hikami *et al.* found "net calcification of *A. kudakajimensis* was reduced under higher pCO_2 , whereas calcification of *C. gaudichaudii* generally increased with increased pCO_2 ." In the second experiment, they found "calcification was not significantly different between treatments in *Amphisorus hemprichii*, a species closely related to *A. kudakajimensis*, or in *C. gaudichaudii*."

Explaining the results of their first experiment, the nine researchers note the upward calcification trend of *Calcarina* with rising pCO_2 "can probably be attributed to the increase in CO₂, possibly through enhancement of symbiont photosynthesis, a phenomenon known as the CO₂-fertilizing effect (e.g., Ries et al., 2009)." They note Calcarina harbor diatoms, and "both a single-species culture experiment (Wu et al., 2010) and a mesocosm bloom experiment (Engel et al., 2008) have shown that high-CO₂ seawater is favorable to diatom growth," which in turn stimulates calcification. They also note Rost et al. (2006) report dinoflagellates, which are harbored by Amphisorus, "use HCO₃ as their carbon source, so their rate of carbon fixation may remain unaffected by fluctuating CO₂ levels."

As for the second experiment, the seawater pH varied but little between the different bicarbonate ion concentration treatments, resulting in little variation in the calcification rates of both species. Hikami *et al.* conclude the different influences of sea-water chemistry they observed in the two forams may have been attributable to the different types of symbiotic algae they hosted.

Vogel and Uthicke (2012) note, "several studies highlight the importance of large benthic foraminifera (LBF) as biological indicators for water quality and ecosystem health," citing Hallock et al. (2003), Uthicke and Nobes (2008), and Uthicke et al. (2010), but "impacts of ocean acidification on LBF physiology are not well studied." They investigated "the influence of increased CO₂ on calcification and photobiology of LBF hosting different types of photosynthetic endosymbionts." The two researchers collected samples of the foraminifers Amphistegina radiata, Heterostegina depressa, and Marginopora vertebralis from two locations on Australia's Great Barrier Reef on several field trips between October 2010 and April 2011. They exposed the samples in a laboratory over a period of six weeks to four seawater conditions (467, 784, 1,169, and 1,662 ppm CO₂), periodically measuring a number of physiological parameters and processes.

The researchers found no negative effects of elevated CO₂ on the calcification of any of the LBF species investigated compared to control conditions. The growth rate of M. vertebralis increased with elevated CO₂, with mean calcification rates at the two highest CO₂ treatments (1,169 and 1,662 ppm) being 63% greater than those at the two lowest treatments (467 and 784 ppm). Increased CO_2 had no effect on chlorophyll a content in either A. radiata or H. depressa, but "chlorophyll a content approximately doubled in M. vertebralis from initial to final measurements." In addition, "the maximum quantum yield of A. radiata, H. depressa and M. vertebralis did not vary significantly between different CO₂ treatments." Nor did they find significant negative impacts on photosynthetic production and respiration in the three LBF species.

Vogel and Uthicke say their study "illustrated that the species investigated were still able to build up their calcite skeletons in CO_2 conditions predicted for the year 2100 and beyond," and "contrary to expectations, *M. vertebralis* showed significantly increased growth rates in elevated CO_2 ."

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6.3.2.1.5 Other Individual Types

Scientists also have studied phytoplankton other than coccolithophores, cyanobacteria, diatoms, and foraminifera, and this brief section reviews the findings of studies where the responses of these species to lower ocean pH levels have been either experimentally or observationally determined, as described in the bullet points below and in the text that follows them.

• Atmospheric CO₂ enrichment induced "a protective effect against the oxidative damage of UV-B-induced stress" in *Platymonas subcordiformis*, suggesting elevated CO₂ should be able to

"enhance the capacity of [UV-B] stress resistance."

- A study of *Stichococcus cylindricus* and *Stichococcus minor* revealed the two marine microalgae "were able to tolerate a broad range of pH from pH 5.0 to 9.5," as well as a broad range of salinities.
- A 2.63-fold increase in the air's CO₂ content led to increases in photosynthetic rates among the 16 ecotypes of a unicellular species of marine green alga (*Ostreococcus tauri*) that ranged from 1.02to 2.18-fold greater than the current mean, while CO₂-induced size differences among ecotypes were found to range from 1.3- to 1.9-fold greater than the current mean. Differences in plastic responses for C/N ratios, which partly determine the food quality of phytoplankton, were found to range from 1.06- to 1.56-fold greater than the current mean.

Gordillo *et al.* (2003) studied the CO₂-induced growth response of the microalgal chlorophyte *Dunaliella viridis*, which possesses a carbonconcentrating mechanism and has been used as a model species for the study of inorganic carbon uptake. They batch-cultured the chlorophyte, one of the most ubiquitous eukaryotic organisms found in hypersaline environments, in 250-ml Perspex cylinders under laboratory conditions at high (5 mM) and low (0.5 mM) nitrate concentrations, while continuously aerating the cultures with air of either 350 or 10,000 ppm CO₂.

They found atmospheric CO₂ enrichment had little effect on dark respiration in both N treatments, and it had little effect on photosynthesis in the low-N treatment. In the high-N treatment, the extra CO₂ increased photosynthesis by 114%. In the case of biomass production, the results were even more divergent: in the low-N treatment elevated CO₂ had no effect, but in the high-N treatment it nearly tripled the cell density of the culture solution. Gordillo *et al.* note "it has long been debated whether phytoplankton species are growth-limited by current levels of CO₂ in aquatic systems, i.e. whether an increase in atmospheric CO₂ could stimulate growth (Riebesell *et al.*, 1993)." Their results clearly indicate it can, if sufficient nitrogen is available.

Gordillo *et al.* also learned that in the high-N treatment, where elevated CO_2 greatly stimulated photosynthesis and biomass production, once the logarithmic growth phase had run its course and

equilibrium growth was attained, approximately 70% of the carbon assimilated by the chlorophyte was released to the water, whereas in the low- CO₂ treatment only 35% was released. Gordillo et al. write, "the release of organic carbon to the external medium has been proposed as a mechanism for maintaining the metabolic integrity of the cell (Ormerod, 1983)," and "according to Wood and Van Valen (1990), organic carbon release would be a sink mechanism protecting the photosynthetic apparatus from an overload of products that cannot be invested in growth or stored." They also note stores of photosynthetic products "are reduced to avoid overload and produce a high demand for photosynthates." Under these conditions, they conclude the process would "divert assimilated C to either the production of new biomass, or the release to the external medium once the culture conditions do not allow further exponential growth."

A second consequence of CO_2 -enhanced organic carbon release is that the internal C:N balance of the phytoplankton is maintained within a rather tight range. This phenomenon has been observed in the green seaweed *Ulva rigida* (Gordillo *et al.*, 2001) and the cyanobacterium *Spirulina platensis* (Gordillo *et al.*, 1999). What the study of Gordillo *et al.* (2003) reveals about the response of *Dunaliella viridis* to atmospheric CO_2 enrichment may be applicable to many, if not most, aquatic plants.

Yu et al. (2004) grew the marine microalgae Platymonas subcordiformis (Wille) Hazen at ambient levels of atmospheric CO₂ concentration and UV-B radiation flux density as well as at elevated levels of 5.000 ppm CO₂ and UV-B radiation characteristic of that anticipated to result from a 25% stratospheric ozone depletion under clear sky conditions in summer. By itself, they report, the elevated UV-B treatment "significantly decreased [microalgal] dry weight, photosynthetic rate, chlorophyll a and carotenoid contents," and the elevated CO2 treatment by itself "enhanced dry weight and photosynthetic rate, but chlorophyll a content and carotenoid content had no major difference compared with those of ambient UV-B and ambient CO2." They also report elevated UV-B by itself significantly increased the production of the toxic superoxide anion and hydrogen peroxide, as well as malonyldialdehyde, which is an end-product of lipid peroxidation, whereas elevated CO₂ by itself did just the opposite. In the treatment consisting of both elevated UV-B and elevated CO₂, the concentrations of these three malevolent substances were lower than those observed in the elevated UV-B and ambient CO₂

treatment. Finally, they note elevated CO_2 decreased the levels of several antioxidant enzymes found in the microalgae, reflecting their reduced need for detoxification of reactive oxygen species in the elevated CO_2 treatment.

Yu *et al.* conclude atmospheric CO₂ enrichment "could reduce the oxidative stress of reactive oxygen species to *P. subcordiformis*, and reduce the lipid peroxidation damage of UV-B to *P. subcordiformis.*" They also state, "CO₂ enrichment showed a protective effect against the oxidative damage of UV-B-induced stress," and, therefore, elevated CO₂ should be able to "enhance the capacity of stress resistance." They conclude microalgae grown under high CO₂ "would better overcome the adverse impact of environmental stress factor[s] that act via generation of activated oxygen species."

Moazami-Goudarzi and Colman (2012) measured the growth rates of two marine microalgae (Stichococcus cylindricus and Stichococcus minor) in artificial seawater, as per Berges et al. (2001), within 125-ml Erlenmeyer flasks at pH values of 5.0, 6.0, 7.0, 8.2, 9.0, and 9.5, as well as at a variety of salinity levels (25, 50, 100, 200, and 470 mM). The two Canadian researchers discovered both species had similar growth rates and grew over the range of pH 5.0 to 9.5, with "cells grown at pH 5.0, 6.0 and 7.0 showing no significant difference in growth rates." They also report "both species were found to have similar growth rates and to grow over a range of salinities at sodium chloride concentrations of 25, 50, 100, 200 and 470 mM." Moazami-Goudarzi and Colman found S. minor and S. cylindricus "were able to tolerate a broad range of pH from pH 5.0 to 9.5," as well as the broad range of salinities they investigated.

Schaum et al. (2013)write. "marine phytoplankton are the foundation of ocean ecosystems," noting "these small but mighty microbes are responsible for roughly half of global carbon fixation" and they "form a fundamental part of the biological carbon pump that exports fixed carbon to the deep ocean." They state "empirical studies so far predict changes [in response to rising atmospheric CO₂ concentrations] in phytoplankton communities using single or a few genotypes to represent functional groups," whereas the real-world variation in responses within functional groups "has not been quantified." The four researchers used "16 ecotypes of Ostreococcus tauri [a unicellular species of marine green alga] from nine habitat types," which "were obtained from the Roscoff Culture Collection and the Plymouth Marine Laboratory, grown in Keller medium and made clonal by dilution, so that each

culture originated from single cells." Those samples were "acclimated for 5–7 asexual generations to 380 ppm CO_2 or 1,000 ppm CO_2 in a closed-system and grown in semi-continuous batch cultures at low densities," allowing the researchers to "quantify variations in plastic responses to elevated CO_2 for ecologically relevant traits such as photosynthesis" while also characterizing "changes in traits affecting food quality for five of these ecotypes."

Schaum et al. note they were able to "link plasticity in photosynthesis rates to changes in the relative fitness of ecotypes during asexual growth," and they were further able to "use this link to predict which ecotypes are likely to rise in frequency in a high-CO₂ environment." They found the 2.63-fold increase in the air's CO₂ content of their experiment led to increases in photosynthetic rates among the 16 ecotypes they studied, ranging from 1.02- to 2.18-fold greater than the current mean, and CO₂-induced size differences among ecotypes were found to range from 1.3- to 1.9-fold greater than the current mean. Differences in plastic responses for C/N ratios, which partly determine the food quality of phytoplankton, were found to range from 1.06- to 1.56-fold greater than the current mean. The four scientists conclude, "as CO₂ levels increase, O. tauri will grow and photosynthesize faster, and have larger cells with a higher C/N ratio than contemporary cells," with the result "Ostreococcus, along with other green algae and cyanobacteria, are likely to increase in abundance in high-CO₂ conditions" with concomitant benefits for the biosphere.

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6.3.2.1.6 Mixtures of All Types

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on mixtures of various types of marine phytoplankton. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Ultra-high CO₂ enrichment (5,000 ppm) promoted the growth of six species of marine microalgae.
- The effects of atmospheric CO₂ enrichment on various marine phytoplankton in a fjord adjacent to the Large-Scale Facilities of the Biological Station of the University of Bergen in Espegrend, Norway revealed no significant species shifts between treatments, and "the ecosystem composition, bacterial and phytoplankton abundances and productivity, grazing rates and total grazer

abundance and reproduction were not significantly affected by CO₂ induced effects."

- "Changes in iron speciation and the resulting potential negative feedback mechanism of phytoplankton productivity on atmospheric CO₂"—i.e., the drawdown of atmospheric CO₂ due to enhanced phytoplanktonic growth and transferral of the carbon thus removed from the atmosphere to the ocean depths—"need to be considered when assessing the ecological effects of ocean acidification."
- The "broad level of pH-tolerance" observed in coastal environments likely results from the adaptation of organisms living there to the large pH fluctuations that routinely occur "as a result of respiratory and photosynthetic processes," as well as "hydrographical events," that alter the "seasonal, and even diurnal, fluctuations in coastal seawater pH" over a large range.
- "Nitrifying organisms in coastal systems tolerate a wide range of pH values," suggesting "the current hypothesis of the negative impacts of ocean acidification on nitrification, at least for the coastal ocean, might need reevaluation."
- Atmospheric CO₂ enrichment is not likely to lead to a degradation of planktonic food quality in Arctic waters.

Wolf-Gladrow *et al.* (1999) examined the direct effects of atmospheric CO_2 enrichment on marine phytoplankton, including the consequences of these phenomena for the world's oceanic carbon pump, finding the ongoing rise in the air's CO_2 content may also benefit the planet's marine biota, producing significant increases in phytoplanktonic growth rates that may "serve as negative feedbacks to anthropogenic CO_2 increase."

More than a decade later, Joint *et al.* (2011) note "the pH of the surface ocean is changing as a result of increases in atmospheric carbon dioxide," and "there are concerns about potential impacts of lower pH and associated alterations in seawater carbonate chemistry on the biogeochemical processes in the ocean." They note "it is important to place these changes within the context of pH in the present-day ocean."

According to the three researchers, "marine and freshwater assemblages have always experienced variable pH conditions." For example, "phytoplankton blooms can rapidly reduce pCO₂, with a

concomitant increase in pH," which subsequently declines as the blooms die out, demonstrating "pH is naturally variable and that marine organismsparticularly microbes-must already be capable of adapting to rapid and sometimes large changes in pH." They also note, "oceanic pH can change by up to 0.06 pH unit during the year even in the oligotrophic Central Pacific, which does not experience the dramatic phytoplankton blooms of temperate oceans." Regarding freshwater ecosystems, Joint et al. report, "Maberly (1996) showed that diel variations in a lake can be as much as 2–3 pH units," and "Talling (2006) showed that in some English lakes, pH could change by >2.5 pH units over a depth of only 14 m," noting "phytoplankton, bacteria, archaea and metazoans are all present in lakes, and appear to be able to accommodate large daily and seasonal changes in pH."

The three researchers conclude, "perhaps the most appropriate null hypothesis to test is that marine microbes possess the flexibility to accommodate pH change and there will be no catastrophic changes in marine biogeochemical processes that are driven by phytoplankton, bacteria and archaea." Many researchers have done just that.

Yu et al. (2006) grew monocultures of six species of marine microalgae (Chlorella sp., Dunaliella salina, Isochrysis galbana Parke 8701, Nitzschia Platymanas subcordiformis, closterium, and Platymanas sp.) in Erlenmeyer flasks under 14:10 dark:light 24-hour cycles through which air of either 360 or 5,000 ppm CO_2 was continuously bubbled for five days. They measured algal cell densities at oneday intervals in order to calculate and compare algal specific growth rates. All six species responded positively to the ultra-high CO₂ enrichment of the air, with the ratios of their specific growth rates in the CO₂-enriched compared to ambient-air treatments being 1.15 for Chlorella sp., 1.35 for Dunaliella salina, 1.35 for Isochrysis galbana, 1.40 for Nitzschia closterium, 1.47 for Platymanas subcordiformis, and 1.60 for *Platymanas* sp.

Yu *et al.* conclude, a "high concentration of CO_2 promotes the growth of microalgae," citing not only their results but also the findings of other researchers, including Lin (1991), Nobutaka *et al.* (1992), Riebesell *et al.* (1993), Hein and Sand-Jensen (1997), Liang and Yonemoto (1999), Hu and Gao (2001), and Xia and Gao (2001, 2002). They note, "possibly, the CO_2 enrichment made the chloroplast[s] more developed," so "both the photosynthesis and cell division rate were increased," and, therefore, "the algal cell density was enhanced."

Vogt *et al.* (2008) studied the effects of atmospheric CO_2 enrichment on various marine microorganisms in nine marine mesocosms maintained within two-meter-diameter polyethylene bags submerged to a depth of 10 meters in a fjord adjacent to the Large-Scale Facilities of the Biological Station of the University of Bergen in Espegrend, Norway. They maintained three of the mesocosms at ambient levels of CO_2 (~375 ppm), three at levels expected to prevail at the end of the current century (760 ppm or 2x CO_2), and three at levels predicted for the middle of the next century (1,150 ppm or 3x CO_2), taking measurements of numerous ecosystem parameters over a period of 24 days.

Vogt et al. detected no significant phytoplankton

species shifts between treatments, and "the ecosystem composition, bacterial and phytoplankton abundances and productivity, grazing rates and total grazer abundance and reproduction significantly were not affected by CO₂ induced effects," citing the work of et al. Riebesell (2007),Riebesell et al. (2008), Egge et al. (2007), Paulino et al. (2007), Larsen et al. (2007), Suffrian et al. (2008), and Carotenuto et al. (2007). The eight researchers say their observations suggest "the system under study was surprisingly resilient to abrupt and large pН changes."

Three oceanic CO₂enrichment experiments (I, II, and III) were carried out in 2001, 2003, and 2005 at the Marine Biological Station of

the University of Bergen at Espegrend, Norway, where researchers maintained nine marine ecosystems in two-meter-diameter polyethylene bags submerged to a depth of 10 meters in an adjacent fjord, keeping three of the mesocosms at ambient levels of CO_2 (1xCO₂), three others at 2xCO₂ and three more at 3xCO₂ (via aeration of the water column and the overlying atmosphere with CO₂-enriched air). They performed this work in the context of the Pelagic Ecosystem CO₂ Enrichment (PeECE) program, enabling the PeECE I, PeECE II, and PeECE III experiments.

After a one-time addition of nutrients intended to initiate a phytoplankton bloom on the day before the start of their 24-day study, Egge *et al.* (2009) measured primary production in the nine mesocosms at two-day intervals during the PeECE III experiment, along with oxygen production and consumption, the presence of transparent exopolymer particles, and the composition of the phytoplanktonic community. The seven scientists report, "in the second half of the experiment there was a tendency of higher production at elevated CO₂ levels," which was "visible from ca. day 10 in the cumulative production, with a significant difference between 3x and 1x CO₂ from day 20 onward," as shown in Figure 6.3.2.1.6.1.



Figure 6.3.2.1.6.1. Cumulative primary production from the start of the PeECE III experiment of Egge *et al.* (2009), adapted from the authors' paper.

Egge *et al.* state their results "demonstrate a small, but statistically significant effect of elevated CO_2 on daily primary production" that is "consistent with the over-consumption of dissolved inorganic carbon at elevated CO_2 reported by Riebesell *et al.* (2007) and Bellerby *et al.* (2008)." These observations once again suggest the planet's rising atmospheric CO_2 concentration may stimulate oceanic primary production and thereby enable the sustaining of a greater population of higher-trophic-level marine organisms.

Breitbarth et al. (2010) write, "studies of artificial and natural iron input have demonstrated iron control of phytoplankton productivity and CO₂ 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 "temporal control of iron on phytoplankton productivity was also observed in a Norwegian fjord system (Ozturk et al., 2002)." 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 natural phytoplanktonic blooms to determine whether lower ocean pH levels may affect iron speciation in seawater. The researchers made measurements in mesocosms consisting of two-meterdiameter polyethylene bags submerged to a depth of 10 meters and maintained in equilibrium with air possessing CO₂ concentrations of either 350, 700, or 1,050 ppm via aeration of the water column and the overlying atmosphere with air of the three CO₂ concentrations (Schulz et al., 2008).

The eight researchers report CO_2 perturbation and phytoplanktonic bloom development resulted in pH value ranges of 8.13–8.26, 7.82–8.08, and 7.67–7.97 at 3570, 700, and 1050ppm CO_2 , respectively. They say their measurements revealed significantly higher dFe concentrations in the high CO_2 treatment compared to the mid and low CO_2 treatments, and the high- CO_2 mesocosms showed higher values of FE(II) compared to the lower CO_2 treatments.

Breitbarth et al. 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 write, "these processes may further fuel increased phytoplankton carbon acquisition and export at future atmospheric CO₂ levels," citing Riebesell et al. (2007). They conclude, "changes in iron speciation and the resulting potential negative feedback mechanism of phytoplankton productivity on atmospheric CO2"-the drawdown of atmospheric CO2 due to enhanced phytoplanktonic growth and transferral of the carbon thus removed from the atmosphere to the ocean depths-"need to be considered when assessing the ecological effects of ocean acidification."

According to Wyatt et al. (2010), "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." The authors 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 NH₄⁺ (Zeebe and Wolf-Gladrow, 2001: Bell et al., 2007, 2008)." As a result, the future decease in ocean pH due to the ongoing rise in the air's CO₂ content could result in the transfer of more gaseous NH₃ from the overlying atmosphere to the ocean, as has been noted by Jacobson (2005).

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, a period of time that included two distinct phases of the annual spring phytoplankton bloom (a pre-bloom period of five weeks and the bloom proper of 11 weeks). They measured ambient pH for carbonate system estimates and dissolved inorganic nutrients, and they equilibrated the samples with CO₂-in-air mixtures that resulted in CO₂ 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, to be compared with the mean ambient value of 8.18.

The six scientists report 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." They also found "an overall increase in NH_x concentrations by 20% was observed between the present day CO₂ treatment (380 ppm) and 1000 ppm." Wyatt et al. write, "as excess CO2 dissociates in the oceans, the increased hydrogen ion concentration ionizes NH₃(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 NH₃(aq) in the surface water and gaseous NH₃ in the overlying atmosphere resulting in the drawdown of atmospheric NH₃ to the surface ocean." Whereas the surface waters of the WEC "are a net source of 150 μ mol/m²/vear of NH₃ to the atmosphere at present (2009)," they say it is likely "the WEC will become a net sink of 300 µmol/m²/year for atmospheric NH₃ as atmospheric CO₂ 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 NH₃ from the air to the surface waters of the WEC. This phenomenon would boost the productivity of higher oceanic trophic levels, help sequester more carbon at the bottom of the sea, and thereby reduce the rate of increase in radiative forcing that is speculated to fuel global warming.

Nielsen et al. (2012) set out to test "whether reduced pH would affect plankton communities over an incubation period of 14 days." They conducted their experiment "in a laboratory microcosm setup using a natural plankton community from the Derwent River estuary, Australia," in which "two treatments with reduced pH (8.0 and 7.7) were compared to an unaltered control of pH 8.3," and "measured parameters included community photosynthesis, nutrient uptake and biomass build-up, as well as enumeration of 25 protist taxa and quantitative HPLC of phytoplankton pigments." They found nutrient uptake and photosynthetic parameters "were all unaffected by pH treatments 8.3-7.7," treatments they say "match the predicted 21st century changes in CO₂ and pH." They note "cellular carbon and total particulate organic carbon were both completely unaffected by pH treatment within this range," and "the same was true for the succession of all 25 enumerated protist species." They report "phytoplankton pigment analysis did not show effects of pH either," and "the investigated plankton community was thus, in all ways, resilient to pH changes between 8.3 and 7.7," noting once again these changes are equivalent to the changes predicted for the next century.

Nielsen et al. write, "others have also found no or very limited changes in phytoplankton communities in response to 21st century predicted changes in pH and CO₂," citing Kim et al. (2006), Riebesell et al. (2007), and Suffrian et al. (2008). They also note, "many coastal plankton communities are impervious to such changes," citing Nielson et al. (2010). One potential reason for this "broad level of pHtolerance," as they describe it, is "pH in coastal waters often fluctuates as a result of respiratory and photosynthetic processes" and "hydrographical events," with the result "seasonal, and even diurnal, fluctuations in coastal seawater pH have been shown to encompass 7.5 to 9.6 (Macedo et al., 2001; Hansen, 2002)." They conclude "it is unlikely that the investigated plankton community would be significantly affected by a pH and CO₂ change as predicted for the 21st century."

Regarding the effects of lower ocean pH levels on the marine nitrogen cycle, Fulweiler *et al.* (2011) write, "the current hypothesis, based on the manipulation of water column pH in laboratory studies, states decreasing pH will impact the nitrogen cycle by decreasing nitrification," and this decrease in the microbial conversion of ammonium to nitrate would likely negatively impact both marine phytoplankton composition and production.

Fulweiler et al. "compiled an existing unique data set of concurrent water column nitrification rates and water column pH values from a temperate New England estuary (Narragansett Bay, Rhode Island, USA)," which had been obtained and reported previously by Berounsky (1990) and Berounsky and Nixon (1985a,b, 1990, 1993). Fulweiler et al. say they "found the exact opposite trend to the current hypothesis: water column nitrification rates were highest at low pH and decreased significantly as pH increased," and "these results are in direct contradiction to some of the more recently published studies examining the impact of ocean acidification on marine nitrification (Huesemann et al., 2002; Beman et al., 2011)." They note their findings "are consistent with previous studies from three decades ago," citing Anthonisen et al. (1976) and Focht and Verstraete (1977).

Fulweiler *et al.* emphasize their results "highlight that nitrifying organisms in coastal systems tolerate a wide range of pH values," and "the degree of negative correlation with pH may depend on site-specific environmental conditions." They conclude their findings indicate "the current hypothesis of the negative impacts of ocean acidification on nitrification, at least for the coastal ocean, might need reevaluation."

Leu et al. (2013) write, "ocean acidification occurs as a consequence of increasing atmospheric CO₂ concentrations, and is thought to represent a major threat for some groups of marine organisms" because polyunsaturated fatty acids or PUFAsessential metabolites that are synthesized only by algae and therefore have to be acquired via their ingestion by all other organisms-may not be as prominent in Arctic plankton in a high-CO₂ world as they are today, leading to a degradation of planktonic food quality. The five researchers studied the effect of lower ocean pH levels on a natural plankton community in the Arctic in a large-scale mesocosm experiment carried out in Kongsfjorden (Svalbard, Norway at 79°N), where nine mesocosms of $\sim 50 \text{ m}^3$ each were exposed to eight CO₂ levels (from natural background conditions to ~1,420 ppm, yielding pH values ranging from ~ 8.3 to 7.5).

Leu et al. report, "no indications were found for a

generally detrimental effect of ocean acidification on the planktonic food quality in terms of essential fatty acids." They write, "it is remarkable that the overall community response with respect to the relative amount of PUFAs to increased CO₂ concentrations was rather positive." They conclude "findings about detrimental effects of ocean acidification on single species in laboratory studies (as, for instance, Riebesell *et al.* (2000) or Tsuzuki *et al.* (1990)), and even their consequences for grazers (Rossoll *et al.*, 2012) are probably less relevant in a natural situation where other, more CO₂-tolerant species take over."

Leu *et al.* write, "the overall availability of essential PUFAs for higher trophic levels seems not to be affected negatively, although the specific fatty acid composition may change." They note "the overall amount of essential PUFAs available to the entire community (or at least within a certain size class) is the important measure for the algal food quality," which "also holds true for the implications for trophic transfer efficiency and consequences for phytoplankton-zooplankton ratios," as discussed by Brett and Muller-Navarra (1997).

Aberle *et al.* (2013) also set out to "test whether Arctic coastal plankton communities will be in any way affected by high pCO₂/low pH and thus susceptible to ocean acidification [(OA)]." They conducted a mesocosm experiment on a natural Arctic plankton community in Kongsfjorden, Svalbard. Over a period of about one month, they deployed and moored nine polyethylene mesocosms and injected CO_2 -enriched seawater into them to achieve three degrees of CO_2 equilibrium concentrations—low (175–250 ppm), intermediate (340–600 ppm), and high (675–1,085 ppm). They added nutrients to all three mesocosm treatments 13 days later "to ensure a sufficient nutrient supply for bloom development."

Aberle *et al.* report they "found almost no direct effects of OA on microzooplankton composition and diversity," and "both the relative shares of ciliates and heterotrophic dinoflagellates as well as the taxonomic composition of microzooplankton remained unaffected by changes in pCO₂/pH." Aberle *et al.* conclude they must reject their hypothesis that a high CO₂ concentration would alter microzooplankton community structure, carrying capacity, or phenology, on the basis of their mesocosm experiment, noting the findings of their study point to "a relatively high robustness of microzooplankton towards elevated CO₂ in coastal waters."

Johnson *et al.* (2013) write, "in response to low ambient CO_2 concentrations, most marine microalgae have evolved a carbon concentrating mechanism

(CCM) to elevate concentrations at the site of carbon fixation (Beardall and Giordano, 2002; Raven and Beardall, 2003; Raven et al., 2011)." They note, since "increases in dissolved CO₂ are predicted to cause down-regulation of microalgal CCM capacity (Giordano et al., 2005; Hopkinson et al., 2011)," which should reduce the energetic costs of CCMs (Raven, 1991), this phenomenon "will potentially allow more energy for other growth processes." They write, "as the carbon acquisition mechanisms and efficiencies of CCMs differ between algae, it is thought that rising CO₂ will benefit different species to varying degrees (Hein and Sand-Jensen, 1997; Tortell et al., 2000; Rost et al., 2003; Beardall and Raven, 2004; Riebesell, 2004; Fu et al., 2008) and may result in dramatic community shifts with profound consequences for marine biogeochemistry (Hutchins et al., 2009)."

Johnson *et al.* compared periphyton assemblages on artificial substrata installed along a coastal CO_2 gradient, ranging from a median value of 419 to 592 to 1,611 ppm, at a shallow-water cold-vent system off the island of Vulcano, NE Sicily, with the aim of testing the hypothesis that periphyton assemblages respond to CO_2 gradients and characterizing any changes in diatom and cyanobacteria populations to better understand the ecological effects of real-world lower ocean pH levels.

The six scientists report periphyton communities indeed "altered significantly CO₂ were as concentrations increased," and "CO2 enrichment caused significant increases in chlorophyll a concentrations and in diatom abundance." Furthermore, "by using chl a as an index of the photosynthetic standing crop (Underwood, 1984)," they say "periphyton biomass was found to increase substantially (fivefold) at the CO₂-enriched stations," indicating "elevations in CO2 stimulate primary productivity in these benthic assemblages." Johnson et al. conclude lower ocean pH levels are "likely to have wide-ranging consequences from local-scale influences on the structure of overlying benthic communities to effects on food web structure and larger-scale biogeochemical cycles."

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6.3.2.2 Macroalgae

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on macroalgae. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Cultures of two red macroalga grown in seawater treatments of + 650-ppm and +1,250-ppm CO₂ were enhanced by 20% and 60%, respectively, for *Gracilaria chilensis*, and by 130% and 190%, respectively, for *Gracilaria sp*.
- The ongoing rise in the air's CO₂ content likely will not "hasten the transformation of reef community structure from coral to algal dominance."
- "Elevated levels of CO₂ in seawater increase the growth rate of many seaweed species despite the variety of ways in which carbon is utilized in these algae."
- At twice the current ambient CO₂ concentration, daily net carbon gain and total wet biomass production rates of a red seaweed common to the Northeast Atlantic intertidal zone were 52 and 314% greater than under ambient CO₂ conditions.
- Slightly less than a doubling of the air's CO₂ concentration increased the mean relative growth rate of a brown seaweed from along the coast of Nanao Island, Shantou, China by about 50%, as well as its mean rate of nitrate uptake during the study's 12-hour light periods by some 200%, and its nitrate reductase activity by approximately 20% over a wide range of substrate nitrate concentrations.
- Elevated CO₂ experiments on eelgrass "led to significantly higher reproductive output, below-ground biomass and vegetative proliferation of new shoots in light-replete treatments."
- "Ocean acidification will stimulate seagrass biomass and productivity, leading to more favorable habitat and conditions for associated invertebrate and fish species."
- The global increase of CO₂ "may enhance seagrass survival in eutrophic coastal waters, where populations have been devastated by algal proliferation and reduced column light transparency."
- High pH values created by seagrass photosynthesis can help increase calcification rates of nearby marine organisms.

Gao et al. (1993) grew cultures of the red alga Gracilaria sp. and G. chilensis in vessels enriched with nitrogen and phosphorus continuously aerated with normal air of 350 ppm CO₂, air enriched with an extra 650 ppm CO₂, or air enriched with an extra 1,250 ppm CO₂ for 19 days. Compared to the control treatment, the relative growth enhancements in the +650-ppm and +1.250-ppm CO₂ treatments were 20% and 60%, respectively, for G. chilensis, and 130% and 190%, respectively, for Gracilaria sp. Gao et al. say these results suggest, "in their natural habitats or cultivation sites, photosynthesis and growth of Gracilaria species are likely to be CO₂-limited, especially when the population density is high and water movement is slow." As the air's CO₂ content continues to rise, these marine marcoalgae should be able to grow increasingly well. That also may be true of many other macroalgae, for Gao et al. note "photosynthesis by most macroalgae is probably limited by inorganic carbon sources in natural seawater," citing Surif and Raven (1989), Maberly (1990), Gao et al. (1991), and Levavasseur et al. (1991).

This finding might be construed to imply corals in a CO_2 -enriched world may be out-competed by marine macroalgae, which, to quote Langdon *et al.* (2003), "are not conspicuous on healthy reefs, but due to various anthropogenic pressures ... are becoming increasingly abundant." In an experiment they conducted at the Biosphere–2 facility near Oracle, Arizona (USA), where they studied gross primary production and calcification in a macrophytedominated ecosystem that had a coral cover of 3%, Langdon *et al.* found the ongoing rise in the air's CO_2 content will not "hasten the transformation of reef community structure from coral to algal dominance."

Xu et al. (2010) 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." They note, "much attention has been paid to the biofiltration capacity of the species (Yang et al., 2005, 2006; Zhou et al., 2006)," and some researchers have suggested it to be "an excellent species for alleviating coastal eutrophication in China (Fei, 2004)." Xu et al. examined how this seaweed might respond to elevated CO₂. They grew plants 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 μ M) or high (30 μ M) dissolved inorganic phosphorus (Pi) concentrations in contact with air of either 370 or 720 ppm CO₂,

measuring their photosynthetic rates, biomass production, and uptake of nitrate and phosphate.

As best as can be determined from Xu *et al.*'s graphical representations of their results, the 95% increase in the air's CO₂ concentration increased algal photosynthetic rates by only 5% in the natural Pi treatment but approximately 41% in the high Pi treatment. With respect to biomass production, the elevated CO₂ elicited a 48% increase in the natural Pi treatment but no increase in biomass in the high Pi treatment. The extra 29.5 μ M Pi in the high Pi treatment itself had boosted biomass production of the low-CO₂ natural-Pi treatment by approximately 83%, and additional CO₂ did not increase growth rates beyond that point.

The three Chinese researchers write, "elevated levels of CO₂ in seawater increase the growth rate of many seaweed species despite the variety of ways in which carbon is utilized in these algae." They note "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 CO2 relieves this limitation and enhances growth." Regarding the results they obtained with Gracilaria lemaneiformis-which they say "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 CO₂ levels," which in their experiment were 40% in the natural Pi treatment, because "high CO2 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."

Kubler *et al.* (1999) grew a red seaweed common to the Northeast Atlantic intertidal zone, *Lomentaria articulata*, for three weeks in hydroponic cultures subjected to various atmospheric CO₂ and O₂ concentrations to determine the effects of these gases on growth. They report oxygen concentrations ranging between 10 and 200% of ambient had no significant effects on daily net carbon gain or total wet biomass production rates in this seaweed. In contrast, CO₂ concentrations ranging between 67 and 500% of ambient had highly significant effects. At twice the current ambient CO₂ concentration, for example, daily net carbon gain and total wet biomass production rates were 52 and 314% greater than under ambient CO₂ conditions. Although this seaweed was likely carbon-saturated, when grown at five times the ambient CO_2 concentration it still exhibited daily net carbon gain and wet biomass production rates 23 and 50%, respectively, greater than those of control plants.

Zou (2005) collected specimens of a brown seaweed (Hizikia fusiforme (Harv.) Okamura) from intertidal rocks along the coast of Nanao Island, Shantou, China, and maintained them in glass aquariums in filtered natural seawater enriched with 60 µM NaNO₃ and 6.0 µM NaH₂PO₄, where they were continuously aerated with ambient air of 360 ppm CO₂ or enriched air of 700 ppm CO₂. He measured the specimens' relative growth and nitrogen assimilation rates and their nitrate reductase activities. The CO₂ enrichment increased the seaweed's mean relative growth rate by about 50%, its mean rate of nitrate uptake during the study's 12-hour light periods by 200%, and its nitrate reductase activity by approximately 20% over a wide range of substrate nitrate concentrations.

Zou notes "the extract of *H. fusiforme* has an immunomodulating activity on humans and this ability might be used for clinical application to treat several diseases such as tumors (Suetsuna, 1998; Shan *et al.*, 1999)." He also reports the alga "has been used as a food delicacy and an herbal ingredient in China, Japan and Korea." He says it "is now becoming one of the most important species for seaweed mariculture in China, owing to its high commercial value and increasing market demand." In addition, Zou notes "the intensive cultivation of *H. fusiforme* would remove nutrients more efficiently with the future elevation of CO_2 levels in seawater, which could be a possible solution to the problem of ongoing coastal eutrophication."

Palacios and Zimmerman (2007) conducted an experiment on eelgrass (Zostera marina) at the Duke Energy-North America Power Plant at Moss Landing, California (USA), where flue gas generated by the power plant furnace was piped approximately 1 km to a site where it was bubbled through outdoor flowthrough seawater aquaria at rates that produced four aqueous CO₂ treatments characteristic of: "(1) the present day atmosphere, with approximately 16 µM $CO_2(aq)$, (2) CO_2 projected for 2100 that increases the $CO_2(aq)$ concentration of seawater to approximately 36 µM CO₂(aq), (3) CO₂ projected for 2200 that increases the $CO_2(aq)$ concentration of seawater to 85 μ M CO₂(aq), and (4) a dissolved aqueous CO₂ concentration of 1123 μ M CO₂(aq), which triples the light-saturated photosynthesis rate of eelgrass (Zimmerman et al., 1997)."

The researchers found elevated CO_2 "led to significantly higher reproductive output, below-ground biomass and vegetative proliferation of new shoots in light-replete treatments," those receiving light at 33% of the surface irradiance level. They write, "shoots growing at 36 μ M CO₂(aq) were 25% larger than those in the unenriched treatment [16 μ M CO₂(aq)]," and "at 85 μ M CO₂(aq) shoots were 50% larger than those in the unenriched treatment and at 1123 μ M CO₂(aq) shoots were almost twice as large as those in the unenriched treatment." They found at 1123 μ M CO₂(aq) "22% of the shoots differentiated into flowers, more than twice the flowering output of the other treatments at this light level."

Noting "increased $CO_2(aq)$ is capable of increasing eelgrass reproductive output via flowering, and area-specific productivity via vegetative shoot proliferation under naturally replete light regimes," Palacios and Zimmerman state "the resulting increases in eelgrass meadow density may initiate a positive feedback loop that facilitates the trapping of sediments and prevents their resuspension, thereby reducing turbidity and increasing light penetration in coastal habitats," such that the resulting increased light penetration "may allow seagrass colonization depths to increase even further."

The two researchers also suggest the CO₂-induced increase in the productivity of eelgrass may "enhance fish and invertebrate stocks as well." They suggest the "deliberate injection of CO₂ to seawater may facilitate restoration efforts by improving the survival rates of recently transplanted eelgrass shoots," noting "it can buffer the negative effects of transplant shock by increasing rhizome reserve capacity and promoting shoot proliferation in light-replete environments." In addition, they say it "may also facilitate eelgrass survival in environments where conditions are periodically limiting, such as long dark winters or unusually warm summers that produce unfavorable productivity to respiration ratios," and "CO2 injection may also promote flowering and seed production necessary for expansion and maintenance of healthy eelgrass meadows." Finally, they suggest "rising concentrations of CO₂(aq) may increase vegetative propagation and seed production of other seagrass populations besides eelgrass."

According to Suarez-Alvarez *et al.* (2012), "the increase of coastal activities which produce important amounts of wastes, including inorganic nutrients (Troell *et al.*, 2003), makes micro- and macroalgae interesting organisms to predict possible impacts, responses, and remediation processes by considering biomass production through cultivation techniques,"

citing Gao *et al.* (1991, 1993), Gao and McKinley (1994), Keffer and Kleinheinz (2002), Doucha *et al.* (2005), and Israel *et al.* (2005). They note, "macroalgae, in particular, have been the object of additional interest for CO_2 remediation (Gao and McKinley, 1994) because of their solar energy conversion capacity, high productivity values (higher than most productive terrestrial crops) and the possibility of being, in many cases, intensively cultivated."

Suarez-Alvarez et al. cultivated 8-gram fragments of the macroalga Hypnea spinella in 1-L flasks containing filtered seawater enriched with 140 µM NH₄Cl and 14 µM KH₂PO₄ for seven days of acclimation. They then culled the plants to their initial density and grew them for nine more days at ambient (360 ppm), 750, or 1,600 ppm atmospheric CO₂, measuring various plant physiological properties and processes. The authors report light-saturated net photosynthesis rates in the 750 ppm and 1,600 ppm CO₂ treatments were 41.5% and 50.5% greater, respectively, than in the 360 ppm treatment. Relative growth enhancements were 85.6% and 63.2% greater, respectively, and maximum ammonium uptake rates were enhanced by 24.2% and 19.9%, respectively. "From a practical point of view," Suarez-Alvarez et al. write, "these results suggest that intensive culture of H. spinella operated in biofilters might be enhanced by CO₂ supply to generate higher biomass productivities and better nitrogen biofiltration efficiencies," and "the use of flue gases for this purpose would also improve the ability of bioremediation of these biofilters, as has already been tested for Gracilaria cornea," citing Israel et al. (2005).

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 Beer et al. (2006). They also observe Thalassia hemprichii "is among the most widely-distributed seagrass species in an Indo-Pacific flora, dominating in many mixed meadows," citing Short et al. (2007). They collected intact vegetative plants of T. hemprichii from Xincun Bay of Hainan Island, Southern China, which they transported to the laboratory and cultured in flowthrough seawater aquaria bubbled with four concentrations of CO₂ representative of the present global ocean, with a pH of 8.10; the projected ocean for 2100, with a pH of 7.75; the projected ocean for 2200, with a pH of 7.50; and the ocean characteristic of "an extreme beyond the current predictions" (a 100-fold increase in free CO_2 , with a pH of 6.2).

The three researchers found the "leaf growth rate of CO₂-enriched plants was significantly higher than that in the unenriched treatment," "nonstructural carbohydrates (NSC) of T. hemprichii, especially in belowground tissues, increased strongly with elevated CO2," and "belowground tissues showed a similar response with NSC." The Chinese scientists list several implications of their finding that "CO₂ enrichment enhances photosynthetic rate, growth rate and NSC concentrations of T. hemprichii." With higher atmospheric CO₂ concentrations, they write, "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 CO₂ may enhance seagrass survival in eutrophic coastal waters, where populations have been devastated by algal proliferation and reduced column light transparency." They conclude "ocean acidification will stimulate seagrass biomass and productivity, leading to more favorable habitat and conditions for associated invertebrate and fish species."

Wu et al. (2008) listed several known effects of a CO₂-enriched atmosphere on micro- and macro-algae living in the world's oceans. According to the authors, "enriched CO₂ up to several times the present atmospheric level has been shown to enhance photosynthesis and growth of both phytoplanktonic and macro-species that have less capacity of CCMs [CO₂-concentrating mechanisms]," and "even for species that operate active CCMs and those whose photosynthesis is not limited by CO₂ in seawater, increased CO₂ levels can down-regulate their CCMs and therefore enhance their growth under lightlimiting conditions," because "at higher CO2 levels, less light energy is required to drive CCM." They report enhanced CO₂ levels have been found to enhance the activity of nitrogen reductase in several marine plants, and this phenomenon "would support enhanced growth rate by providing adequate nitrogen required for the metabolism under the high CO₂ level." They write, "altered physiological performances under high-CO₂ conditions may cause genetic alteration in view of adaptation over long time scales," and "marine algae may adapt to a high CO2 oceanic environment so that evolved communities in [the] future are likely to be genetically different from contemporary communities."

Semesi et al. (2009) investigated whether diel variations in seawater pH caused by the photosynthetic activity of seagrass meadows within Chwaka Bay (Zanzibar, Tanzania) could affect the calcification and photosynthesis rates of calcareous red algae (Hydrolithon sp. and Mesophyllum sp.) and green algae (Halimeda renschii) growing within the They measured rates marine meadows. of calcification and relative photosynthetic electron transport (rETR) of the algae in situ in open-bottom incubation cylinders either in the natural presence of the rooted seagrasses or after their leaves had been removed.

Semesi et al. report "seagrass photosynthesis increased the seawater pH within the cylinders from 8.3-8.4 to 8.6-8.9 after 2.5 hours (largely in conformity with that of the surrounding seawater), which, in turn, enhanced the rates of calcification 5.8fold for Hydrolithon sp. and 1.6-fold for the other 2 species." They also found "the rETRs of all algae largely followed the irradiance throughout the day and were (in Mesophyllum sp.) significantly higher in the presence of seagrasses." The three researchers "algal calcification within conclude seagrass meadows such as those of Chwaka Bay is considerably enhanced by the photosynthetic activity of the seagrasses, which in turn increases the seawater pH."

They state the high pH values created by seagrass photosynthesis are what caused the elevated calcification rates of the macroalgae, and this observation has further implications. It suggests, for example, the lowering of seawater pH caused by higher atmospheric CO₂ concentrations—which results in a lowering of the calcium carbonate saturation state of seawater, and which has been predicted to lead to reductions in coral calcification rates-may be counteracted by CO₂-induced increases in the photosynthetic activity of the symbiotic zooxanthellae of Earth's corals, which may boost the pH of seawater in intimate contact with the coral host, allowing the host to increase its calcification rate in CO₂-enriched seawater, or at least not suffer a major reduction in calcification.

Smith *et al.* (2013) provide additional support for this thesis. They state, "benthic marine primary producers affect the chemistry of their surrounding environment through metabolic processes." They note, "photosynthesis and respiration will elevate or depress the concentration of oxygen in the diffusive boundary layer," and "acid-base regulation and biomineralization/dissolution for calcifying species can alter the relative concentration of inorganic carbon species and thus pH."

To compare species-specific rates of change in pH and oxygen concentrations over a diel cycle for several species of common benthic coral reef organisms-including corals, turf algae, and fleshy and calcifying macroalgae—Smith et al. assessed the generality of results across divergent types of reefs in the Caribbean and Pacific. They found "more productive fleshy taxa have the potential to raise both oxygen and pH during the day to a greater extent than calcified species." This discovery, as well as similar observations reported by Anthony et al. (2011) and Kleypas et al. (2011), suggest "non-calcifying primary producers, especially those driving large amplitudes in diurnal pH fluctuations, may be important 'buffer organisms' against potential ocean acidification on coral reefs." They write, "while particular species of macroalgae can negatively affect corals in a variety of ways," some fleshy algae "may provide a buffering capacity to future ocean acidification scenarios."

Johnson et al. (2012) note, "CO₂ gradients in natural settings, where whole ecosystems have been exposed to elevated levels of CO₂, allow us to investigate changes in the interactions, competition, predation and/or herbivory that involve long-lived metazoan species in benthic marine ecosystems." They observe, "volcanic CO₂ gradients are beginning to reveal the ecological shifts that can be expected to occur with globally increasing atmospheric CO₂ in both temperate (Hall-Spencer et al., 2008) and tropical ecosystems (Fabricius et al., 2011)." Johnson et al. assessed the abundance of herbivores (sea urchins) and the response of brown macroalgae (Padina spp.) to increasing levels of CO₂ in two natural settings. One of the sites was a set of shallow. volcanic CO₂ seeps on the island of Vulcano, NE Sicily, where P. pavonica was studied. The other site, where they studied P. australis, was a comparable set of seeps in the D'Entrecasteaux Island group, Papua New Guinea.

The five scientists found "a reduction in sea urchin abundances alongside a proliferation of *Padina* spp., as CO_2 levels increased" along both temperate and tropical rocky shores. The predator sea urchins were absent from locations that had the highest CO_2 levels (lowest pH), while "even in the lowest pH conditions, *P. pavonica* and *P. australis* were still able to calcify, seemingly from the enhancement of photosynthesis under high levels of CO_2 ."

Johnson et al. suggest the absence of sea urchins

in the CO₂-enriched areas "may be one explanation for the proliferation of *Padina* spp., as it becomes released from the top-down control by these keystone grazers," noting "this effect of sea urchin removal has been observed in other *Padina* sp. populations (Sammarco *et al.*, 1974) and across other Phaeophyte assemblages (Leinaas and Christie, 1996; Ling *et al.*, 2010)." They note "increased photosynthetic activity at high CO₂ has also been observed in other calcified macroalgae (Reiskind *et al.*, 1988; Semesi *et al.*, 2009)," and in "non-calcified macroalgae (Kubler *et al.*, 1999; Connell and Russell, 2010; Russell *et al.*, 2011)."

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6.3.3 Effects on Marine Animals

6.3.3.1 Bivalves

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on marine bivalves. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Juvenile king scallops display a tolerance to lower ocean pH levels at *p*CO₂ levels below 1,600 ppm.
- Mussel larvae (*Mytilus edulis*) reared in a laboratory setting mimicking a cold-water environment revealed "no marked effect on fertilization success, development time, or abnormality to the D-shell stage, or on feeding of mussel larvae" from lower ocean pH levels , and under such conditions (pH 7.6) the larvae "were still able to develop a shell in seawater under-saturated with respect to aragonite."
- A laboratory experiment examining "the combined effects of elevated *p*CO₂ and food availability on juvenile *M. edulis* growth and calcification" showed "only minor impacts of *p*CO₂ up to 3350 μatm."
- At a naturally CO₂-enriched ocean site, growth and calcification rates of *M. edulis* were "seven times higher" at an "inner fjord field station (mean pCO_2 ca. 1000 µatm) in comparison to a low pCO_2 outer fjord station (ca. 600 µatm)," demonstrating "a high inherent resilience of calcifying benthic communities in an estuarine, eutrophic habitat to elevated seawater pCO_2 ," where "food supply, and not pCO_2 , appears to be the primary factor driving biomass and biogenic CaCO₃ production, as well as community structure."
- "Selective breeding may be a solution to 'climateproof' [the Sydney rock oyster] from the impacts of ocean acidification."

- Larvae spawned from adult Sydney rock oysters (*Saccostrea glomerata*) growing in elevated CO₂ (reduced pH) seawater "were larger and developed faster" than those spawned from adults growing under ambient conditions, suggesting "previous studies that have investigated the effects of elevated CO₂ on the larvae of molluscs and other marine organisms [whose predecessors had not been exposed to elevated CO₂] may overestimate the severity of their responses" to lower ocean pH levels.
- Sperm swimming speeds and fertilization success of the Pacific oyster (*Crassostrea gigas*) are slightly increased under lower ocean pH levels.
- Effects of lower ocean pH levels on *Crassostrea* gigas larvae "during the first three days of development are not significant as long as CO₃²⁻ concentrations remain above aragonite saturated conditions."
- The "pre-adapted ability to resist a wide range of decreased pH may provide *C. gigas* with the necessary tolerance to withstand rapid pH changes over the coming century."
- The discovery of four-decades-old mussels living "in natural conditions of pH values between 5.36 and 7.29" attest to "the extent to which long-term adaptation can develop tolerance to extreme conditions."

Sanders et al. (2013) "investigated the effects on oxygen consumption, clearance rates and cellular turnover in juvenile [king scallop] Pecten maximus following three months' laboratory exposure to four pCO₂ treatments (290, 380, 750, and 1140 ppm)." The four researchers state "none of the exposure levels were found to have significant effects on the clearance rates, respiration rates, condition index or cellular turnover (RNA:DNA) of individuals." These findings are compatible with those of Anderson et al. (2013), who also studied the growth, development, and survival of the initial larval stages of P. maximus and found them to be susceptible to the deleterious effects of lower ocean pH levels only at pCO_2 levels of 1,600 ppm and above. Sanders et al. conclude their results suggest "where food is in abundance, bivalves like juvenile P. maximus may display a tolerance to limited changes in seawater chemistry."

Berge *et al.* (2006) collected blue mussels (*Mytilus edulis* L.) from the outer part of the

Oslofjord outside the Marine Research Station Solbergstrand in Norway and placed them in five 5-L aquariums continuously supplied with low-foodsupply seawater extracted from the top meter of the Oslofjord outside the Marine Research Station Solbergstrand in Norway, continuously adding CO₂ to the waters of the aquaria so as to maintain them at five pH values (means of 8.1, 7.6, 7.4, 7.1, and 6.7) for 44 days. Shell lengths at either the time of death or at the end of the study were determined and compared to lengths measured at the start of the study.

According to the authors, "the increased concentration of CO_2 in the water and the correspondingly reduced pH had no acute effects on the mussels." The Norwegian researchers report, "mean increments of shell length were much lower for the two largest CO_2 additions compared to the values in the controls, while for the two smallest doses the growth [was] about the same as in the control, or in one case even higher," such that there were "no significant differences between the three aquaria within the pH range 7.4–8.1."

Berge et al. conclude their results "indicate that future reductions in pH caused by increased concentrations of anthropogenic CO_2 in the sea may have an impact on blue mussels," but "comparison of estimates of future pH reduction in the sea (Caldeira and Wickett, 2003) and the observed threshold for negative effects on growth of blue mussels [which they determined to lie somewhere between a pH of 7.4 and 7.1] do however indicate that this will probably not happen in this century." Caldeira and Wickett's calculation of the maximum level to which the air's CO₂ concentration might rise yields a value that approaches 2,000 ppm around the year 2300, representing a surface oceanic pH reduction of 0.7 units, which drops the pH only to 7.4, the upper limit of the "threshold for negative effects on growth of blue mussels" found by Berge et al.

Noting "there is a particular need to study effects of OA [lower ocean pH levels] on organisms living in cold-water environments due to the higher solubility of CO₂ at lower temperatures," Bechmann *et al.* (2011) maintained mussel (*Mytilus edulis*) larvae in a laboratory setting under the OA scenario predicted for the year 2100 (pH 7.6) and compared them against batches of larvae held under the current oceanic pH of 8.1 (the control treatment), keeping water temperature at a constant 10°C. They found "no marked effect on fertilization success, development time, or abnormality to the D-shell stage, or on feeding of mussel larvae in the low-pH treatment," and the *M. edulis* larvae "were still able to develop a shell in seawater under-saturated with respect to aragonite (a mineral form of CaCO₃)." They also found after two months of exposure the mussels were 28% smaller in the pH 7.6 treatment than in the control treatment. They write, "if only the larger larvae settle and survive in the field, the effects of OA on the mussel population may not be dramatic."

Thomsen et al. (2010) note, "as most laboratory experiments cannot account for species genetic adaptation potential, they are limited in their predictive power." Thus studies investigating "naturally CO₂-enriched habitats" have "recently gained attention, as they could more accurately serve as analogues for future, more acidic ecosystems." Thomsen et al. studied the macrobenthic community in Kiel Fjord, a naturally CO₂-enriched site in the Western Baltic Sea dominated by calcifying marine invertebrates. They determined in 34%, 23%, and 9% of the 42 weeks they were there, the partial pressure (p) of CO_2 in the water exceeded preindustrial pCO_2 (280 ppm) by a factor of three (>840 ppm), four (>1,120 ppm), and five (>1,400 ppm), respectively.

The German scientists report juvenile blue mussel (*Mytilus edulis*) recruitment "peaks during the summer months, when high water pCO_2 values of ~1000 ppm prevail." Their short-term laboratory research indicates "blue mussels from Kiel Fjord can maintain control rates of somatic and shell growth at a pCO_2 of 1400 ppm." At 4,000 ppm pCO_2 , however, both shell mass and extension rates were significantly reduced; but "regardless of the decreased rates of shell growth at higher [1,400] pCO_2 , all mussels increased their shell mass at least by 150% during the 8-week trial, even at Ω arg (Ω calc) as low as 0.17 (0.28)," where Ω is the calcium carbonate saturate state of either aragonite (arg) or calcite (calc).

Thomsen *et al.* conclude it is likely "long-term acclimation to elevated pCO_2 increases the ability to calcify in *Mytilus* spp.," citing Michaelidis *et al.* (2005) and Ries *et al.* (2009) in addition to their own study. They say they could find "no causal relationship between the acid-base status and metabolic depression in this species at levels of ocean acidification that can be expected in the next few hundred years (IPCC, 2007)," after discovering in the laboratory) "communities dominated by calcifying invertebrates can thrive in CO_2 -enriched coastal areas."

Working at the same location three years later with a different set of coauthors in a similarly coupled laboratory and field study, Thomsen *et al.* (2013)

examined "the annual pCO_2 variability in [the Kiel Fjord] habitat and the combined effects of elevated pCO_2 and food availability on juvenile *M. edulis* growth and calcification." In the laboratory experiment, "mussel growth and calcification were found to chiefly depend on food supply, with only minor impacts of pCO_2 up to 3,350 µatm." In the field location (Kiel Fiord), where maximum pCO_2 values experienced during the summer were about 2,500 µatm at the surface of the fjord and more than 3,000 µatm at its bottom, they observed "seven times higher growth and calcification rates of M. edulis at a high pCO_2 inner fjord field station (mean pCO_2 ca. 1,000 μ atm) in comparison to a low *p*CO₂ outer fjord station (ca. 600 µatm)." They note this high inner fjord productivity "was enabled by higher particulate organic carbon concentrations," as a result of the fjord's "being "highly impacted by eutrophication, which causes bottom water hypoxia and consequently high seawater pCO_2 ." Thomsen *et al.* conclude their study demonstrates "a high inherent resilience of calcifying benthic communities in an estuarine, eutrophic habitat to elevated seawater pCO_2 ," where "food supply, and not pCO_2 , appears to be the primary factor driving biomass and biogenic CaCO₃ production, as well as community structure."

Range et al. (2011) conducted a 75-day controlled CO₂ perturbation experiment designed to test the effects of increased pCO_2 and reduced pH of seawater on the calcification, growth, and mortality of juvenile Ruditapes decussatus clams. They manipulated the carbonate chemistry of seawater by diffusing pure CO₂ into natural seawater to attain two reduced pH levels (by -0.4 and -0.7 pH unit compared to unmanipulated seawater). The authors hypothesized the juvenile clams would exhibit reduced net calcification, reduced growth of the shell and soft tissue, and increased mortality in the lower-pH conditions. At the conclusion of their experiment, however, the eight researchers found "no differences among pH treatments in terms of net calcification, size or weight of the clams," disproving the first two of their three hypotheses. Their third hypothesis also proved to be wrong-doubly wrong, in fact-for not only was juvenile clam mortality not increased in the low-pH seawater, mortality was significantly reduced in the acidified treatments, which they describe as an "unexpected result."

The Portuguese scientists conclude by noting life is intriguingly complex and "the generalized and intuitively attractive perception that calcification will be the critical process impacted by ocean acidification is being increasingly challenged," citing Widdicombe and Spicer (2008) and Findlay et al. (2009).

To provide a better understanding of the potential for the Sydney rock oyster (Saccostrea glomerata) to adapt to the threat of lower ocean pH levels, Parker et al. (2011) measured the within- and betweenpopulation variability in the species' growth response to elevated pCO_2 , working with oysters (denoted as wild) they collected from intertidal and shallow subtidal habitats along the southeast coast of Australia, as well as two lines (QB and LKB) of the same species that had been selectively bred to support the country's oyster aquaculture industry. The authors report the wild oysters experienced a 64% reduction in growth after four days in an elevated pCO_2 environment of 1,000 ppm (with a water pH of 7.84) compared to wild ovsters reared in the ambient pCO_2 environment of 375 ppm (with a water pH of 8.20). The growth reduction experienced by OB ovsters growing in the same two environments was 45%, and that experienced by LKB oysters was 25%. They report the LKB oysters reared at elevated pCO_2 "grew slightly better than the wild ovsters reared at ambient pCO₂." Such observations, Parker et al. write, provide "preliminary evidence that selective breeding may be a solution to 'climate-proof' important aquaculture industries from the impacts of ocean acidification."

Parker et al. (2012) introduce their follow-up study by noting analyses of the impact of lower ocean pH levels on marine organisms conducted to date "have only considered the impacts on 'adults' or 'larvae,' ignoring the potential link between the two life-history stages and the possible carry-over effects that may be passed from adult to offspring," citing Dupont et al. (2010), Hendriks et al. (2010), and Kroeker et al. (2010). Parker et al. placed adults of wild-collected and selectively bred populations of the Sydney rock oyster (Saccostrea glomerata), obtained at the beginning of reproductive conditioning, in seawater equilibrated with air of either 380 ppm CO₂ or 856 ppm CO₂ which produced seawater pH values of 8.2 and 7.9, respectively, after which they measured the development, growth, and survival responses of the two sets of larvae.

The six scientists found "larvae spawned from adults exposed to elevated PCO_2 were larger and developed faster." In addition, "selectively bred larvae of *S. glomerata* were more resilient to elevated CO_2 than wild larvae," as "measurement of the standard metabolic rate (SMR) of adult *S. glomerata* showed that at ambient CO_2 , SMR is increased in selectively bred compared with wild oysters," and it is further increased "during exposure to elevated CO_2 ." These findings suggest "previous studies that have investigated the effects of elevated CO_2 on the larvae of molluscs and other marine organisms [whose predecessors had not been exposed to elevated CO_2] may overestimate the severity of their responses." They conclude "marine organisms may have the capacity to acclimate or adapt to elevated CO_2 over the next century."

Miller *et al.* (2009) grew larvae of two oyster species—the Eastern oyster (*Crassostrea virginica*) and the Suminoe oyster (*Crassostrea ariakensis*)—for up to 28 days in estuarine water in equilibrium with air of four CO₂ concentrations (280, 380, 560, and 800 ppm) 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 IPCC. They maintained these levels by periodically aerating the aquaria with air containing 1% CO₂, assessing larval growth via image analysis and determining calcification 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 CO₂ concentrations, they "appeared to grow, calcify and develop normally with no obvious morphological deformities, conditions of significant aragonite despite undersaturation." The scientists state these findings "run counter to expectations that aragonite shelled larvae should be especially prone to dissolution at high pCO2." They note, "both oyster species generated larval shells that were of similar mean thickness, regardless of pCO_2 , Ω arag [aragonite compensation point] or shell area," remarking they "interpret the pattern of similar shell thickness as further evidence of normal larval shell development."

Working with another oyster species (Crassostrea gigas). Havenhand and Schlegel (2009) observed and measured sperm swimming behavior and fertilization kinetics in response to lower ocean pH levels . The ovsters, collected from a mixed mussel/ovster bed on the coast of western Sweden, were kept in flowthrough tanks of filtered sea water the scientists maintained at either the normal ambient pH level or a level reduced by about 0.35 units they created by bubbling CO₂ through the water. In water of pH 8.15, mean sperm swimming speeds were $92.1 \pm 4.8 \mu m/s$, whereas in water of pH 7.8 they were slightly higher, at 94.3 \pm 5.5µm/s, although the difference was not statistically significant. Mean fertilization success in water of pH 8.15 was 63.4%, whereas in water of pH 7.8 it was also slightly higher, at 64.1%; this difference, too, was not statistically significant.

The Swedish scientists state "the absence of significant overall effects of pH on sperm swimming behavior and fertilization success is remarkable," emphasizing power analyses they conducted "showed clearly that these results were not due to inadequate statistical power," and "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 CO₂-induced acidification expected by the end of this century."

Gazeau et al. (2011) assessed "the impact of several carbonate-system perturbations on the growth of Pacific oyster (Crassostrea gigas) larvae during the first three days of development (until shelled Dveliger larvae)." They used filtered seawater obtained from the Oosterschelde (a nearby tidal inlet) with five chemistries obtained "by separately manipulating pH, total alkalinity and aragonite saturation state." The seven scientists report "developmental success and growth rates were not directly affected by changes in pH or aragonite saturation state but were highly correlated with the availability of carbonate ions ... as long as carbonate ion concentrations were above aragonite saturation levels." When carbonate ion concentrations dropped below aragonite saturation levels, they found growth and development "strongly decreased."

Gazeau *et al.* conclude, "the effects of ocean acidification on larvae of *Crassostrea gigas* from the Oosterschelde estuary during the first three days of development are not significant as long as $CO_3^{2^-}$ concentrations remain above aragonite saturated conditions." They add, "due to relatively high levels of total alkalinity in this area, it is not expected that seawater will become corrosive for aragonite following a decrease of 0.3 to 0.4 pH unit."

The French, English, and Dutch researchers also write, "most calcifying species, including mollusks, are able to concentrate Ca^{2+} and CO_3^{2-} ions at the site of calcification (McConnaughey and Gillikin, 2008)," and the bivalves they studied "should therefore be able to regulate calcification rates under suboptimal concentrations of Ca^{2+} and CO_3^{2-} ." They note, "Thomsen *et al.* (2010) have shown that blue mussels are actively growing in a bay of the Western Baltic Sea naturally enriched with high CO_2 water," and "juvenile recruitment occurs in summer time coinciding with low pH levels and aragonite undersaturated conditions." Thus the evidence indicates lower ocean pH levels will not seriously affect mollusks.

Ginger *et al.* (2013) note, "our knowledge of the effect of reduced pH on *C. gigas* larvae presently

relies presumptively on four short-term (< 4 days) survival and growth studies." They studied "the effects of long-term (40 days) exposure to pH 8.1, 7.7 and 7.4 on larval shell growth, metamorphosis, respiration and filtration rates at the time of metamorphosis," as well as the juvenile shell growth and structure of C. gigas. The seven scientists discovered "mean survival and growth rates were not affected by pH"; "the metabolic, feeding and metamorphosis rates of pediveliger larvae were similar, between pH 8.1 and 7.7"; "the pediveligers at pH 7.4 showed reduced weight-specific metabolic and filtration rates, yet were able to sustain a more rapid post-settlement growth rate"; and "no evidence suggested that low pH treatments resulted in alterations to the shell ultra-structures or elemental compositions (i.e., Mg/Ca and Sr/Ca ratios)." Ginger et al. conclude "larval and post-larval forms of the C. gigas in the Yellow Sea are probably resistant to elevated CO₂ and decreased near-future pH scenarios." They note "the pre-adapted ability to resist a wide range of decreased pH may provide C. gigas with the necessary tolerance to withstand rapid pH changes over the coming century."

Working with juvenile Mytilus galloprovincialis specimens obtained from a mussel raft in the Ria de Ares-Betanzos of Northwest Spain and reared in an experimental bivalve hatchery in Tavira, Portugal, Fernandez-Reiriz et al. (2012) tested the effects of three levels of seawater acidification caused by increasing concentrations of atmospheric CO₂: a natural control level plus two lesser levels of pH, one reduced by 0.3 pH unit and another reduced by 0.6 pH unit. They measured several responses of the mussels after 78 days of exposure to the three sets of pH conditions, focusing on clearance and ingestion rate, absorption efficiency, oxygen consumption, ammonia excretion, oxygen to nitrogen ratio, and scope for growth. The five researchers found no significant differences for clearance, ingestion, and respiration rates. The absorption efficiency and ammonium excretion rate of the juvenile mussels were inversely related to the 0.6 pH reduction, while the maximal scope for growth and tissue dry weight also were observed in the mussels exposed to the pH reduction of 0.6 unit. Fernandez-Reiriz et al. conclude their results suggest M. galloprovincialis "could be a tolerant ecophysiotype to CO₂ acidification, at least in highly alkaline coastal waters," noting, "mytilids are also able to dominate habitats with low alkalinity and high pCO₂," citing Thomsen et al. (2010).

Working with the same species of mussels obtained from the same location off the coast of Northwest Spain under an identical pH regime, Range et al. (2012) tested the effects of seawater acidification on growth, calcification, and mortality of six-month-old juveniles. The eight researchers found the growth of the mussels, measured as relative increases in shell size and body weight during the 84 days of the experiment, "did not differ among treatments." A tendency for faster shell growth under elevated CO₂ was apparent, "at least during the first 60 days of exposure." They note calcification was reduced under elevated CO₂, but by only up to 9%. They state, "given that growth was unaffected, the mussels clearly maintained the ability to lay down CaCO₃, which suggests post-deposition dissolution as the main cause for the observed loss of shell mass." They also write, "mortality of the juvenile mussels during the 84 days was small (less than 10%) and was unaffected by the experimental treatments." The Portuguese scientists conclude "there is no evidence of CO2-related mortalities of juvenile or adult bivalves in natural habitats, even under conditions that far exceed the worst-case scenarios for future ocean acidification (Tunnicliffe et al., 2009)."

Tunnicliffe et al. (2009) studied Bathymodiolus brevior, "a vent-obligate species that relies partly on symbiotic sulphide-oxidizing bacteria for nutrition (von Cosel and Metivier, 1994)" and is found "at many sites in the western Pacific Ocean, where it occupies habitats of low hydrothermal fluid flux." Using remotely operated vehicles to collect mussel specimens, water samples, and imagery, Tunnicliffe et al. examined dense clusters of the vent mussel "in natural conditions of pH values between 5.36 and 7.29 on the northwest Eifuku volcano, Mariana arc, where liquid carbon dioxide and hydrogen sulfide emerge in a hydrothermal setting." They studied the vent mussels clusters along with mussels from "two sites in the southwestern Pacific: Hine Hina in the Lau backarc basin and Monowai volcano on the Kermadec arc," where "the same mussel species nestles in cracks and rubble where weak fluid flow emerges."

Based on the pH values they observed, the authors calculated saturation ratios for calcite (Ω_{calc}) ranging from 0.01 to 0.61, with an average value of only 0.18. They discovered "a dense mussel population, along with many other associated species (Limen and Juniper, 2006), on NW Eifuku, where chemosynthetic symbiosis provides an energetic benefit to living in a corrosive, low-pH environment." Tunnicliffe *et al.* say these findings attest to "the extent to which long-term adaptation can develop tolerance to extreme conditions." They report discovering four-decades-old mussels living at the sites they visited, stating "the mussels' ability to precipitate shells in such low-pH conditions is remarkable."

In another study using extreme environmental conditions, Hammer et al. (2011) exposed specimens of the deep-sea bivalve Acesta excavata collected from cold-water reefs to water maintained in equilibrium with an atmospheric CO₂ concentration of approximately 33,000 ppm, which resulted in a pH value of 6.35-corresponding to conditions reported for water in close proximity to natural CO₂ seeps on the ocean floor-for periods of 0.5, 1, 4, 12, 24, or 96 hours, after which they retuned the bivalves to normal CO₂/pH conditions for 1, 4, 12, 24, or 96 hours. The three researchers report the exposure of A. excavata to water in equilibrium with the super-high CO₂ concentration "induced extra- and intra-cellular acidosis that remained uncompensated during exposure," and "oxygen consumption dropped significantly during the initial phase." They found it "approached control values at the end of exposure" and "no mortality was observed in exposed animals."

These observations, the researchers write, show "A. excavata displays higher tolerance to severe environmental hypercapnia [a condition where there is too much CO_2 in the blood] than what may be expected for deep-sea animals." They note Tunnicliffe et al. (2009) "found evidence that permanent exposure to similar conditions causes reduced growth rates and shell thickness in mussels adapted to live at deep-sea vents," and they speculate "such long-term effects may also develop in A. excavata." They note previous studies on other species that mostly involved exposure of fish to moderate hypercapnia ($P_{CO2} = 10,000$ ppm or less) frequently observed complete compensation of extracellular acidosis, citing Heisler (1984, 1986), and "marine invertebrates are often able to partially counteract acidosis through accumulation of bicarbonate ions," citing Lindinger et al. (1984), Portner et al. (1988), Michaelidis et al. (2005), Miles et al. (2007), Pane and Barry (2007), and Gutowska et al. (2010).

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6.3.3.2 Corals

Some scientists predict the ongoing rise in the air's CO_2 content will play havoc with Earth's coral reefs in two ways: by stimulating global warming, which has been predicted to dramatically enhance coral bleaching, and by lower ocean pH levels , which is projected to lower the calcium carbonate saturation state of seawater and thereby reduce coral calcification rates. The first of these predictions was examined in Section 6.1.2 of this chapter. The topic of lower ocean pH levels is addressed here.

Several researchers have postulated many of Earth's corals are destined to die, with some species even facing extinction, because of the hypothesized connection between the ongoing rise in the air's CO₂ content and reduced rates of coral calcification (Buddemeier, 1994; Buddemeier and Fautin, 1996a,b; Gattuso et al., 1998; Buddemeier, 2001). Kleypas et al. (1999), for example, calculated calcification rates of tropical corals already should have declined by 6 to 11% or more since 1880, as a result of the increase in atmospheric CO₂ concentration, and they predict the reductions could reach 17 to 35% by 2100 as a result of expected increases in the air's CO₂ content in the coming decades. Langdon et al. (2000) calculated a decrease in coral calcification rate of up to 40% between 1880 and 2065.

IPCC claimed in its most recent assessment report:

Elevated temperature along with ocean acidification reduces the calcification rate of corals (*high confidence*), and may tip the calcium carbonate balance of reef frameworks towards dissolution (*medium evidence and agreement*).

— p. 67 of the *Technical Summary*, Working Group II, IPCC Fifth Assessment Report, dated March 28, 2013

Ocean acidification will cause a decrease of calcification of corals, which will cause not only a reduction in the coral's ability to grow its skeleton, but also in its contribution to reef building (*high confidence*).

— p. 73 of the *Technical Summary*, Working Group II, IPCC Fifth Assessment Report, dated March 28, 2013)

Ocean warming and acidification expected under RCP 8.5 will reduce calcification, elevate coral mortality and enhance sediment dissolution (*high confidence*; Manzello *et al.*, 2008). Coral reefs may stop growing and start dissolving when atmospheric CO_2 reaches 560 ppm due to the combined effects of both drivers (*medium evidence*).

— p. 19 of *Chapter 5. Coastal Systems and Low-Lying Areas*, Working Group II, IPCC Fifth Assessment Report, dated March 28, 2013

The research summarized below reveals the dire assessment of IPCC is tenuous at best and more likely wholly incorrect. As Idso et al. (2000) have noted, coral calcification is more than a physical-chemical process described by a set of well-defined equations. It is a biologically driven physical-chemical process that may not be amenable to explicit mathematical description. They state, for example, "photosynthetic activity of zooxanthellae is the chief source of energy for the energetically-expensive process of calcification," and much evidence suggests "long-term reef calcification rates generally rise in direct proportion to increases in rates of reef primary production." They also note "the calcium carbonate saturation state of seawater actually rises with an increase in temperature, significantly countering the direct adverse oceanic chemistry consequences of an increase in atmospheric and/or hydrospheric CO₂ concentration." They conclude "the negative predictions of today could well be replaced by positive predictions tomorrow."

As revealed below, numerous scientific studies point toward a much more optimistic view of the future for the planet's corals.

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6.3.3.2.1 Laboratory Studies

Researchers have predicted rates of coral calcification, and the photosynthetic rates of their symbiotic algae, will dramatically decline in response to what is typically referred to as an "acidification" of the world's oceans, as the atmosphere's CO_2 concentration continues to rise. This section examines evidence to the contrary obtained from laboratory-based studies. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Larvae from *Acropora* coral species (A. *digitifera* and A. *tenuis*) "may be able to tolerate ambient pH decreases of at least 0.7 pH units."
- "Scleractinian coral species will be able to acclimate to a high CO₂ ocean even if changes in seawater pH are faster and more dramatic than predicted."
- Though short-term exposure to lower ocean pH levels resulted in a decline of calcification and net dissolution of calcium carbonate in *Lophelia pertusa*, longer-term (six months) exposure revealed *L. pertusa* was able to acclimate and experience slightly enhanced rates of calcification, maintaining net growth in waters sub-saturated with aragonite.
- Using "carbonate concentration or aragonite saturation state as the sole predictor of the effects of ocean acidification on coral calcification" is unreliable.

- "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."
- A "firmer grasp of the biological component of biomineralization is paramount" in determining the response of corals to lower ocean pH levels .
- The future increase in oceanic bicarbonate ions may "stimulate photosynthesis and calcification in a wide variety of hermatypic corals," reducing and potentially overcoming theoretical effects of lower ocean pH levels.
- Reef corals may mitigate the effects of seawater acidification by regulating pH in the fluid at the tissue-skeleton interface, and this mechanism "may explain how several coral species continue to calcify even in low pH seawater, which is undersaturated with respect to aragonite."
- The fleshy tissues in octocorals may act as a protective barrier against rising levels of *p*CO₂, helping to maintain a stable internal environment that avoids the adverse effects of lower ocean pH levels.
- Based "purely on thermodynamic grounds, the predicted change in surface ocean pH in the next decades would appear to have minimal effect on the capacity of [important] acid-rich proteins to precipitate carbonates," which suggests "these proteins will continue to catalyze calcification reactions at ocean pH values projected in the coming century."

Suwa *et al.* (2010) employed controlled infusions of pure CO₂ to create mean pH values of 8.03, 7.64, and 7.31 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*) collected during a natural spawning event. Seven days later they determined their survival percentage, and after 10 more days they documented the size of the developing polyps. After 14 days they documented the percentage of polyps that had acquired zooxanthellae the researchers had collected from the giant clam *T. crocea* and released into the several treatment tanks.

They found "A. digitifera larval survival rate did not differ significantly among pH treatments," and the graphs of their data reveal survivorship in A. tenuis was about 18.5% greater in the lowest pH (highest CO₂) treatment than in the ambient seawater treatment. At the end of the subsequent 10-day study, polyp size was reduced in the lowest pH treatment, by about 14%, which is not too bad for an atmospheric CO_2 concentration reported by the authors to be in the range of 2,115-3,585 ppm. In the A. tenuis coral, this reduction in individual size was more than compensated by the greater percentage increase in survivorship. In addition, after only four days of exposure to the zooxanthellae derived from giant clams, all polyps in all treatments had acquired a full complement of the symbiotic zooxanthella.

The seven scientists say "the survival of coral larvae may not be strongly affected by pH change," or "in other words," as they continue, "coral larvae may be able to tolerate ambient pH decreases of at least 0.7 pH units." A pH decrease of that magnitude is likely never to occur, as it implies atmospheric CO₂ concentrations in the range of 2,115 to 3,585 ppm. If such high concentrations ever were to occur, they would be a long, long time in coming, giving corals far more than sufficient time to acclimate—and even evolve (Idso and Idso, 2009)—to cope with the slowly developing situation.

Takahashi and Kurihara (2013) measured the rates of calcification, respiration, and photosynthesis of the tropical coral *Acropora digitifera*, along with the coral's zooxanthellae density, under near-natural summertime temperature and sunlight conditions for five weeks. Their analysis revealed these "key physiological parameters" were not affected by either predicted mid-range CO₂ concentrations ($pCO_2 =$ 744 ppm, pH = 7.97, $\Omega_{arag} = 2.6$) or by high CO₂ concentrations ($pCO_2 = 2,142$ ppm, pH = 7.56, $\Omega_{arag} = 1.1$) over the 35-day period of their experiment. They found "no significant correlation between calcification rate and seawater aragonite saturation (Ω_{arag})" and "no evidence of CO₂ impact on bleaching."

Kreif *et al.* (2010) collected two colonies of massive *Porites* corals (which form large multicentury-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 adjacent to the Interuniversity Institute for Marine Science in Eilat (Israel) 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 CO₂ 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, the researchers sampled several fragments and analyzed them for a number of properties. Fourteen months from the start of the experiment, they analyzed fragments of each coral species from each CO₂ treatment for zooxanthellae cell density, chlorophyll *a* concentration, and host protein concentration.

They report, "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 occurred 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, the scientists report, "tissue biomass (measured by protein concentration) was found to be higher in both species after 14 months of growth under increased CO2." They further note Fine and Tchernov (2007) observed the same phenomenon, having "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 CO2." Krief et al. also report "a decrease in zooxanthellae cell density with decreasing pH was recorded in both species," but "this trend was accompanied by an increase in chlorophyll concentration per cell at the highest CO₂ level."

The Israeli, French, and UK researchers say "the inverse response of skeleton deposition and tissue biomass to changing CO₂ conditions is consistent with the hypothesis that calcification stimulates zooxanthellae photosynthesis by enhancing CO₂ concentration within the coelenteron (McConnaughey and Whelan, 1997)," and "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). 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).

Krief et al. conclude "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." 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."

Form and Riebesell (2012) studied branches of Lophelia pertusa, collected from reefs off the coast of Norway, which they describe as "the most common reef framework-forming and ecosystem engineering cold-water coral with a cosmopolitan distribution (Zibrowius, 1980; Cairns, 1994; Freiwald et al., 2004)." They conducted a short-term (eight-day) experiment and a long-term (178-day) experiment, in which they employed different atmospheric CO₂ treatments to create a range of water pH treatments from 8.029 to 7.768 in the eight-day study and from 7.944 to 7.755 in the 178-day study, measuring the corals' growth rates over these intervals. They report "short-term (1-week) high CO₂ exposure resulted in a decline of calcification by 26-29% for a pH decrease of 0.1 unit and net dissolution of calcium carbonate." In contrast, "L. pertusa was capable to acclimate to acidified conditions in long-term (6 months) incubations, leading to even slightly enhanced rates of calcification." In the long-term low-pH treatment, "net growth is sustained even in waters sub-saturated with respect to aragonite."

Crook et al. (2013) note "almost all tropical corals have algal symbionts (zooxanthellae)," while "most deep and cold-water corals lack zooxanthellae." Because the latter corals have no symbionts and rely solely on heterotrophy for energy, they "provide a simplified system for exploring the roles of nutrition (and energy) in coral calcification." Studving Balanophyllia elegans, а solitary azooxanthellate scleractinian coral common in shallow coastal waters around Monterey Bay, California (USA), where it is exposed seasonally to low-pH, high- pCO_2 upwelling waters, the five researchers conducted an eight-month factorial laboratory experiment in which they "measured the effects of three pCO_2 treatments (410, 770, and 1,220 µatm) and two feeding frequencies (3-day and 21-day intervals) on 'planulation' (larval release) by adult B. elegans, and on the survival, skeletal growth and calcification of newly settled juveniles."

Crook *et al.* report " pCO_2 had no effect on the numbers of brooded planulae larvae released," "higher food levels increased the number of larvae released by 50-200%," and "excess food enables corals to counteract partially some of the negative impacts of lower [aragonite] saturation states under higher pCO_2 conditions." They found "after 8 months of growth, high-food skeletons were up to 7 times larger (by volume) than low-food skeletons at every pCO_2 level," and "in every pCO_2 treatment, higher food led to both greater linear extension and greater calcification (skeletal weight) over the 8-month experiment." They also found "calcification by high pCO_2 , high-food corals was 4 times greater than in low-food corals at ambient pCO_2 ," and "even feeding on planktonic crustaceans only once every 21 days was still sufficient to maintain positive growth at high pCO_2 , albeit very slowly." The five U.S. researchers conclude, "as long as food availability remains high, B. elegans may be able to largely compensate for the extra energy required for calcification at low saturations, even if calcification occurs at slightly lower rates than at modern pCO_2 ." They reinforce this conclusion in the last sentence of their paper's abstract, writing, "we conclude that food abundance is critical for azooxanthellate coral calcification, and that B. elegans may be partially protected from adverse consequences of ocean acidification in habitats with abundant heterotrophic food."

Nash et al. (2012) write, "coral reef ecosystems develop best in high-flow environments," but "their fragile frameworks are also vulnerable to high wave energy." They say the wave-resistant algal rims, which surround many shallow coral reefs and are predominantly made of crustose coralline algae (CCA), are critical structural elements for the survival of such coral reefs. The scientists note "concerns have been growing about the susceptibility of CCA to ocean acidification, because CCA Mg-calcite skeletons are more susceptible to dissolution under low pH conditions than are coral aragonite skeletons." They further note the recent discovery by Nash et al. (2011) of the stable carbonate known as dolomite in the CCA Porolithon onkodes necessitates a reappraisal of the impacts of lower ocean pH levels on it and other CCAs, such as *P. pachydermum*.

The 11 researchers "carried out dissolution experiments on fragments of CCA collected fresh, but then dried, from the Heron Island reef front (Great Barrier Reef, Australia)," after which the fragments were exposed to ambient sea water as a control and an enriched CO_2 treatment, where "pH ranged from 7.85 to 8.55 (control) and 7.69–8.44 (treatment), tracking

natural diurnal changes measured in the lagoon water." Nash et al. (2012) determined "dried dolomite-rich CCA have 6-10 times lower rates of dissolution than predominantly Mg-calcite CCA in both high-CO₂ (~700 ppm) and control (~380 ppm) environments." They found this stabilizing mechanism resulted from "a combination of reduced porosity due to dolomite infilling and selective dissolution of other carbonate minerals." Noting "the prevailing theories that Mg-calcites with higher Mg content will undergo greatest dissolution," they write, "we were surprised to find a trend in the opposite direction." As dolomite-rich CCA frameworks are common in shallow coral reefs globally, Nash et al. conclude "it is likely that they will continue to provide protection and stability for coral reef frameworks as CO2 rises."

Egilsdottir et al. (2013) note "it has been suggested that organisms presently surviving in highly variable environments are likely to be more robust to ocean acidification," citing Moulin et al. (2011) and Raven (2011), and they hypothesize "the ability of organisms to tolerate significant pH/pCO_2 fluctuations may be a result of adaptation (a genetic trait shared by the population) and/or acclimation (owing to phenotypic plasticity of the individual)." The authors investigated the effect of elevated pCO_2 "in the articulated coralline red alga Corallina elongata from an intertidal rock pool on the north coast of Brittany (France), where pCO_2 naturally varied daily between 70 and 1,000 µatm." They grew the algae at four pCO_2 values (380, 550, 750, and 1,000 µatm) in laboratory mesocosms and measured several physiological responses of the coral.

The French and Icelandic researchers report "algae grown under elevated pCO_2 formed fewer new structures and produced calcite with a lower *mMg/Ca* ratio relative to those grown under 380 µatm." They also observe "respiration, gross primary production and calcification in light and dark were not significantly affected by increased pCO_2 ." Egilsdottir *et al.* conclude their study "supports the assumption that *C. elongata* from a tidal pool, where pCO_2 fluctuates over diel and seasonal cycles, [are] relatively robust to elevated pCO_2 ." They also state these observations portend "a greater resilience" of such organisms to the projected "highly variable pH/pCO_2 environments of future ocean acidification."

Ragazzola *et al.* (2013) note coralline algae have been shown to be a major contributor to the formation and stabilization of coral reefs and in enhancing coral larvae settlement, citing Chisholm (2000). Given "their crucial role in shallow water ecosystems and their worldwide distribution," the scientists write, "understanding the impact of ocean acidification on calcifying algae is fundamental," especially because "their high-Mg calcite skeleton is the most soluble polymorph of CaCO₃ (50% more soluble than calcite and 20% more soluble than aragonite)." Coralline algae are, therefore, "likely to be particularly sensitive to a reduction in Ω ," which is the calcium carbonate saturation state of seawater, citing Ries (2011), Burdett *et al.* (2012), and Martin *et al.* (2013).

Because "species with wide geographic ranges, such as coralline algae, are in general very plastic and able to acclimatize to a variety of habitats through morphological and functional responses (Brody. 2004)," Ragazzola et al. cultured Lithothamnion glaciale, one of the main maerl-forming species in the northern latitudes, under different elevated CO₂ levels (410, 560, 840, and 1,120 ppm = 8.02, 7.92, 7.80, and 7.72 pH, respectively) for 10 months, with initial analyses of the various parameters they measured conducted at the three-month point of the study, as reported by Ragazzola et al. (2012). The six scientists report the growth rates of the plants in the three CO₂enriched treatments after the first three months of their study were not significantly different from either each other or those of the ambient-treatment plants. At the end of the 10-month experiment, however, the CO₂-enriched plants' growth rates were approximately 60% lower than that of the ambient-treatment plants. However, the individual cell wall thicknesses of both inter and intra filaments at the three-month point of the study were significantly thinner than those of the control plants, while at the end of the 10month study they were equivalent to those of the control plants.

Ragazzola et al. (2013) note a possible explanation of their findings is "a shift from what could be termed a 'passive' phase during the first three months to an 'active' phase by the end of ten months," whereby "during the 'passive' phase, the increased energy requirement for calcification due to higher CO₂ results in a reduction in the amount of calcite deposited in each cell well," but during the "active phase," L. glaciale reduces its growth rate so the cell wall structure can be better maintained. Because maintaining skeletal integrity is one of the main priorities of marine organisms living in high CO₂ environments, the German and UK researchers say "the results of this study indicate that seawater chemistry can drive phenotypic plasticity in coralline algae," and "the ability to change the energy allocation between cell growth and structural support is a clear adaptive response of the organism," which

"is likely to increase its ability to survive in a high CO_2 world."

Ries et al. (2010) "investigated the impact of CO₂-induced ocean acidification on the temperate scleractinian coral Oculina arbuscula by rearing colonies for 60 days in experimental seawaters bubbled with air-CO₂ gas mixtures of 409, 606, 903, and 2,856 ppm CO₂, yielding average aragonite saturation states (Ω_A) of 2.6, 2.3, 1.6 and 0.8." The authors observed "following the initial acclimation phase, survivorship in each experimental treatment was 100%," 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," with the latter values corresponding to pH reductions from current conditions of 0.08 and 0.26, respectively. Ries et al. "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."

Herfort et al. (2008) note an increase in atmospheric CO₂ will cause an increase in the abundance of HCO_3^- (bicarbonate) ions and dissolved CO_2 , and they also report several studies on marine plants have observed "increased photosynthesis with higher than ambient DIC [dissolved inorganic carbon concentrations," citing Gao et al. (1993), Weis (1993), Beer and Rehnberg (1997), Marubini and Thake (1998), Mercado et al. (2001, 2003), Herfort et al. (2002), and Zou et al. (2003). The three researchers employed a wide range of bicarbonate concentrations "to monitor the kinetics of bicarbonate use in both photosynthesis and calcification in two reef-building corals, Porites porites and Acropora sp." Additions of HCO₃⁻ to synthetic seawater continued to increase the calcification rate of Porites porites until the bicarbonate concentration exceeded three times that of seawater, and photosynthetic rates of the coral's symbiotic algae were stimulated by HCO_3^- addition until they became saturated at twice the normal HCO_3 concentration of seawater.

Similar experiments conducted on Indo-Pacific *Acropora* sp. showed calcification and photosynthetic rates in these corals were enhanced to an even greater extent, with calcification continuing to increase above a quadrupling of the HCO₃⁻ concentration and photosynthesis saturating at triple the concentration of seawater. The scientists monitored calcification rates of the *Acropora* sp. in the dark, writing, "although these were lower than in the light for a given HCO₃⁻ concentration, they still increased dramatically with

HCO₃⁻ addition, showing that calcification in this coral is light stimulated but not light dependent."

Herfort *et al.* suggest "hermatypic corals incubated in the light achieve high rates of calcification by the synergistic action of photosynthesis," which, as they have shown, is enhanced by elevated concentrations of HCO_3^- ions caused by the rise in the air's CO_2 content. The three researchers note over the next century the predicted increase in atmospheric CO_2 concentration "will result in about a 15% increase in oceanic HCO_3^- ," and this development "could stimulate photosynthesis and calcification in a wide variety of hermatypic corals."

Jury et al. (2010) explain why some corals show positive responses to lower ocean pH levels in laboratory studies whereas others do not. They note, "physiological data and models of coral calcification indicate that corals utilize a combination of seawater bicarbonate and (mainly) respiratory CO₂ for calcification, not seawater carbonate," but "a number of investigators are attributing observed negative effects of experimental seawater acidification by CO₂ or hydrochloric acid additions to a reduction in seawater carbonate ion concentration and thus aragonite saturation state." They identify "a physiological discrepancy between the and geochemical views of coral biomineralization" and "not all calcifying organisms respond report. negatively to decreased pH or saturation state." They note, "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."

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." Amongtreatment 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, "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," stating "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."

Venn et al. (2013) also focused on how lower ocean pH levels impact the physiological mechanisms that drive calcification, to provide knowledge helpful in predicting how corals and other marine calcifiers will respond and potentially acclimate to lower ocean pH levels. In corals, the authors note, the capacity to regulate pH in the fluid at the tissue-skeleton interface [subcalicoblastic medium (SCM)] and in the calcifying cells [calicoblastic epithelium (CE)] "has been widely proposed to be important in shaping calcification responses to ocean acidification." They studied the impact of seawater acidification on pH_{SCM} and pH_{CE} in the coral Stylophora pistillata, "using in vivo imaging of pH in corals exposed to reduced seawater pH and elevated pCO_2 in the laboratory for [both] long and short durations." This work included "exposures to levels of acidification and elevated pCO_2 many times greater than those predicted to occur at the end of this century."

Venn et al. say they "observed calcification (measured by growth of skeletal crystals and whole colonies) in all our treatments, including treatment pH 7.2, where aragonite was undersaturated." They continue, "this finding agrees with previous work with S. pistillata conducted elsewhere, where net calcification was also observed over a similar range of pH and pCO₂ (Krief et al., 2010)." Such findings suggest, they write, "S. pistillata may have a high tolerance to decreases in seawater pH and changes in seawater chemistry," leading them to conclude "maintenance of elevated pH_{SCM} relative to the surrounding seawater may explain how several coral species continue to calcify even in low pH seawater, which is undersaturated with respect to aragonite (this study and Rodolfo-Metalpa et al. (2011) and Cohen et al., (2009))." Venn et al. report, "reductions in calcification rate, both at the level of crystals and whole colonies, were only observed in our lowest pH treatment [pH 7.2] when pH was significantly depressed in the calcifying cells in addition to the SCM." "Overall," they say their findings suggest "reef corals may mitigate the effects of seawater acidification by regulating pH in the SCM."

Gabay *et al.* (2013) note octocorals possess "an internal calcium carbonate skeleton comprised of

microscopic sclerites embedded in their tissue," citing Fabricius and Alderslade (2001), Jeng *et al.* (2011), and Tentori and Ofwegen (2011). They also note octocorals are "the second most important faunistic component in many reefs, often occupying 50% or more of the available substrate." They say "it is important to predict their response to a scenario of increased pCO_2 ."

Gabay *et al.* studied three species of octocorals from two families found in the Gulf of Aqaba at Eilat—the zooxanthellate *Ovabunda macrospiculata* and *Heteroxenia fuscens* (family Xeniidae) and *Sarcophyton* sp. (family Alcyoniidae)—which they maintained for five months under normal (8.2) and reduced (7.6 and 7.3) pH conditions, assessing their pulsation rate, protein concentration, polyp weight, density of zooxanthellae, and chlorophyll concentration per cell.

The three Israeli scientists found "no statistically significant difference between the octocorals exposed to reduced pH values compared to the control." They say "these findings indicate that octocorals may possess certain protective mechanisms against rising levels of pCO_2 ," and they suggest "their fleshy tissues act as a barrier, maintaining a stable internal environment and avoiding the adverse effects of the ambient elevated pCO_2 ." That notion accords with the observations of Rodolfo-Metalpa et al. (2011), and Gabay et al. note "this suggestion is further supported by our finding that the ultrastructural features of O. macroscipulata sclerites are not affected by increased ambient seawater acidity." They conclude, "octocorals might be able to acclimate and withstand rising levels of ocean acidification, even under conditions that are far beyond what is expected to occur by the end of the present century (pH 7.9)."

Mass et al. (2013) write, "despite the broad interest in coral calcification and the potential for climate-driven adverse effects, the molecules and biophysical mechanism responsible for the precipitation of carbonates are poorly understood." They note, "to date, we lack both a characterization of molecules involved in calcification and a mechanistic understanding of processes that lead to and control calcification," and this "lack of knowledge limits our ability to predict the response of corals to increasing atmospheric CO2." The seven scientists "for the first time," identified, cloned, determined the amino acid sequence of, and characterized four highly acidic proteins they derived from the expression of genes obtained from the common stony coral Stylophora pistillata. Each of these proteins can spontaneously catalyze the precipitation of calcium carbonate in

vitro.

They found "coral acid-rich proteins (CARPs) not only bind Ca²⁺ stoichiometrically but also precipitate aragonite in vitro in seawater at pH 8.2 and 7.6 via an electrostatic interaction with protons on bicarbonate anions." The seven U.S. researchers conclude, "based purely on thermodynamic grounds, the predicted change in surface ocean pH in the next decades would appear to have minimal effect on the capacity of these acid-rich proteins to precipitate carbonates." They note their findings "strongly suggest that these proteins will continue to catalyze calcification reactions at ocean pH values projected in the coming century."

Maier et al. (2013) note "previous experiments examining the effect of ocean acidification on the cold-water corals L. pertusa and M. oculata have indicated that their rates of calcification remain positive even in waters where Ω_a is < 1 (Maier *et al.*, 2009; Thresher et al., 2011; Form and Riebesell, 2012)." They add that Form and Riebesell (2012) and Maier et al. (2012, 2013) found "calcification rates of these species remained positive at a partial pressure of CO_2 (pCO₂) of 1000 µatm, a value that is at the high end of projected changes by 2100." Maier et al. measured respiration rates "for both short and long periods of time at pCO_2 levels ranging from ambient (350 µatm) to elevated (1100 µatm) levels," using "the same experimental setup as a previous study demonstrating that elevated pCO_2 had no effect on the rate of calcification in these two species (Maier et al., 2013)."

The six scientists report, "in the range of pCO_2 studied so far, up to 1215 µatm, no significant change in respiration was found as a function of increasing pCO_2 ." As for what "this means," Maier *et al.* write, "for the maintenance of high calcification rates over a large range of pCO_2 of up to 1,000 ppm, there is no evidence for a direct energy allocation from food uptake to calcification in order to compensate for higher energy required to maintain calcification constant despite a decrease in pH."

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6.3.3.2.2 Field Studies

Some scientists have predicted rates of coral calcification and the photosynthetic rates of their symbiotic algae will decline dramatically in response to lower ocean pH levels as the atmosphere's CO_2 concentration continues to rise. As research evidence accumulates, however, the true story appears to be just the opposite. This section examines such evidence obtained from field-based studies conducted in the natural ocean. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Theoretical calculations suggest rising atmospheric CO₂ over the past century should have led to a 6–14% decline in coral calcification via lower ocean pH levels , yet several studies show coral calcification rates have remained stable or increased.
- In contrast to model-based assumptions, the process of calcification in many corals is not correlated with aragonite saturation state or pH.
- Increases in calcification observed over the past century in many ocean regions have been shown to correlate strongly with increases in water temperature.
- Changes in pH did not affect the composition of associated microbial communities in two Mediterranean coral species.
- Cold-water corals are "likely to be much more resilient to decreasing seawater pH from ocean acidification than previously realized," because of their ability "to ameliorate or buffer external changes in seawater pH by up-regulating their internal (extracellular) pH at the site of calcification."
- The distribution and composition of deep-sea corals "are not constrained by carbonate levels below saturation."
- "The drawdown of total dissolved inorganic carbon due to photosynthesis and calcification of reef communities can exceed the drawdown of

total alkalinity due to calcification of corals and calcifying algae, leading to a net increase in aragonite saturation state." Although "carbon fluxes of benthic reef communities cannot significantly counter changes in carbon chemistry at the scale of oceans, they provide a significant mechanism of buffering ocean acidification impacts at the scale of habitat to reef."

Field studies hold an advantage over laboratory-based studies in more aptly representing conditions in the real world, as many of those conditions are impossible or impractical to recreate in a laboratory setting. The findings produced in field studies tend to hold more weight and establish greater clarity on a scientific topic or question under investigation than findings produced in a laboratory setting. Such is the case with lower ocean pH levels . Whereas positive, negative, and neutral effects from this phenomenon have been observed on corals in laboratories, fieldbased studies in the ocean reveal the situation is much less dire than IPCC predicts. Many studies suggest a modest decline in oceanic pH may actually favor coral calcification and growth.

Pelejero et al. (2005), for example, developed a reconstruction of seawater pH spanning the period 1708–1988, based on the boron isotopic composition $(\delta^{11}B)$ of a long-lived massive coral (*Porites*) from Flinders Reef in the western Coral Sea of the southwestern Pacific. They found "no notable trend toward lower δ^{11} B values" over the 300-year period investigated. They write, "the dominant feature of the coral δ^{11} B record is a clear interdecadal oscillation of pH, with δ^{11} B values ranging between 23 and 25 per mil (7.9 and 8.2 pH units)," which "is synchronous with the Interdecadal Pacific Oscillation." They also calculated changes in aragonite saturation state from the Flinders pH record that varied between ~3 and 4.5, and these values encompass "the lower and upper limits of aragonite saturation state within which corals can survive." They report, "skeletal extension and calcification rates for the Flinders Reef coral fall within the normal range for *Porites* and are not correlated with aragonite saturation state or pH." Thus, contrary to claims of great sensitivity of coral calcification to changes in pH and aragonite saturation, they found large cyclical changes in these parameters had essentially no detectable effect on either coral calcification or skeletal extension rates.

In a study of historical calcification rates determined from coral cores retrieved from 35 sites on the Great Barrier Reef, Lough and Barnes (1997) observed a statistically significant correlation between coral calcification rate and local water temperature. They found a 1°C increase in mean annual water temperature increased mean annual coral calcification rate by about 3.5 percent, but they also report there were "declines in calcification in *Porites* on the Great Barrier Reef over recent decades." They point out their data depict several extended periods of time when coral growth rates were either above or below the long-term mean, cautioning, "it would be unwise to rely on short-term values (say averages over less than 30 years) to assess mean conditions."

They report, "a decline in calcification equivalent to the recent decline occurred earlier this century and much greater declines occurred in the 18th and 19th centuries," long before anthropogenic CO_2 emissions had much of an impact on the air's CO_2 concentration. Over their entire dataset, Lough and Barnes write, "the 20th century has witnessed the second highest period of above average calcification in the past 237 years," not exactly to be expected in light of how dangerous high water temperatures are often said to be for corals, the claim that Earth is currently warmer than it has been at any other time during the entire past millennium, and the air's CO_2 content is currently much higher than it has been for more than a thousand years.

Bessat and Buigues (2001) reported similar findings after deriving a history of coral calcification rates, covering the period 1801–1990, from a core extracted from a massive *Porites* coral head on the French Polynesian island of Moorea. They note "recent coral-growth models highlight the enhanced greenhouse effect on the decrease of calcification rate," but instead of relying on theoretical calculations, they wanted to work with real-world data because the records preserved in ancient corals "may provide information about long-term variability in the performance of coral reefs, allowing unnatural changes to be distinguished from natural variability."

Bessat and Buigues found a 1°C increase in water temperature increased coral calcification rates at the site they studied by 4.5 percent. Then they found, "instead of a 6–14% decline in calcification over the past 100 years computed by the Kleypas group, the calcification has increased, in accordance with [the results of] Australian scientists Lough and Barnes." They also observed patterns of "jumps or stages" in the record, characterized by an increase in the annual rate of calcification, particularly at the beginning of the past century "and in a more marked way around 1940, 1960 and 1976," stating once again their results "do not confirm those predicted by the Kleypas *et al.* (1999) model." Lough and Barnes (2000) delivered another major blow to the Kleypas *et al.* model when they assembled and analyzed the calcification characteristics of 245 similar-sized massive colonies of *Porites* corals obtained from 29 reef sites located along the length, and across the breadth, of Australia's Great Barrier Reef (GBR). The data spanned a latitudinal range of approximately 9° and an annual average sea surface temperature (SST) range of 25–27°C. To these data they added other published data from the Hawaiian Archipelago (Grigg, 1981, 1997) and Phuket, Thailand (Scoffin *et al.*, 1992), thus extending the latitudinal range of the expanded dataset to 20° and the annual average SST range to 23–29°C.

Lough and Barnes found the GBR calcification data were linearly related to the average annual SST data, as "a 1°C rise in average annual SST increased average annual calcification by 0.39 g cm⁻² year⁻¹." Results were much the same for the extended dataset. They report, "the regression equation [calcification = 0.33(SST) - 7.07] explained 83.6% of the variance in average annual calcification (F = 213.59, p less than 0.00)," and "this equation provides for a change in calcification rate of 0.33 g cm⁻² year⁻¹ for each 1°C change in average annual SST."

Lough and Barnes say their findings "allow assessment of possible impacts of global climate change on coral reef ecosystems," and between the two 50-year periods 1880-1929 and 1930-1979, they calculate a calcification increase of 0.06 g cm⁻² year⁻¹, noting "this increase of ~4% in calcification rate conflicts with the estimated decrease in coral calcification rate of 6-14% over the same time period suggested by Kleypas et al. (1999) as a response to changes in ocean chemistry." Even more stunning is their observation that between the two 20-year periods 1903-1922 and 1979-1998. "the SSTassociated increase in calcification is estimated to be less than 5% in the northern GBR, ~12% in the central GBR, ~20% in the southern GBR and to increase dramatically (up to \sim 50%) to the south of the GBR." Lough and Barnes conclude coral calcification rates "may have already significantly increased along the GBR in response to global climate change."

Carricart-Ganivet (2004) developed relationships between coral calcification rate and annual average SST based on data collected from colonies of the reefbuilding coral *Montastraea annularis* at 12 locations in the Gulf of Mexico and Caribbean Sea. He found the calcification rate in the Gulf of Mexico increased 0.55 g cm⁻² year⁻¹ for each 1°C increase, and in the Caribbean Sea it increased 0.58 g cm⁻² year⁻¹ for each
1°C increase. Pooling these data with data regarding *M. annularis* and *M. faveolata* growing to a depth of 10 m at Carrie Bow Cay, Belize, data from reefs at St. Croix in the U.S. Virgin Islands, and data of *M. faveolata* growing to a depth of 10 m at Curacao, Antilles, Carricart-Ganivet reports a mean increase in calcification rate of ~0.5 g cm⁻² year⁻¹ for each 1°C increase in annual average SST, even greater than what Lough and Barnes found for *Porites* corals.

Working 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—Carricart-Ganivet and Gonzalez-Diaz (2009) measured yearly coral extension rates and densities of dominant Caribbean reef-building the coral Montastraea annularis for the period 1991 to 2003, from which data they calculated annual coral calcification rates. They plotted their results against mean annual sea surface temperature (SST, obtained from the UK's Hadley Centre) and compared their results with the earlier study of Carricart-Ganivet (2004). The results of these two investigations are illustrated in Figure 6.3.3.2.2.1, where it can be seen they are completely compatible with each other.



Figure 6.3.3.2.2.1. 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 the authors (red circles). The line that has been fit to the data is defined by Calcification Rate = 0.51 SST - 12.85 (r² = 0.82, p < 0.002). Adapted from Carricart-Ganivet and Gonzalez-Diaz (2009).

Crabbe et al. (2006) determined the original growth rates of long-dead Quaternary corals found in limestone deposits on islands in the Wakatobi Marine National Park of Indonesia, which they compared to the growth rates of present-day corals of the same genera living in the same area. They found the Quaternary corals grew "in a comparable environment to modern reefs"-except, of course, for the air's CO₂ concentration, which is currently higher than it has been at any other time throughout the Ouaternary, which spans the past 1.8 million years. Their measurements indicated the radial growth rates of the modern corals were 31 percent greater than those of their ancient predecessors in the case of Porites species, and 34 percent greater in the case of Favites species.

Cohen and Holcomb (2009) highlight several about the process of calcification in facts zooxanthellate corals. First, they report what is perhaps the most fundamental fact: "calcification is an active, physiological process that requires significant amounts of energy to drive it." Second, they note "increased photosynthesis [of coral symbiotic zooxanthellae] means increased photosynthate and more energy for calcification." Third, they report Atkinson et al. (1995) have shown "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-saturationstate seawaters." Fourth, the two researchers write, "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 CO₂ 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 from these observations, Cohen and Holcomb write, is "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." This further suggests Earth's corals, with their genetically diverse symbiotic zooxanthellae, are likely well-equipped to deal successfully with future increases in the air's CO_2

content.

The same phenomenon that powers the twin processes of coral calcification and phytoplanktonic growth (photosynthesis) tends to increase the pH of marine waters (Gnaiger *et al.*, 1978; Santhanam *et al.*, 1994; Brussaard *et al.*, 1996; Lindholm and Nummelin, 1999; Macedo *et al.*, 2001; Hansen, 2002). This phenomenon has been shown to have the ability to dramatically increase the pH of marine bays, lagoons, and tidal pools (Gnaiger *et al.*, 1978; Macedo *et al.*, 1978; Macedo *et al.*, 2001; Hansen, 2002) and significantly enhance the surface water pH of areas as large as the North Sea (Brussaard *et al.*, 1996).

In an example of this phenomenon, Middelboe and Hansen (2007) studied the pH of a wave-exposed boulder reef in Aalsgaarde on the northern coast of Zealand, Denmark, and a sheltered shallow-water area in Kildebakkerne in the estuary Roskilde Fjord, Denmark. They report, in line with what would be expected if photosynthesis tends to increase surfacewater pH, "daytime pH was significantly higher in spring, summer and autumn than in winter at both study sites," often reaching values of 9 or more during peak summer growth periods vs. 8 or less in winter. They also found "diurnal measurements at the most exposed site showed significantly higher pH during the day than during the night," sometimes reaching values above 9 during daylight hours but typically dipping below 8 at night, and "diurnal variations were largest in the shallow water and decreased with increasing water depth."

Middelboe and Hansen cite the work of Pearson *et al.* (1998), who found pH averaged about 9 during the summer in populations of *Fucus vesiculosus* in the Baltic Sea; Menendez *et al.* (2001), who found maximum pH was 9 to 9.5 in dense floating macroalgae in a brackish coastal lagoon in the Ebro River Delta; and Bjork *et al.* (2004), who found pH values as high as 9.8 to 10.1 in isolated rock pools in Sweden. Noting "pH in the sea is usually considered to be stable at around 8 to 8.2," the two Danish researchers conclude "pH is higher in natural shallow-water habitats than previously thought."

Meron *et al.* (2012) state ocean acidification "has the potential to cause significant perturbations to the physiology of ocean organisms, particularly those such as corals that build their skeletons/shells from calcium carbonate," and this phenomenon "could also have an impact on the coral microbial community, and thus may affect coral physiology and health." They note most studies of declining pH effects on corals and/or their associated microbiota typically have been done under "controlled laboratory

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conditions." This approach clearly ignores any impacts declining pH values may have on the coral holobiont, some of which may be negative and some positive, which in the latter case is referred to as the probiotic hypothesis, as per Reshef *et al.* (2006).

The six scientists took advantage of a natural pH gradient off the coast of Ischia (Gulf of Naples, Italy) created by an underwater CO_2 flux from volcanic vents (Hall-Spencer *et al.*, 2008). They examined the potential impacts of a range of pH conditions (7.3 to 8.1) on coral microbial communities living under real-world conditions, focusing on two Mediterranean coral species: *Balanophyllia europaea* and *Cladocora caespitosa*.

The research team reports "pH did not have a significant impact on the composition of associated microbial communities in both coral species." They note "corals present at the lower pH sites exhibited only minor physiological changes" and "no microbial pathogens were detected." They conclude "at least for these two coral species, reduced pH does not seem to significantly reduce coral health," which suggests some of the contrary results obtained in laboratory studies could be due to the fact "laboratory environments cannot mimic the dynamism and microbial diversity present in nature," and the conditions possibility "aquarium themselves contribute to stress or disturbance in the microbial community." This view is supported in part by the finding of Kooperman et al. (2007), who noted, "the same coral species has different associated microbial communities in the laboratory compared with field conditions."

Shamberger et al. (2011) deployed "autosamplers" to collect water samples from the barrier coral reef of Kaneohe Bay, Oahu, Hawaii, every two hours for six 48-hour periods, two each in June 2008, August 2009, and January/February 2010. Based on these seawater measurements, they calculated net ecosystem calcification (NEC) and net photosynthesis (NP) rates for these periods. The six scientists found "daily NEC was strongly negatively correlated with average daily pCO_2 , which ranged from 421 to 622 ppm." They report, "daily NEC of the Kaneohe Bay barrier reef is similar to or higher than daily NEC measured on other coral reefs, even though Ω_{arag} levels (mean $\Omega_{arag} = 2.85$) are some of the lowest measured in coral reef ecosystems." Shamberger et al. conclude "it appears that while calcification rate and Ω_{arag} are correlated within a single coral reef ecosystem," as in the case of the barrier reef of Kaneohe Bay, "this relationship does not necessarily hold between different coral reef systems," and it can

thus be expected "ocean acidification will not affect coral reefs uniformly and that some may be more sensitive to increasing pCO_2 levels than others." That implies (taking a more positive view of the subject) some coral reefs may be less sensitive to increasing pCO_2 than others.

McCulloch *et al.* (2012) state "for cold-water corals, which are already living at low levels of carbonate saturation, the shoaling of the saturation horizon as carbonate saturation states decrease [in response, for example, to rising atmospheric CO_2 concentrations] has the potential to cause dramatic declines in rates of calcification, or the dissolution of the carbonate skeletons of those living at or close to the saturation horizon." Since these corals are indeed living there, they speculate "they may have evolved adaptive strategies to counter the effects of low carbonate saturation states," one of which is to upregulate their internal pH to a value that allows calcification to occur.

McCulloch *et al.* extended the novel approach of Trotter *et al.* (2011), based on boron isotopic systematics, to determine the relationship between seawater pH and the internal (extracellular) pH_{cf} at the site of calcification for several azooxanthellate coldwater scleractinian corals, collected from a large range of depths and geographically disparate sites, including southeast Australia, Chile's Comau Fjord, the Marmara Sea, a number of sites in the Mediterranean Sea, the northeast Atlantic Ocean, and the northwestern Hawaiian Islands.

The suite of "aragonitic cold-water coral species," as the 11 researchers describe them, "collectively show an overall trend of higher ΔpH [= pH_{cf} seawater pH] values that is anti-correlated with seawater pH, with systematics generally consistent with biologically controlled pH up-regulation." This result indicates, "like symbiont-bearing tropical corals (Trotter *et al.*, 2011), they have the ability to ameliorate or buffer external changes in seawater pH by up-regulating their pH_{cf} at the site of calcification."

McCulloch *et al.* conclude "cold-water corals are likely to be much more resilient to decreasing seawater pH from ocean acidification than previously realized," because, as they see it, "decreasing seawater pH alone will only marginally affect calcification rates since this process would be largely countered by pH_{cf} up-regulation in cold-water corals, together with enhanced calcification rates from warming of the deep oceans."

Jantzen *et al.* (2013) write ocean acidification "is thought to negatively affect most marine-calcifying organisms, notably cold-water corals (CWC)," which

might be expected to be especially sensitive due to the deep and cold waters in which they are typically found. They measured water profiles with a CTD (conductivity, temperature, depth) multi-probe profiler along the Comau fjord, extending down to 50–60 meters in 2010 and down to 225 meters in 2011, which allowed them to detect and describe the spatial distribution of the cold-water coral *Desmophyllum dianthus*.

The seven scientists determined *D. dianthus* grows along the fjord over its entire pH range, where "it occurs in shallow depths (below 12 m, pH 8.1) as part of a deep-water emergence community, but also in [water of] 225 m depth at a pH of 7.4." They report the cold-water coral thrives close to the aragonite saturation horizon and even below it, where they found "flourishing coral banks."

Jantzen *et al.* note other studies "question reduced calcification rates of corals in environments with lowered aragonite saturation state (Ω_{arg})," citing Marubini *et al.* (2008) and Jury *et al.* (2010), but they note "very recent studies hint at a higher acclimatization potential of cold-water corals to ocean acidification," citing Rodolfo-Metalpa *et al.* (2010), Trotter *et al.* (2011), Form and Riebesel (2012), and McCulloch *et al.* (2012a,b).

Thresher et al. (2011) state concerns about the effects of lower ocean pH levels on marine ecosystems "are based primarily on modeling studies and short-term laboratory exposure to low-carbonate conditions," citing Riegl et al. (2009), Veron et al. (2009), and Ries et al. (2010). They say "their relevance to long-term exposure in the field and the potential for ecological or evolutionary adjustment are uncertain," citing Maynard et al. (2008). In an effort "to determine the sensitivity of corals and allied taxa to long-term exposure to very low carbonate concentrations." Thresher et al. examined "the depth distribution and life-history characteristics of corals and other shell-forming megabenthos along the slopes of deep-sea seamounts and associated structure in the SW Pacific," where the gradient of water chemistry ranged from super-saturated in the case of aragonite and high-magnesium calcite (HMC) to undersaturated with calcite.

The five researchers "found little evidence that carbonate under-saturation to at least -30% affected the distribution, skeletal composition, or growth rates of corals and other megabenthos on Tasmanian seamounts." They found "both solitary scleractinian corals and colonial gorgonians were abundant at depths well below their respective saturation horizons and appeared healthy," and HMC echinoderms were common as deep as they sampled (4,011 m), in water approximately 45% under-saturated. They also report, "for both anthozoan and non-anthozoan taxa, there was no obvious difference in species' maximum observed depths as a function of skeletal mineralogy." In other words, the community "was not obviously shifted towards taxa with either less soluble or no skeletal structure at increasing depth." They conclude, "it is not obvious from our data that carbonate saturation state and skeletal mineralogy have any effect on species' depth distributions to the maximum depth sampled," and they saw "little evidence of an effect of carbonate under-saturation on growth rates and skeletal features."

Thresher *et al.* write, "the observation that the distributions of deep-sea corals are not constrained by carbonate levels below saturation is broadly supported by the literature," noting "solitary scleractinians have been reported as deep as 6 km (Fautin *et al.*, 2009) and isidid gorgonians as deep as 4 km (Roark *et al.*, 2005)." They say their own data also "provide no indication that conditions below saturation per se dictate any overall shifts in community composition."

Explaining these results, the researchers note one or more cell membranes may envelop the organisms' skeletons, largely isolating the calcification process and its associated chemistry from the bulk seawater, citing McConnaughey (1989), Adkins et al. (2003), and Cohen and McConnaughey (2003), and this phenomenon could presumably protect "the skeleton itself from the threat of low carbonate dissolution." In addition, Thresher et al. note, "calcification is energetically expensive, consuming up to 30% of the coral's available resources, and ... normal calcification rates can be sustained in relatively lowcarbonate environments under elevated feeding or nutrient regimes," as described in detail by Cohen and Holcomb (2009). Thresher et al. conclude, "Although saturation levels in those studies are considerably higher than those experienced by the deep-sea taxa we observed, the principle that elevated food availability could compensate for the higher costs of calcification in heterotrophic deepsea species appears plausible."

Thresher *et al.* say their data clearly suggest, whatever the cause, "a change in carbonate saturation horizons per se as a result of ocean acidification is likely to have only a slight effect on most of the live deep-sea biogenic calcifiers."

Anthony *et al.* (2011) used "a carbon flux model for photosynthesis, respiration, calcification and dissolution coupled with Lagrangian transport to examine how key groups of calcifiers (zooxanthellate corals) and primary producers (macroalgae) on coral reefs contribute to changes in the seawater carbonate system as a function of water residence time." The examination showed "the carbon fluxes of corals and macroalgae drive Ω_a in opposing directions," and "areas dominated by corals elevate pCO₂ and reduce Ω_{a} , thereby compounding ocean acidification effects in downstream habitats, whereas algal beds draw CO₂ down and elevate Ω_a , potentially offsetting ocean acidification impacts at the local scale." They also report simulations for two significantly elevated CO₂ scenarios (600 and 900 ppm CO₂) suggest "a shift in reef community composition from coral to algal dominance in upstream areas under ocean acidification will potentially improve conditions for calcification in downstream areas."

Klevpas *et al.* (2011) provided field validation of the simulations of Anthony et al. by examining the roles of three key members of benthic reef communities-corals, macroalgae, and sand-in modifying the chemistry of open-ocean source water. They found "the drawdown of total dissolved inorganic carbon due to photosynthesis and calcification of reef communities can exceed the drawdown of total alkalinity due to calcification of corals and calcifying algae, leading to a net increase in aragonite saturation state." They note there were no seagrasses on the reef flat they studied, and "research suggests that seagrasses may have an additional impact on reef seawater chemistry because they enhance the alkalinity flux from sediments (Burdige and Zimmerman, 2002), and they respond to CO_2 fertilization (Palacios and Zimmerman, 2007)."

These observations suggest reef communities gradually could alter their spatial compositions in a CO_2 -acreting world to the point where seagrasses and other macroalgae take up residence in upstream regions, while corals and other calcifying organisms lay claim to downstream regions. Anthony *et al.* (2011) conclude, "although the carbon fluxes of benthic reef communities cannot significantly counter changes in carbon chemistry at the scale of oceans, they provide a significant mechanism of buffering ocean acidification impacts at the scale of habitat to reef."

Manzello *et al.* (2012) note although many people expect future ocean acidification (OA) resulting from rising atmospheric CO_2 concentrations to reduce the calcification rates of marine organisms, we have little understanding of how OA will manifest in dynamic, real-world systems, because "natural CO_2 , alkalinity, and salinity gradients can significantly alter local carbonate chemistry, and thereby create a range of susceptibility for different ecosystems to OA." "To determine if photosynthetic CO_2 uptake associated with seagrass beds has the potential to create OA refugia," Manzello *et al.* repeatedly measured carbonate chemistry across an inshore-to-offshore gradient in the upper, middle, and lower Florida Reef Tract over a two-year period.

During times of heightened oceanic vegetative productivity, the five U.S. researchers found, "there is a net uptake of total CO₂ which increases aragonite saturation state (Ω_{arag}) values on inshore patch reefs of the upper Florida Reef Tract," and "these waters can exhibit greater Ω_{arag} than what has been modeled for the tropical surface ocean during preindustrial times, with mean Ω_{arag} values in spring equaling 4.69 ± 0.10." They report Ω_{arag} values on offshore reefs "generally represent oceanic carbonate chemistries consistent with present day tropical surface ocean conditions."

Manzello et al. hypothesize the pattern described above "is caused by the photosynthetic uptake of total CO₂ mainly by seagrasses and, to a lesser extent, macroalgae in the inshore waters of the Florida Reef Tract." They conclude these inshore reef habitats are "potential acidification refugia that are defined not only in a spatial sense, but also in time, coinciding with seasonal productivity dynamics," which further implies "coral reefs located within or immediately downstream of seagrass beds may find refuge from acidification." They cite Palacios and ocean Zimmerman (2007), whose work they describe as indicating "seagrasses exposed to high-CO₂ conditions for one year had increased reproduction, rhizome biomass, and vegetative growth of new shoots, which could represent a potential positive feedback to their ability to serve as ocean acidification refugia."

Noonan *et al.* (2013) write, "ocean acidification (OA) is expected to negatively affect coral reefs," but "little is known about how OA will change the coralalgal symbiosis on which reefs ultimately depend." They state, "to date it remains unknown if corals are able to respond to rising CO₂ concentrations by changing to better adapted dominant *Symbiodinium* types after long-term exposure to elevated pCO_2 in the field," the field being the ocean, in this case. Noonan *et al.* investigated "the dominant types of *Symbiodinium* associating with six species of scleractinian coral that were exposed to elevated partial pressures of carbon dioxide (pCO_2) *in situ* from settlement and throughout their lives." They did so "at three naturally occurring volcanic CO₂ seeps $(pCO_2 \sim 500 \text{ to } 900 \text{ ppm}, \text{pH}_{\text{Total}} 7.8-7.9)$ and adjacent control areas $(pCO_2 \sim 390 \text{ ppm}, \text{pH}_{\text{Total}} \sim 8.0-8.05)$ in Papua New Guinea," and "*Symbiodinium* associated with corals living in an extreme seep site $(pCO_2 > 1000 \text{ ppm})$ were also examined."

In five of the six species studied, the researchers report, "85-95% of samples exhibited the same *Symbiodinium* type across all sites, with remaining rare types having no patterns attributable to CO₂ exposure." The sixth species of coral did display "site specific differences in *Symbiodinium* types," but these were "unrelated to CO₂ exposure." The scientists write, "*Symbiodinium* types from the coral inhabiting the extreme CO₂ seep site were found commonly throughout the moderate seeps and control areas." These findings suggest the six species of coral Noonan *et al.* studied, plus the various *Symbiodinium* types they encountered, were able not only to survive but to function well throughout the full range of CO₂induced pH values to which they had been exposed.

Wall and Edmunds (2013) note laboratory studies "typically are performed under conditions that do not replicate the natural environment perfectly, notably by providing light at a constant low intensity throughout the day, and with a spectral composition differing from ambient sunlight," citing Kinzie *et al.* (1984) and Schlacher *et al.* (2007). "Also of great importance," they write, "is the hydrodynamic regime of reef environments (Monismith, 2007), which is difficult to recreate in tanks and yet is critical for multiple aspects of coral physiology (Dennison and Barnes, 1988; Patterson *et al.*, 1991)."

Wall and Edmunds collected juvenile *Porites* spp. from 2–3 m depths on the back reef of Moorea, attached them to plastic bases with epoxy, and after allowing them to recover in a 1,000-L flow-through tank placed them in nine 150-L reservoirs consisting of three replicates each of filtered seawater maintained at three conditions: Treatment 1 (unmanipulated seawater), Treatment 2 (seawater equilibrated with pCO_2 at 98.9 Pa), and Treatment 3 (same as Treatment 2 but augmented with baking soda to increase [HCO₃⁻] to 2730 µmol kg⁻¹ at a pH_T of 7.69). They conducted three experiments on 4, 6, and 8 February 2012, where in each case the customcast, UV-transparent acrylic chambers they created remained on the reef for 28 hours.

They found no differences between the behaviors of the juvenile massive *Porites* corals in Treatments 1 and 2, but calcification was enhanced by fully 81% in Treatment 3 relative to Treatments 1 and 2. The two U.S. researchers conclude, "these findings indicate that juvenile massive *Porites* spp. are resistant to short exposures to OA *in situ*," and "they can increase calcification at low pH and low Ω_{arg} if [HCO₃⁻] is elevated." The latter finding leads them also to suggest calcification of juvenile *Porites* spp. may "be limited by dissolved inorganic carbon under ambient pCO₂ condition."

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6.3.3.3 Crustaceans

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on marine crustaceans. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Survival of shrimp larvae was not reduced by lower ocean pH levels .
- At reduced seawater pH the velvet swimming crab was able to "buffer changes to extra-cellular pH over 30 days exposure" and do so "with no evidence of net shell dissolution." In addition, "tolerance to heat, carapace mineralization, and aspects of immune response were not affected by hypercapnic conditions."
- The early life larval stages of the bay barnacle "are generally tolerant to near-future levels of ocean acidification," and this observation "is in line with findings for other barnacle species." In addition, its "substantial genetic variability in response to low pH may confer adaptive benefits under future ocean acidification."
- Vertically migrating adult Arctic copepods daily cross a *p*CO₂ range of less than140 μatm and show

"only minor responses to manipulated high CO_2 ," suggesting "the natural range of pCO_2 experienced by an organism determines its sensitivity to future OA."

Noting "there is a particular need to study effects of OA [ocean acidification] on organisms living in coldwater environments due to the higher solubility of CO₂ at lower temperatures," Bechmann et al. (2011) maintained shrimp (Pandalus borealis) larvae, from day 1 through day 36 post-hatching, under the OA scenario predicted for the year 2100 (pH 7.6) and compared them against batches of larvae held under the current oceanic pH of 8.1 (the control treatment), while water temperature was kept at a constant 5°C. Bechmann et al. report survival of the larvae was not reduced at any time during the experiment, but there was "a significant delay in zoeal progression (development time)," which "may increase the chance of loss by predation." They note "a multi-generation experiment with the copepod Acartia tonsa showed that effects of OA observed in the first generation were no longer present in the second and third generation (Dupont and Thorndyke, 2009)," implying that could also prove true in the situation they investigated. The eight Norwegian researchers conclude, "there are different opinions about how to extrapolate the effects of OA from a single species examined in relatively short-term experiments to the population and ecosystem level," noting "all agree that more data from relevant long-term experiments are needed to better predict effects at higher levels of biological organization," citing Dupont et al. (2010a,b), Hendriks and Duarte (2010), and Hendricks et al. (2010).

Small et al. (2010) investigated the potential effects of lower ocean pH levels on the velvet swimming or "devil" crab (Necora puber). Working with adult individuals collected from the lower intertidal zone of Mount Batten Beach, Plymouth, UK, the authors tested the effect of 30 days' exposure of the crabs to seawater maintained in 4-L aquaria at pH values of 8.0 (control), 7.3, and 6.7. They found "Necora puber was able to buffer changes to extracellular pH over 30 days exposure," and to do so "with no evidence of net shell dissolution." They report, "tolerance to heat, carapace mineralization, and aspects of immune response were not affected by hypercapnic conditions"— i.e., conditions that lead to more than the normal level of carbon dioxide in an organism's blood. About the only negative finding was a decline in whole-animal oxygen consumption, which they described as being "marginal" between the control and medium hypercapnic conditions, but "significant" at the unrealistic future pH value of 6.7. Small *et al.* conclude their results "confirm that most physiological functions in *N. puber* are resistant to low pH/hypercapnia over a longer period than previously investigated."

In two experiments conducted over two successive years. Pansch et al. (2013) first assessed larval survival and development of the bay barnacle Amphibalanus improvisus while rearing nauplius larvae in six-well plates over 10 days in response to three pH treatments (8.02, 7.80, and 7.59). In the second experiment they assessed larval stage and size by rearing nauplius larvae in 5-L glass bottles over six days with two pH treatments (8.09 and 7.80). The three scientists report the "larval development of the barnacle was not significantly affected by the level of reduced pH that has been projected for the next 150 years," noting, "after 3 and 6 days of incubation, we found no consistent effects of reduced pH on developmental speed or larval size at pH 7.8 compared with the control pH of 8.1." They write, "after 10 days of incubation, there were no net changes in survival or overall development of larvae raised at pH 7.8 or 7.6 compared with the control pH of 8.0." In their many individual trials, they determined "there was significant variation in responses between replicate batches (parental genotypes) of some larvae," with some batches responding positively to reduced pH.

Pansch *et al.* say their results suggest "the noncalcifying larval stages of *A. improvisus* are generally tolerant to near-future levels of ocean acidification," and "this result is in line with findings for other barnacle species and suggests that barnacles do not show the greater sensitivity to ocean acidification in early life history reported for other invertebrate species." They also state the barnacle's "substantial genetic variability in response to low pH may confer adaptive benefits under future ocean acidification."

According to Lewis *et al.* (2013), "copepods comprise the dominant Arctic zooplankton; hence, their responses to OA [ocean acidification] have important implications for Arctic ecosystems, yet there is little data on their current under-ice winter ecology on which to base future monitoring or make predictions about climate-induced change." Lewis *et al.* examined "the natural distributions of the dominant Arctic copepods found under winter sea ice in relation to the current seawater carbonate chemistry conditions and compared these with their short-term responses to future high CO₂ conditions." They conducted this work "at the temporary Catlin Arctic Survey Ice Base (CIB) during late winter to early spring in 2011," where "the zooplankton were dominated by adult calanoid copepods, comprising mainly the Arctic endemics *Calanus glacialis* and *Calanus hyperboreus* but also the smaller, globally occurring *Oithona similis*, together with the nauplii of various copepod species." They conducted a series of OA experiments "using these copepod species and life history stages to compare their response to future high CO_2 conditions with natural under-ice pCO_2 exposures."

The five researchers' data revealed "species and life stage sensitivities to manipulated conditions were correlated with their vertical migration behavior and with their natural exposures to different pCO_2 ranges," and "vertically migrating adult *Calanus* spp. crossed a pCO_2 range of >140 µatm daily and showed only minor responses to manipulated high CO_2 ," whereas "*Oithona similis*, which remained in the surface waters and experienced a pCO_2 range of <75 µatm, showed significantly reduced adult and nauplii survival in high CO_2 experiments."

Lewis *et al.* conclude, "the natural range of pCO_2 experienced by an organism determines its sensitivity to future OA," adding, "certainly, ubiquitous species in their adult form, living across a range of physicochemical conditions, are likely capable of surviving change." They also note the "larvae of many marine organisms are released at very specific times to coincide with favorable environmental or food conditions," and it seems logical to conclude the same would hold true in the future, making it easier for copepod larvae to survive future OA conditions as well.

Pedersen et al. (2013) investigated "the impact of medium-term exposure to CO₂ acidified seawater on survival, growth and development ... in the North Atlantic copepod Calanus finmarchicus." Using a custom-developed experimental system, "fertilized eggs and subsequent development stages were exposed to normal seawater (390 ppm CO₂) or one of three different levels of CO₂-induced acidification (3,300, 7,300, 9,700 ppm CO₂)." The four Norwegian researchers report, "following the 28-day exposure period, survival was found to be unaffected by exposure to 3,300 ppm CO₂, but significantly reduced at 7,300 and 9,700 ppm CO₂," values far beyond any atmospheric concentration predicted under even the most extreme of circumstances. Pedersen et al. conclude, "the absence of any apparent reduction in the overall survival during the present medium-term exposure to 3,300 ppm CO₂, indicates that survival of Calanus eggs and nauplii may be robust against the

direct effects of the worst-case CO_2 scenario predicted for year 2300."

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6.3.3.4 Echinoderms

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on marine echinoderms. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- The common sea star *C. papposus* is "positively impacted by ocean acidification," as "larvae and juveniles raised at low pH grow and develop faster, with no negative effect on survival or skeletogenesis."
- Adults of the sea star *Luidia clathrata* exposed to end-of-century pH conditions "are relatively unimpaired in their regenerative capacity," which "encompasses not only their ability to re-grow their arms, but their ability to allocate materials and energy to regenerated somatic body components."
- "*Paracentrotus lividus* appears to be extremely resistant to low pH, with no effect on fertilization success or larval survival."
- "Polar and sub-polar sea urchin larvae can show a certain degree of resilience to acidification" and do not appear to be more susceptible to lower seawater pH than their temperate and tropical counterparts.
- Gametes from *Sterechinus neumayeri* are "relatively robust to pH change, especially to changes within the range predicted for the near future (i.e. a decrease of 0.3–0.5 pH units)."
- "Sea urchins inhabiting stressful intertidal environments produce offspring that may better resist future ocean acidification."
- In studies designed to reveal the effects of atmospheric CO₂ enrichment upon marine life, treatment comparisons should be made at equivalent development stages of the organism being studied. At such points along the life cycle, studies have shown there to be no significant physical differences between individuals raised under control or CO₂-enriched conditions.

- Lower ocean pH levels induced a developmental delay in *P. lividus*, yet "at a given developmental state (or size), larvae present the same calcium incorporation rate regardless of pH."
- Strongylocentrotus purpuratus sea urchins "demonstrate the capacity for rapid evolution in the face of ocean acidification and show that standing genetic variation could be a reservoir of resilience to climate change in [a] coastal upwelling ecosystem."

According to Dupont *et al.* (2010), "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 normally would be thought to make it much more difficult for echinoderms (relative to most other calcifying organisms) to produce calcification-dependent body parts.

Dupont et al. studied 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). They regulated the pH of the tanks to values of either 8.1 or 7.7 by adjusting environmental CO₂ levels to either 372 ppm or 930 ppm, documenting settlement success as the percentage of initially free-swimming larvae that affixed themselves to the aquarium walls, larval length at various time intervals, and degree of calcification. The three researchers report results the opposite of what is often predicted: The echinoderm larvae and juveniles were "positively impacted by ocean acidification." 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)." They report the sea stars' growth rates were "two times higher" in the low pH seawater, and "C. papposus seem to be not only more than simply resistant to ocean acidification, but are also performing better."

The Swedish scientists conclude, "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," leading the sea stars to become "better competitors in an unpredictable environment."

Schram *et al.* (2011) investigated the effects of lower ocean pH levels on another sea star, *Luidia clathrata.* The write, "two groups of sea stars, each with two arms excised, were maintained on a formulated diet in seawater bubbled with air alone (pH 8.2, approximating a pCO_2 of 380 ppm) or with a controlled mixture of air/CO₂ (pH 7.8, approximating a pCO_2 of 780 ppm)," and "arm length, total body wet weight, and righting responses were measured weekly." After 97 days, "a period of time sufficient for 80% arm regeneration," they state "protein, carbohydrate, lipid and ash levels were determined for body wall and pyloric caecal tissues of intact and regenerating arms of individuals held in both seawater pH treatments."

The four U.S. researchers report, "adults of the common soft bottom predatory sea star Luidia clathrata exposed to end-of-century conditions of ocean acidification (pH 7.8) are relatively unimpaired in their regenerative capacity," which "encompasses not only their ability to re-grow their arms, but their ability to allocate materials and energy to regenerated somatic body components." They found "no discernable pattern arising from exposure to a reduced seawater pH of 7.8 for 97 days on righting behavior," which they say is "an integrative measure of stress." Schram et al. conclude, "the demonstration of an organism's ability to sustain normal functions under these conditions is as equally important to document as those that are negatively impacted," because "this information will be critical to future assessments of prospective impacts of ocean acidification at the community level."

Schlegel et al. (2012) note "environmental factors directly affect populations by selecting resilient individuals," and "selection at the gametic level, or during early life, has strong and immediate effects at the population level, carrying over into subsequent life stages," as "heritability of this resilience leads to cascading adaptive effects in subsequent generations." As an example of this process, they report, "in free-spawning marine organisms, sperm selection during fertilization plays a key role by determining the nature and diversity of genotypes in the subsequent generation (Levitan, 1996; 2008) and thus their resilience to environmental change."

Schlegel *et al.* investigated "the effects of CO_2 -induced ocean acidification on the early life history

stages in the Australasian sea urchin Heliocidaris erythrogramma, focusing on intra-specific variation in responses, which can be highly variable for this species (Evans and Marshall, 2005)." They followed "the A1FI-scenario from IPCC's 4th assessment report" and "compared the effects of present day conditions for southeast Australia with the end-ofcentury scenario (pCO₂=970 ppm; pH=0.3 unit reduction) and a high-CO₂ scenario (pCO₂=1600 ppm; pH=0.5 unit reduction)." The write, "observed effects on sperm swimming behavior were applied within an established fertilization kinetics modeling framework (Vogel et al., 1982; Styan et al., 2008) to predict fertilization outcomes of single urchin pairs at each pCO_2 level." These results "were then compared to observed results from fertilization experiments conducted in the laboratory."

Schlegel et al. found "acidification significantly decreased the proportion of motile sperm but had no effect on sperm swimming speed," and the four the subsequent fertilization researchers state experiments "showed strong inter-individual variation in responses to ocean acidification, ranging from a 44% decrease to a 14% increase in fertilization success." They say their results indicate "some individuals will exhibit enhanced fertilization success in acidified oceans, supporting the concept of 'winners' and 'losers' of climate change at an individual level." If these differences are heritable, they say, it is likely "ocean acidification will lead to selection against susceptible phenotypes as well as to rapid fixation of alleles that allow reproduction under more acidic conditions," and these phenomena "may ameliorate the biotic effects of climate change if taxa have sufficient extant genetic variation upon which selection can act."

Moulin et al. (2011) supplied real-world data indicating phenotypic adaptation to seawater of lower pH by conducting a field experiment on the sea urchin Paracentrotus lividus in an attempt "to compare the effect of pH on the progeny of individuals collected from the same shore, i.e., same population, but from distinct tide pools: one where night pH was significantly reduced and the other where this decline was not so important." The four Belgian researchers report the pH of coastal seawater at the site they studied (Aber, Crozon peninsula, southern Brittany, France) was 8.14, but they say at the end of the night low tides, tide pools 1 (subtidal) and 2 (intertidal) had pH values of, respectively, 7.8 and 7.4. Under these conditions, they detected "no significant difference in gonad maturity between individuals from the two tide pools," and "the offspring of sea urchins from the tide

pool with higher pH decrease (tide pool 2) showed a better resistance to acidification at pH 7.4 than that of sea urchins from the tide pool with low pH decrease (tide pool 1) in terms of fertilization, viz. a reduction of over 30% [for tide pool 1] compared to about 20% for tide pool 2."

Moulin *et al.* conclude "sea urchins inhabiting stressful intertidal environments produce offspring that may better resist future ocean acidification." They also note "the fertilization rate of gametes whose progenitors came from the tide pool with higher pH decrease was significantly higher," suggesting "a possible acclimation or adaptation of gametes to pH stress."

Martin et al. (2011) write, "ocean acidification is predicted to have significant effects on benthic calcifying invertebrates, in particular on their early developmental states," and "echinoderm larvae could be particularly vulnerable to decreased pH, with major consequences for adult populations." The authors explored the effect of a gradient of decreasing pH from 8.1 to 7.0-corresponding to atmospheric CO₂ concentrations of ~400 ppm to ~6,630 ppm—on the larvae of the sea urchin Paracentrotus lividus, a common, economically and ecologically important species widely distributed throughout the Mediterranean Sea and the northeast Atlantic from Ireland to southern Morocco. The scientists used "multiple methods to identify the response of P. lividus to CO₂driven ocean acidification at both physiological (fertilization, growth, survival and calcification) and molecular (expression of genes involved in calcification and development) levels."

They found "Paracentrotus lividus appears to be extremely resistant to low pH, with no effect on fertilization success or larval survival." They reported "larval growth was slowed when exposed to low pH," as larvae of *P. lividus* "collected at pH 7.5 at 46 hours post-fertilization (real age) were smaller than in the control treatment [pH 8.1] and corresponded to a virtual age of 36 hours (a delay in development of 10 hours)." They further report, "down to a pH of 7.25, the larvae at Day 3 have a normal morphology but are delayed in development," so the apparent decrease in calcification at that point in time is, as they put it, "simply an indirect consequence of the impact of low pH on developmental rate." They continue, "at a given developmental state (or size), larvae present the same calcium incorporation rate regardless of pH." The scientists also report "genes involved in development and biomineralization were upregulated by factors of up to 26 at low pH," which suggests "plasticity at the gene expression level" in P. lividus "allows a normal, but delayed, development under low pH conditions."

Ericson *et al.* (2010) note in polar latitudes "the effects of changing pCO_2 and pH on gametes may be influenced by the carbonate chemistry of cold water, such as the already higher pCO_2 and lower seawater pH," and "it has also been predicted that ocean acidification effects on organisms may be more apparent and appear earliest in polar waters." Ericson *et al.* "investigated the effects of present-day pH 8.0, predicted ocean surface pH for the years 2100 and 2300 (pH 7.7 and pH 7.3, respectively) and an extreme pH (pH 7.0) on fertilization and embryogenesis in the Antarctic nemertean worm *Parborlasia corrugatus* and sea urchin *Sterechinus neumayeri.*"

The four researchers found "fertilization success was not affected by pH in P. corrugatus across a range of sperm concentrations," and "fertilization success in S. neumaveri declined significantly in pH 7.0 and 7.3 seawater, but only at low sperm concentration." They observe, "seawater pH had no effect on the rate of egg cleavage in S. neumayeri, or the proportion of abnormal embryos 1-day postfertilization," and "P. corrugatus embryogenesis was also relatively robust to pH changes, with a significant effect detected only when the seawater pH was decreased to 7.0." Ericson et al. conclude, "as in a number of other studies (see reviews by Byrne et al., 2010; Dupont et al., 2010), that gametes appeared relatively robust to pH change, especially to changes within the range predicted for the near future (i.e. a decrease of 0.3-0.5 pH units)," and they say their initial findings "do not support a view that polar species are more affected by lowered pH compared with temperate and tropical counterparts (as has also been shown for the later developmental stages of S. neumayeri (Clark et al., 2009))."

Yu et al. (2013) tested the effects of high CO₂/low pH on early development and larval growth by exposing Sterechinus neumayeri to environmental levels of CO₂ in McMurdo Sound (control: 410 ppm) and mildly elevated CO₂ levels, both near the level of the aragonite saturation horizon (510 ppm), and to under-saturating conditions (730 ppm). Over the course of development from egg to late four-arm pluteus, they found, "(1) early embryological development was normal with the exception of the hatching process, which was slightly delayed, (2) the onset of calcification as determined by the appearance of CaCO₃ spicule nuclei was on schedule, (3) the lengths of the spicule elements, and the elongation of the spicule nuclei into the larval skeleton, were significantly shorter in the highest CO₂ treatment four

days after the initial appearance of the spicule nuclei, and (4) finally, without evidence of true developmental delay, larvae were smaller overall under high CO_2 treatments; and arm length, the most plastic morphological aspect of the echinopluteus, exhibited the greatest response to high CO_2 /low pH/low carbonate conditions." Yu *et al.* conclude, "effects of elevated CO_2 representative of near future climate scenarios are proportionally minor on these early development stages."

Yu et al. (2011) raised larvae of the purple sea urchin (Strongylocentrotus purpuratus) in seawater maintained at pCO₂ levels ranging from ambient to 1,000 and 1,450 ppm CO₂ (pH 7.7 and 7.5, respectively) while measuring, after three and six days of development, "total larval length (from the spicule tip of the postoral arm to the spicule tip of the aboral point) along the spicules, to assess effects of low pH upwelling water on morphology." They found "even at the highest pCO_2 treatments, larval development was normal in terms of timing and morphological appearance," although at both days 3 and 6 larvae in the 1,450 ppm CO₂ treatment were 7-13% smaller than control larvae. Yu et al. also report "the observed developmental progression and survival of cultures was within the norm typically observed for this species at this temperature range." They note, "a lack of developmental deformities at early stages for $pCO_2 \sim 1000$ ppm has been previously reported for this species (Todgham and Hofmann, 2009), and another local species, Lytechinus pictus, with a similar overlapping portion of its range in southern California (O'Donnell et al., 2010)." They also remark, "there are even reports survival is increased in this species and its congener S. droebachiensis under some low pH conditions (Dupont and Thorndyke, 2008)."

Yu *et al.* conclude, "the effects of small magnitude in these urchin larvae are indicative of a potential resilience to near-future levels of ocean acidification."

Stumpp *et al.* (2011a) evaluated the impacts of elevated seawater pCO_2 (1,264 ppm vs. 375 ppm) on the early development of, and the larval metabolic and feeding rates of, *Strongylocentrotus purpuratus*. The researchers assessed growth and development daily, for three weeks, in terms of total body length, body rod length, postoral rod length, and posterolateral rod length, as well as mortality and feeding and metabolic rates. They found daily mortality rate (DMR) was higher under control conditions (DMR = 2.7% per day) than under high seawater pCO_2 (DMR = 2.2% per day). They also observed, in the elevated

 CO_2 treatment, larval development was about 8% slower, such that it took slightly longer for the organisms to reach equivalent development stages in the high CO_2 treatment.

As a result of the slower development of the larvae in the high CO_2 treatment, at any given time the individuals in this treatment were smaller and less well-developed than those in the control treatment, and if that were the only comparison made in this study, the effects of elevated CO_2 would seem to be negative. However, the researchers also made comparisons on the basis of development stage, and they found there were no long-term physical differences between the larvae living in the high and low CO_2 treatments.

Thus in studies designed to reveal the effects of atmospheric CO₂ enrichment on various species of marine life, treatment comparisons should be made at equivalent development stages of the organism being studied. At such points along the life cycle of the purple sea urchin, there were no significant physical differences between individuals raised in the control and CO₂-enriched conditions. Stumpp et al. conclude, "we suggest that body length is a useful scale of reference for studies in sea urchin larvae where a morphological delay in development occurs," and "using time post-fertilization as a reference may lead to misinterpretation of data"-by wrongfully assuming a negative result when in fact there may be no deleterious effect of lower ocean pH levels. Stumpp et al. (2011b) reached essentially the same conclusion in a companion paper, writing, "in studies in which a stressor induces an alteration in the speed of development, it is crucial to employ experimental designs with a high time resolution in order to correct for developmental artifacts," as this protocol "helps prevent misinterpretation of stressor effects on organism physiology."

Pespeni *et al.* (2013) note "little is known about the adaptive capacity of species to respond to an acidified ocean," and, as a result, "predictions regarding future ecosystem responses remain incomplete." They demonstrated lower ocean pH levels generate striking patterns of genome-wide selection in purple sea urchins (*Strongylocentrotus purpuratus*) cultured under CO₂ levels of 400 and 900 ppm. Working with seven populations collected along a 1,200 km mosaic of coastal upwelling-driven acidification of the California Current System, Pespeni *et al.* combined sequencing across the transcriptome of the purple sea urchin, growth measurements under experimental acidification, and tests of frequency shifts in 19,493 polymorphisms during development, detecting in the process "the widespread occurrence of genetic variation to tolerate ocean acidification."

Although larval development and morphology showed little response to elevated CO₂, the 11 researchers found "substantial allelic change in 40 functional classes of proteins involving hundreds of loci," They state "pronounced genetic changes. including excess amino acid replacements, were detected in all populations and occurred in genes for biomineralization, lipid metabolism, and ion homeostasis-gene classes that build skeletons and interact in pH regulation." They note "such genetic change represents a neglected and important impact of ocean acidification that may influence populations that show few outward signs of response to acidification." The researchers conclude "our results demonstrate the capacity for rapid evolution in the face of ocean acidification and show that standing genetic variation could be a reservoir of resilience to climate change in this coastal upwelling ecosystem."

Catarino et al. (2012) studied the development of larvae produced by adults of the Arbacia dufresnei urchin, which they collected from a sub-Antarctic population in the Straits of Magellan near Punta Arenas, Chile, immersed in high (8.0), medium (7.7), and low (7.4) pH seawater. The five scientists found "the proportion of abnormal larvae did not differ according to [pH] treatment." Although "lower pH induced a delay in development," which also was noted by Dupont et al. (2010), it "did not increase abnormality." Catarino et al. report, "even at calcium carbonate saturation states <1, skeleton deposition occurred," and they note specimens of Heliocidaris erythrogramma also "seem not to be affected by a pH decrease (until 7.6)," citing Byrne et al. (2009a,b). They note the Antarctic Sterechinus neumayeri is thought to be "more robust to ocean acidification than tropical and temperate sub-tidal species," citing Clark et al. (2009) and Ericson et al. (2010). The findings of Catarino *et al.*, and those of the other researchers they cite, indicate "polar and sub-polar sea urchin larvae can show a certain degree of resilience to acidification." They conclude A. dufresnei has the potential to "migrate and further colonize southern regions."

Sunday *et al.* (2011) note the presumed acidification of Earth's oceans is predicted to impact marine biodiversity via "physiological effects impacting growth, survival, reproduction and immunology, leading to changes in species abundances and global distributions." They point out "the degree to which these changes will play out

critically depends on the evolutionary rate at which populations will respond to natural selection imposed by ocean acidification," and this phenomenon "remains largely unquantified," citing Stockwell *et al.* (2003) and Gienapp *et al.* (2008). Sunday *et al.* measured the potential for an evolutionary response to lower ocean pH levels in the larval development rate of the two coastal invertebrates, a sea urchin (*Strongylocentrotus franciscanus*) and a mussel species (*Mytilus trossulus*).

The four researchers report their experiment revealed "the sea urchin species Stronglyocentrotus franciscanus has vastly greater levels of phenotypic and genetic variation for larval size in future CO₂ conditions compared to the mussel species Mytilus trossulus." They demonstrate "S. franciscanus may have faster evolutionary responses within 50 years of the onset of predicted year-2100 CO₂ conditions despite having lower population turnover rates." Sunday et al. conclude their comparisons suggest "information on genetic variation, phenotypic variation, and key demographic parameters, may lend valuable insight into relative evolutionary potentials across a large number of species," thereby also indicating simplistic climate envelope models of species redistributions in a future CO₂-enriched and possibly warmer world are not up to the task of providing an accurate picture of future biological reality. They note "a genetic basis for variation in CO₂ responses has been found in the three previous studies in which it has been sought (Langer et al., 2009; Parker et al., 2011; Pistevos et al., 2011), supporting the notion that genetic variation exists at some level for almost all quantitative characters (Roff, 1997)."

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6.3.3.5 Fish

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on marine fish. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Negative effects of lower ocean pH levels on fish are generally not manifested until the water reaches pH concentrations associated with atmospheric CO₂ levels several times the present value.
- Otoliths of fish grown in seawater of lower pH and aragonite saturation associated with higher CO₂ conditions are usually significantly larger than those of fish grown under present-day conditions.
- "CO₂-induced acidification up to the maximum values likely to be experienced over the next 100 years had no noticeable effect on embryonic duration, egg survivorship and size at hatching for *A. percula*, and tended to have a positive effect on the length and weight of larvae."
- "Most shallow-water fish tested to date appear to compensate fully their acid-base balance within several days of exposure to mild hypercapnia."
- "Future ocean acidification will probably not pose a problem for sperm behavior, and hence fertilization success, of Baltic cod."
- Lower ocean pH levels "neither affected the embryogenesis nor the hatch rate" of Atlantic herring. It also "showed no linear relationship between CO₂ and total length, dry weight, yolk sac area and otolith area of the newly hatched larvae."
- "Cobia exhibited resistance to treatment effects on growth, development, swimming ability, and swimming activity at 800 and 2100 µatm pCO₂," whereas "these scenarios resulted in a significant increase in otolith size (up to 25% larger area)."
- The larval clown fish "is robust to levels of ocean chemistry change that may occur over the next 50–100 years."

- Lower ocean pH levels significantly increased the size, density, and relative mass of larval cobia otoliths, which changes "could affect auditory sensitivity including a ~50% increase in hearing range at 2100 ppm CO₂."
- Lower ocean pH levels "did not appear to negatively affect size or condition of early larval walleye pollock." It induced "a trend toward larger body sizes among fish reared at elevated CO₂ levels."

Ishimatsu *et al.* (2005) note fish "constitute a major protein source in many countries," and the "potential reduction of fish resources by high-CO₂ conditions due to the diffusion of atmospheric CO₂ into the surface waters ... can be considered as another potential threat to the future world population." They conducted a survey of the scientific literature regarding the potential negative consequences for the health of marine fish of atmospheric CO₂ enrichment that could arise from continued anthropogenic CO₂ emissions.

Focusing on the possible threat of hypercapnia-a condition characterized by an excessive amount of CO_2 in the blood that typically results in acidosis, a serious and sometimes fatal condition-they say their survey revealed "hypercapnia acutely affects vital physiological functions such as respiration. circulation, and metabolism, and changes in these functions are likely to reduce growth rate and population size through reproduction failure." Although this potential threat sounds dire, it represents an egregious flight of the imagination away from what could realistically be expected to happen to fish in the future.

Ishimatsu *et al.* report "predicted future CO_2 concentrations in the atmosphere are lower than the known lethal concentrations for fish," noting "the expected peak value is about 1.4 torr [just under 1,850 ppm CO_2] around the year 2300 according to Caldeira and Wickett (2003)." As to just how far below the lethal CO_2 concentration for fish 1.4 torr is, in the case of short-term exposures on the order of a few days, Ishimatsu *et al.* cite a number of studies that yield median lethal concentrations ranging from 37 to 50 torr, values 26 and 36 times greater than the maximum CO_2 concentration expected some 300 years from now.

Regarding long-term exposures, the results are even more comforting. Ishimatsu *et al.* report Fivelstad *et al.* (1999) observed only 5 and 8% mortality at the end of 62 days of exposure to CO_2

concentrations of 5 and 9 torr, respectively, for freshwater Atlantic salmon smolts, and mere 1 and 5% mortalities for seawater postsmolts of the same species at 12 and 20 torr after 43 days (Fivelstad *et al.*, 1998). Ishimatsu *et al.* note Smart *et al.* (1979) found little difference in mortality for freshwater rainbow trout reared for 275 days at 4 to 17 torr, and no mortality occurred by the tenth week of exposure of juvenile spotted wolf fish to 20 torr (Foss *et al.*, 2003).

Fish embryos and larvae are often more vulnerable to environmental stresses than are adult fish. Yet even here, Ishimatsu *et al.* report the 24-hour median lethal concentration of CO_2 for eggs and larvae of several marine fish studied by Kikkawa *et al.* (2003) "ranged widely from 10 torr to 70 torr among species," with the smaller of these two values being more than seven times greater than the CO_2 concentration expected 300 years from now.

Ishimatsu *et al.*'s review reveals growth reductions of 24 to 48%, but again the CO_2 concentrations that induced those growth reductions ranged from 17 to 20 torr, or 12 to 14 times more than the CO_2 concentration expected 300 years from now. Consequently, Ishimatsu *et al.*'s scientific literature review suggests both freshwater and marine fish will most likely never experience any ill effects from elevated atmospheric CO_2 concentrations.

Melzner et al. (2009) state several of Earth's 30,000 species of teleost fish, which include virtually all the important sport and commercial fishes, have been shown able to "fully compensate extra cellular fluid pH" and "maintain oxygen consumption rates and growth performance under ocean acidification conditions (e.g. Larsen et al., 1997; Foss et al., 2003; Fivelstad et al., 1998, 2003; Deigweiher et al., 2008)." Noting no studies of these phenomena have lasted for more than a few days, they maintained a group of Atlantic Cod (Gadus morhua) for four months in a recirculating aquaculture system of 15 cubic meters at an atmospheric CO₂ partial pressure of 0.3 kPa (~3,000 ppm) and another group for 12 months at a CO₂ partial pressure of 0.6 kPa (~6,000 ppm). They then investigated the fishes' swimming metabolism in a swim-tunnel respirometer and took tissue samples of their gills for various chemical analyses, including gill Na⁺/K⁺-ATPase capacity, which serves as a general indicator for ion regulatory effort.

The six German scientists report, "motor activity in adult Atlantic Cod is not compromised by longterm exposure to water pCO_2 levels of 0.3–0.6 kPa," which are "scenarios exceeding the 0.2 kPa value predicted for surface ocean waters around the year 2300 (Caldeira and Wickett, 2003)." Melzner *et al.* conclude "adults of active fish species with a high ion regulatory capacity [which is employed to eliminate metabolic CO_2] are well equipped to cope with projected scenarios of global climate change."

Checkley *et al.* (2009) report on their work with fish otoliths—bony structures consisting of aragoniteprotein bilayers which fish use to sense orientation and acceleration. Noting atmospheric CO_2 enrichment had been calculated 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 "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."

"Contrary to expectations," Checkley *et al.* write, "the otoliths of fish grown in seawater with high CO₂, and hence lower pH and aragonite saturation, were significantly larger than those of fish grown under simulations of present-day conditions." They found "for 7- to 8-day-old fish grown under 993 and 2558 ppm CO₂, the areas of the otoliths were 7 to 9% and 15 to17% larger, respectively, than those of control fish grown under 380 ppm CO₂." The marine researchers note young fish are "able to control the concentration of ions (H⁺ and Ca²⁺) ... in the endolymph surrounding the otolith," where "with constant pH, elevated CO₂ increases CO_3^{2-} concentration and thus the aragonite saturation state, accelerating formation of otolith aragonite."

Munday *et al.* (2009) note "there is concern that continued increases in atmospheric CO_2 over the next century could have significant impacts on a wide range of marine species, not just those with calcified skeletons." In the case of fish, which "control their tissue pH by bicarbonate buffering and the exchange of ions, mostly across the gills," they write, "small changes in internal or external pH can readily be compensated (Heisler, 1989; Claiborne *et al.*, 2002)." Fish embryos and young larvae are possibly "more sensitive to pH changes than are juveniles and adults," and "significant effects of ocean acidification are most likely to be detected in these early life stages."

Munday *et al.* grew wild-caught pairs of the orange clownfish (*Amphiprion percula*) in a 70,000-liter recirculating seawater system at James Cook University's experimental marine aquarium facility.

They filled 70-liter tanks with seawater simulating a range of ocean acidification scenarios for the next 50-100 years—390 (current day), 550, 750, and 1.030 ppm atmospheric CO₂—while documenting egg, embryo, and larval development. The four researchers from the School of Marine and Tropical Biology of Australia's James Cook University determined "CO₂ acidification had no detectable effect on embryonic duration, egg survival and size at hatching," and it "tended to increase the growth rate of larvae." They observed, for example, 11 days after hatching, "larvae from some parental pairs were 15 to 18 per cent longer and 47 to 52 per cent heavier in acidified water compared to controls." There was a "positive relationship between length and swimming speed," and, they note, "large size is usually considered to be advantageous for larvae and newly settled juveniles."

Munday et al. note "the most common prediction is that ocean acidification could [negatively] affect individual performance (e.g. development, growth, survival, swimming ability)," especially during the early life history of the fish. However, they write, "contrary to expectations," their findings indicate "CO₂-induced acidification up to the maximum values likely to be experienced over the next 100 years had no noticeable effect on embryonic duration, egg survivorship and size at hatching for A. percula, and tended to have a positive effect on the length and weight of larvae." As for adult fish, they state "most shallow-water fish tested to date appear to compensate fully their acid-base balance within several days of exposure to mild hypercapnia," citing Michaelidis et al. (2007) and Ishimatsu et al. (2008).

Frommel et al. (2010) state, "elevated CO₂ concentrations can disturb the acid-base regulation, blood circulation, and respiration, as well as the nervous system of marine organisms, leading to long term effects such as reduced growth rates and reproduction," especially in fish, because most "are external fertilizers, and sperm are activated by seawater as they are expelled into the open ocean during a spawning event," citing Westin and Nissling (1991). Frommel et al. collected sperm from ripe adult male cod fish (Gadus morhua) caught during an August cruise through their spawning grounds in the Baltic Sea's Bornholm Basin. They exposed the fish to seawater that had been brought into equilibrium (by bubbling) with air of either 380 or $1,400 \text{ ppm CO}_2$ (leading to seawater pH values of 8.080 and 7.558, respectively), and they recorded sperm swimming behavior during the exposure period using a digital camera.

The scientists "found no significant effect of decreased pH on sperm speed, rate of change of direction or percent motility for the population of cod analyzed." Frommel *et al.* conclude "future ocean acidification will probably not pose a problem for sperm behavior, and hence fertilization success, of Baltic cod."

Franke and Clemmesen (2011) conducted a study in which eggs of Atlantic herring (Clupea harengus L.) were fertilized and incubated in artificially acidified seawater corresponding to atmospheric CO₂ concentrations of 1,260, 1,859, 2,626, 2,903, and 4,635 ppm and compared to a control treatment of 480 ppm CO₂ until the main hatch of the herring larvae occurred. "The development of the embryos was monitored daily and newly hatched larvae were sampled to analyze their morphometrics." The scientists report elevated CO₂ "neither affected the embryogenesis nor the hatch rate," and "the results showed no linear relationship between CO₂ and total length, dry weight, yolk sac area and otolith area of the newly hatched larvae." Franke and Clemmesen conclude "herring eggs can cope at current temperature conditions with an increase in CO₂," even one "exceeding future predictions of CO2-driven ocean acidification."

Bignami *et al.* (2013a) state "there is a critical need to understand the effects of acidification on the vulnerable larval stages of marine fishes, as there is a potential for large ecological and economic impacts on fish populations and the human economies that rely on them." They studied "the larvae of *Rachycentron canadum* (cobia), a large, highly mobile, pelagic-spawning, widely distributed species with a life history and fishery value contrasting other species studied to date." Bignami *et al.* raised larval cobia through the first three weeks of ontogeny under conditions of predicted future ocean pH levels to determine effects on somatic growth, development, swimming ability, swimming activity, and the formation of otoliths.

The three U.S. researchers report "cobia exhibited resistance to treatment effects on growth, development, swimming ability, and swimming activity at 800 and 2100 μ atm *p*CO₂," and "these scenarios resulted in a significant increase in otolith size (up to 25% larger area)." Bignami *et al.* conclude, "this study demonstrates that cobia is unlikely to experience a strong negative impact from CO₂-induced acidification predicted to occur within the next several centuries," which they speculate "may be due to the naturally variable environmental conditions this species currently encounters throughout ontogeny

in coastal environments," and "may lead to an increased acclimatization ability even during long-term exposure to stressors."

Munday et al. (2011a) state "in general, marine fish appear to be relatively tolerant to mild increases in ambient CO₂, presumably because well-developed mechanisms for acid-base regulation allow them to compensate for cellular acidosis caused by exposure to elevated pCO₂ (Portner et al., 2005; Ishimatsu et al., 2008; Melzner et al., 2009)." However, because "fish otoliths (earbones) are composed of aragonite," there is a concern they "could be susceptible to the declining carbonate ion concentrations associated with ocean acidification." Such an effect could be quite serious because "fish ears detect sound, body orientation and acceleration from the position of the otoliths in the inner ear and movement of the otoliths over sensory hair cells (Helfman et al., 1997; Popper and Lu, 2000)."

Munday et al. reared larvae of the marine clown fish Amphiprion percula throughout their larval phase at three pH levels-ambient or control conditions $(CO_2 \sim 390 \text{ ppm, pH} \sim 8.15)$ and higher CO_2 /lower pH conditions (CO₂ ~ 1,050 ppm, pH ~ 7.8; CO₂ ~ 1,721 ppm, pH \sim 7.6) representative of conditions predicted to prevail in AD 2100 and AD 2200-2300, respectively-to ascertain whether the elevated CO₂/reduced pH conditions would alter otolith size, shape, symmetry (between left and right otoliths), or chemistry compared to current conditions. The four researchers report "there was no effect of the intermediate treatment on otolith size, shape, symmetry between left and right otoliths, or otolith elemental chemistry, compared with controls." In the more extreme treatment, otolith area and maximum length were slightly larger than for the controls, and "no other traits were significantly affected." Munday et al. state the larval clown fish appears "capable of regulating endolymphic fluid chemistry even in waters with pH values significantly lower than open ocean values," and they conclude "the larval clown fish is robust to levels of ocean chemistry change that may occur over the next 50-100 years." This conclusion is similar to that reached by Munday et al. (2011b), who "detected no effects of \sim 850 ppm CO₂ on size, shape or symmetry of otoliths on juvenile spiny damselfish, a species without a larval phase."

Miller *et al.* (2013) assessed the impact of lower ocean pH levels on the breeding success of cinnamon anemone fish. They employed three 8,000-L recirculating aquarium systems, each set to a different CO_2 and corresponding pH level. The treatments consisted of a current-day Control CO_2 (430 µatm), a mid-century Moderate CO₂ (584 µatm), and an endof-century High CO₂ (1,032 µatm). They placed 18 pairs of cinnamon anemone fish (Amphiprion melanopus) collected from Australia's Great Barrier Reef into each of these three aquariums after all individuals had been weighed and measured for length. At the start of the experiment, they placed pairs of fish in individual 45-L tubs with continuous water flow at winter non-breeding temperatures and ambient pCO_2 values, which the scientists gradually adjusted over a two-week period to the desired levels. Then, they increased temperature by 0.5°C per week, until the average summer breeding temperature was reached, after which they kept the pairs of fish in these conditions for a nine-month period that included the summer breeding season, and the researchers recorded various assessments of breeding success.

Australian researchers report, The four "unexpectedly, increased CO₂ dramatically stimulated breeding activity." More than twice as many pairs of the fish bred in the Moderate and High CO₂ treatments (67% and 55%) compared to the Control treatment (27%). In addition, "pairs in the High CO₂ group produced double the number of clutches per pair and 67% more eggs per clutch compared to the Moderate and Control groups." The researchers determined "reproductive output in the High group was 82% higher than that in the Control group and 50% higher than that in the Moderate group." They note, "despite the increase in reproductive activity, there was no difference in adult body condition among the three treatment groups," and "there was no significant difference in hatchling length between the treatment groups." Miller et al. conclude "this study provides the first evidence of the potential effects of ocean acidification on key reproductive attributes of marine fishes and, contrary to expectations, demonstrates an initially stimulatory effect in response to increased pCO2."

Bignami *et al.* (2013b) write, "the days- to month-long pelagic larval period is an ecologically vital ontogenetic phase in marine fishes because it constitutes the primary mode of dispersal in many species (Cowen and Sponaugle, 2009) and represents the life stage most susceptible to mortality (Houde, 1997)." They say, "during this phase, the sensory abilities of larval fishes are important determinants of survival (Montgomery *et al.*, 2006) and ultimately influence the persistence of viable populations." The five researchers "used new 3D microcomputed tomography to conduct *in situ* analysis of the impact of ocean acidification on otolith (ear stone) size and density of larval cobia (*Rachycentron canadum*), a

large, economically important pantropical fish species that shares many life history traits with a diversity of high-value, tropical pelagic fishes."

According to the researchers, at an atmospheric partial pressure of 2,100 ppm CO_2 there was a significant increase in otolith size (up to 49% greater volume and 58% greater relative mass) and a 6% increase in otolith density, and the estimated relative mass of larval cobia otoliths in an end-of-century 800 ppm CO_2 treatment was 14% greater. Bignami *et al.* demonstrate "these changes could affect auditory sensitivity including a ~50% increase in hearing range at 2100 ppm CO_2 ." They say "this is a potentially optimistic result, indicating some resistance to acidification and suggesting that under near-future scenarios these impacts may be most relevant in habitats already experiencing high p CO_2 levels."

Hurst et al. (2013) examined the direct effects of projected ocean pH levels on the eggs and larvae of walleye pollock in a series of laboratory experiments to determine the effects of elevated CO₂ levels on size-at-hatch and early larval growth rates. They selected treatments to reflect ambient conditions and conditions predicted to occur in high latitude seas in the next century (a 400-600 ppm increase), as well as a significantly higher CO₂ treatment (~1,200 ppm). The three U.S. researchers report, "ocean acidification did not appear to negatively affect size or condition of early larval walleye pollock." They found "a trend toward larger body sizes among fish reared at elevated CO₂ levels," and they note this trend also has been observed in experiments with orange clownfish (Munday et al., 2009) and in a study of juvenile walleve pollock conducted by Hurst et al. (2012). Such findings, the authors write, suggest "the growth dynamics of early life stages of walleye pollock are resilient to projected levels of ocean acidification."

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6.3.3.6 Miscellaneous Animal Studies

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on other marine animals not discussed in prior subsections. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- For the common cuttlefish (*Sepia officinalis*), a decrease in pH to 7.85 "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," and these phenomena "may improve the survival [of] the newly hatched juveniles."
- Adults of the branched calcitic bryozoan *Myriapora 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."

- The gastropod *Concholepas concholepas* demonstrates "the ability to maintain calcification even at pCO_2 levels of 1036 µatm." In addition, exposure to elevated pCO_2 during their early ontogeny "may actually increase the likelihood of *C. concholepas* surviving after being overturned by an exogenous cause."
- Juveniles of the Arctic pteropod *Limacina helicina* are able to extend their shells at an aragonite saturation state as low as 0.6, which may result from "the presence of a thin periostracal layer covering the calcareous surface" that might act to protect the shell in seawater of reduced pH.
- "Copepods, as a group, may be well equipped to deal with the chemical changes associated with ocean acidification."
- Sea anemone abundance along a natural seawater pH gradient of 8.2–7.6 was observed to be higher at the lowest pH.
- Lower ocean pH levels will have no impact on the oceans' "transparency to sound."

Lacoue-Labarthe *et al.* (2009) placed fertilized eggs of the common cuttlefish (*Sepia officinalis*) in fiveliter plastic bottles filled with filtered and UVsterilized Mediterranean seawater pumped from a depth of 30 meters at a site adjacent to Monaco Bay, after which the eggs were maintained throughout their full development time at controlled conditions of temperature (16 or 19°C) and pH (8.1, 7.85 or 7.6), with the latter values maintained within \pm 0.05 of a pH unit by periodically bubbling pure CO₂ into the bottles (which were continuously aerated with CO₂free air), resulting in mean CO₂ concentrations of the air in contact with the surface of the water of 400, 900, or 1,400 ppm.

According to the authors, "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)." 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 a greater accumulation of potentially detrimental silver in the tissues of the hatchlings, but any deleterious effects of the extra silver apparently were overcome by the positive effects of lowered pH on beneficial zinc accumulation. Toxic cadmium accumulation was reduced in the lower pH (higher CO_2) treatments.

The seven scientists conclude, "decreasing pH until 7.85," 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, they write, "may improve the survival [of] the newly hatched juveniles." They note Gutowska *et al.* (2008) demonstrated "calcification was enhanced in sub-adult cuttlefish reared at $6,000 \text{ ppm CO}_2$."

Gutowska et al. found, over a six-week test period, "juvenile *S*. officinalis maintained calcification under ~4000 and ~6000 ppm CO₂, and grew at the same rate with the same gross growth efficiency as did control animals," gaining approximately 4% body mass daily and increasing the mass of their calcified cuttlebone by more than 500%. Gutowska et al. conclude "active cephalopods possess a certain level of pre-adaptation to long-term increments in carbon dioxide levels," and they suggest 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."

Rodolfo-Metalpa *et al.* (2010) conducted "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.*" Bryozoans or "moss animals" are a geologically important group of small animals that resemble corals; they 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.

Rodolfo-Metalpa *et al.* transplanted colonies of the species to normal (pH 8.1), high (pH 7.66), and

extremely high (pH 7.43) CO₂ conditions at gas vents located just off Italy's Ischia Island in the Tyrrhenian Sea. 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). They found throughout the first and cooler observation period, "dead M. truncata colonies dissolved at high CO₂ levels (pH 7.66), whereas live specimens maintained the same net calcification rate as those growing at normal pH." At the extremely high CO_2 level, the net calcification rate of the live specimens was reduced to only about 20% of what it was at normal pH, though the moss animals survived. Throughout the second and warmer observation period, by contrast, calcification ceased in both the normal and the high CO₂ treatments, and in the extremely high CO₂ treatment the transplants died.

The five scientists conclude, "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." That level is far below what even IPCC predicts will occur in response to continued burning of fossil fuels.

According to Manriquez *et al.* (2013), in Chile "the gastropod *Concholepas concholepas* is both an economically and ecologically important species inhabiting subtidal and intertidal marine habitats." In these rocky environments, "the gastropods are often exposed to highly turbulent conditions," during which times they adhere tightly to the rock surface with their foot. The scientists note, "when feeding and handling prey items the foot of *C. concholepas* is often removed from the rock leaving it vulnerable to being dislodged." Thus it is in the gastropod's best interests to right itself as quickly as possible whenever this occurs.

To explore the impact of lower ocean pH levels on this self-preservation response, as well as the more basic phenomena of growth and calcification, Manriquez *et al.* collected small individuals of *C. concholepas* from a rocky intertidal area in northern Chile, transported them to a laboratory, and reared them in natural seawater for one month, after which 10 individuals were randomly assigned to one of three pCO_2 concentrations: 388 µatm (current), 716 µatm (medium), or 1,036 µatm (high). There they remained, under well-fed conditions, for 83 days, while the researchers made various measurements on days 0, 11, 45, 52, 62, 73, and 83 after the beginning of treatments.

At the end of the study period, the 11 researchers report, there were no significant among-treatment differences in peristomal length, wet weight, or buoyant weight, nor the shell weight of empty shells. They also determined, "on average, self-righting time was three times faster in individuals reared under increased pCO_2 levels than under normal seawater conditions." Manriquez et al. conclude "C. concholepas have the ability to maintain calcification even at pCO_2 levels of 1036 µatm ... in agreement with similar results reported in the literature for other invertebrates (Ries et al., 2009; Manzello, 2010; Rodolfo-Metalpa et al., 2011)." And they state, "during their early ontogeny, exposure to elevated pCO_2 may actually increase the likelihood of C. concholepas surviving after being overturned by an exogenous cause."

Citing Hunt *et al.* (2008), authors Comeau *et al.* (2012) write, "pteropods are pelagic mollusks that play an important role in the food web of extensive oceanic regions, particularly at high latitudes, where they are a major dietary component for zooplankton and higher predators, such as herring, salmon, whales and birds." Comeau *et al.* investigated the effect of lower ocean pH levels "using juveniles of the Arctic pteropod *Limacina helicina* from the Canada Basin of the Arctic Ocean," where they caught and extracted overwintering individuals from depths of 100 to 200 meters through a hole in the ice, thereafter maintaining the mollusks at three pH levels (8.05, 7.90, and 7.75) for eight days, after which they assessed them for mortality and shell growth.

Comeau et al. found pH did not impact the mortality of the pteropods, but the degree of linear extension of their shells decreased as pH declined. Nevertheless, the pteropods were able to extend their shells at an aragonite saturation state as low as 0.6, suggesting "the presence of a thin periostracal layer covering the calcareous surface, as shown on the Antarctic pteropod Limacina helicina antarctica (Sato-Okoshi et al., 2010), might, among other mechanisms, protect the shell from a corrosive environment." Although much remains to be known about pteropod responses to a potential decline in seawater pH, these findings indicate pteropods possess a certain degree of adaptability to low pH levels, and the results of similar studies of other calcifying sea creatures suggest pteropods may be able to evolve in their ability to cope with declining seawater pH.

Weydmann et al. (2012) note the Arctic copepod Calanus glacialis "can comprise up to 70-80% of the zooplankton biomass in Arctic shelf seas (Blachowiak-Samolyk et al., 2008; Conover, 1988; Hirche and Mumm, 1992), and is a key herbivore (Mumm et al., 1998; Soreide et al., 2008; Tande, 1991) as well as an important prev item for other zooplankton species (Falk-Petersen et al., 2002, 2004), fish (Fortier et al., 2001), and seabirds (Karnovsky et al., 2003; Weslawski et al., 1999; Wojczulanis et al., 2006)." Noting "testing the potential impacts of ocean acidification on C. glacialis reproduction is vital," they investigated "how the reduction of sea surface pH from present day levels (pH 8.2) to a realistic model-based level of pH 7.6, and to an extreme level of pH 6.9, would affect the egg production and hatching success of C. glacialis under controlled laboratory conditions," where "reduced pH seawater was prepared by bubbling compressed CO₂ through filtered seawater, until the appropriate level of pH was reached."

The four researchers report, " CO_2 -induced seawater acidification had no significant effect on *C. glacialis* egg production," and a reduction in pH to 6.9 only delayed hatching at what they called this "extreme level of pH." They also state there was no significant effect "on the survival of adult females"; this observation, they write, "is in agreement with previous studies on other copepod species," citing Mayor *et al.* (2007) and Kurihara and Ishimatsu (2008). Weydmann *et al.* conclude their results are "in agreement with previous studies on other copepod species and would indicate that copepods, as a group, may be well equipped to deal with the chemical changes associated with ocean acidification."

Suggett et al. (2012) state "non-calcifying anthozoans such as soft corals and anemones, play important ecological and biogeochemical roles in reef environments (e.g. Fitt et al., 1982; Bak and Borsboom, 1984; Muller-Parker and Davy, 2001)." They collected pertinent data from 11-26 May 2011 on a sea anemone (Anemonia viridis) along a natural seawater pH gradient of 8.2-7.6-which would be expected to prevail across an atmospheric CO₂ gradient of 365-1,425 ppm-produced by a shallow cold vent system (Johnson et al., 2011; 2012) that released CO₂ to coastal waters near Vulcano, Italy, about 25 km northeast of Sicily. The nine researchers found an increase in gross maximum photosynthesis, respiration rates, and dinoflagellate endosymbiont abundance (but unchanged diversity) with increasing CO₂. Sea anemone abundance increased with CO₂ and

"dominated the invertebrate community at high CO_2 conditions." The enhanced productivity in the sea anemones they studied, Suggett *et al.* write, implies "an increase in fitness that may enable non-calcifying anthozoans to thrive in future environments, i.e. higher seawater CO_2 ." As they declare in the title of their paper, "Sea anemones may thrive in a high CO_2 world."

Meron et al. (2013) studied the physiology of Anemonia viridis growing naturally along a CO₂-ventinduced pH gradient near Ischia, Italy, also studying the nature of the associated microbial community (bacteria and endosymbiotic Symbiodinium), focusing on two specific locations that could be characterized as ambient (pCO₂ 330 ppm, pH 8.1) and very CO₂enriched (pCO₂ 9,341 ppm, pH 7.0). Although the four researchers found reduction in pH had an impact on the composition and diversity of the anemones' associated microbial communities, "no significant changes were observed in A. viridis physiology, and no microbial stress indicators (i.e., pathogens, antibacterial activity, etc.) were detected." Meron et al. conclude, "it appears that elevated CO_2 does not have a negative influence on A. viridis that live naturally in the [very CO₂-enriched] site." They say "this suggests that natural long-term exposure and dynamic diverse microbial communities may contribute to the acclimation process of the host in a changing pH environment."

Mukherjee et al. (2013) "investigated the proteomic response of metamorphosing larvae of the tubeworm Hydroides elegans, challenged with two climate change stressors, ocean acidification (pH 7.6) and hypoxia (2.8 mg O_2 per liter)," as well as with both of the stressors combined. The seven scientists found concomitant exposure to the two climate change stressors "caused several proteins involved in energy metabolism, calcification and stress tolerance to be differentially expressed." This phenomenon "seemed to allow the tubeworm larvae to successfully metamorphose and carry out calcification." Mukherjee et al. conclude "the aragonite tubeforming tubeworm larvae have a high tolerance to hypoxia and may possess the capacity to acclimate over time, even in the face of ocean acidification."

Some researchers have recently looked at the possible effects of lower ocean pH levels on the oceans' "transparency to sound." Reeder and Chiu (2010) state "it has been reported that, given a 0.3 reduction in pH, from 8.1 to 7.8, a reduction in the acoustic absorption at low frequencies could result, suggesting a significant increase in ocean noise," and more recently "it has been suggested that low-frequency sound will travel farther due to the ocean pH reduction expected by 2050," and most recently, researchers have suggested "in an ocean more transparent to sound, the resultant changes in propagation range will be noticeable in the operation of scientific, commercial and naval applications that are based on ocean acoustics."

Reeder and Chiu reviewed "the fundamental principles of acoustic transmission loss in the ocean and how the multiple transmission loss mechanisms impact ocean noise levels within the context of changing ocean pH." They conducted "an analytical analysis involving physical and empirical models of all relevant transmission loss mechanisms," focusing on "three ocean acoustic environments ... to elucidate the expected change in ocean noise level from sources at the surface as a function of frequency: shallow water, the acoustic surface duct and the deep ocean."

The two researchers in the Department of Oceanography of the Naval Postgraduate School in Monterey California (USA) report for even a large reduction in ocean pH from 8.1 to 7.4, there was "no observable change in ocean noise in the shallow water and surface duct environments for all frequencies two environments which host a large portion of the marine mammal population." They also found "a negligible change in ocean noise level in the deep water environment for all frequencies ... which also provides an upper bound to the maximum expected increase in ocean noise level due to the fact that it does not fully account for the range-dependent water column sound speed, bottom topography and distributed sources."

Putting their results in the context of average background ocean noise levels as represented by Wenz (1962) curves, they found "a statistically insignificant change compared to the inherent variability of ocean noise associated with shipping and surface-generated mechanisms." Thus, "after 250 years," they write, "there would still be no significant modifications to the Wenz curves," which suggests lower ocean pH levels will have no negative impact on ocean noise.

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6.3.3.7 Multiple Animal Studies

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on animals as obtained from studies in which multiple species are discussed. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- The impact of elevated atmospheric CO₂ on marine calcification "is more varied than previously thought."
- Different stress effects on interacting species resulting from lower ocean pH levels "may not only enhance but also buffer community level effects."
- "Biological processes can provide homeostasis against changes in pH in bulk waters of the range predicted during the 21st century."
- 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" and "may not be the widespread problem conjured into the 21st century."

Ries et al. (2009) "reared 18 calcifying species for 60 days in isothermal (25°C) experimental seawaters equilibrated with average [atmospheric] CO₂ values of 409, 606, 903 and 2856 ppm, corresponding to modern CO₂, and \sim 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," after which "the organisms' net rates of calcification (total calcification minus total dissolution) under the various CO₂ treatments were estimated from changes in their buoyant weight and verified with dry weight measurements after harvesting." The three Woods Hole Oceanographic Institution (USA) researchers report, "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 CO2," 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 CO₂ treatment."

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)." Finally, they write, "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 ."

Ries *et al.* conclude "the impact of elevated atmospheric CO_2 on marine calcification is more varied than previously thought," with responses ranging from negative to neutral to positive.

Kurihara *et al.* (2007) extracted sedimentary mud from the seafloor of Tanabe Bay on the Kii Peninsula of Japan and incubated it in marine microcosms continuously aerated for 56 days with air of either 360 or 2,360 ppm CO₂ while they periodically measured the abundance and biomass of different members of the meiobenthic community contained in the sediments. Meiofauna are small benthic invertebrates larger than microfauna but smaller than macrofauna; they are metazoan animals that can pass through a 0.5-1 mm mesh but are retained by a 30–45 µm mesh. In marine environments, they typically are found between grains of damp sand on the seashore or in muddy sediments at the bottoms of water bodies.

The authors "observed no significant differences in the abundance of total meiofauna, nematodes, harpacticoid copepods (including adults and and nauplii by the end of the copepodites) experiment." They say there "may have been recruitments successful under elevated CO_2 conditions" and "elevated CO2 had not impacted the reproduction of nematodes and harpacticoid copepods." These observations, the three researchers write, "suggest that the projected atmospheric CO₂ concentration in the year 2300 does not have acute effects on the meiofauna."

Appelhans et al. (2012) note "the impact of seawater acidification on calcifying organisms varies at the species level," and "if the impact differs between predator and prey in strength and/or sign, interactions may be altered." trophic This consequence, if true, could play havoc with many marine ecosystems as currently constituted. In a study designed to explore the potential for such interactions in the brackish western Baltic Sea, Appelhans et al. investigated the impacts of three seawater pCO_2 levels (650, 1,250 and 3,500 ppm) on the growth of two predatory species (the common sea star Asterias rubens and the shore crab Carcinus maenas), also determining whether the conditions affected the quantity or size of prey consumed (the blue mussel Mytilus edulis). The five German scientists found "growth of Mytilus edulis was generally very low and not significantly affected by acidification." They write, "a trend toward a lower shell mass with increasing seawater pCO_2 was observed," and "the mean maximum breaking resistance of mussel shells

was significantly lowered by ~20% at the highest level of 3500 ppm."

As for the predators, they report, "acidification did not provoke a measurable shift in prev size preferred by either predator." They also found intermediate acidification levels (corresponding to 1,250 ppm CO₂) "had no significant effect on growth or consumption in either predator species," but the highest acidification level (corresponding to $3,500 \text{ ppm CO}_2$) "reduced feeding and growth rates in sea stars by 56%, while in crabs a 41% decrease in consumption rates of mussels could be demonstrated." "Interestingly," Appelhans et al. conclude, "the enhanced vulnerability of mussels seems to be neutralized by the decreased consumption of the predators under high acidification." They write, "these results illustrate that different stress effects on interacting species may not only enhance but also buffer community level effects," noting, "when stress effects are similar (and weak) on interacting species, biotic interactions may remain unaffected."

Hurd et al. (2011) observe, "most ocean acidification studies so far have been simplistic" because they have not "jointly considered physical, chemical and biological interactions." They note "the emerging discipline of marine ecomechanics (Denny and Helmuth, 2009; Denny and Gaylord, 2010) provides a valuable framework in which such inter-disciplinary research can be conducted." The old experimental approach, they write, "overlooks the existence of a discrete micro-layer (i.e., diffusion boundary layer, DBL) at the surface of many aquatic organisms that buffers them from the surrounding mainstream seawater (Vogel, 1996)." This is achieved by metabolic processes that alter the water chemistry within the DBL, with photosynthesis increasing pH, and calcification and respiration reducing pH (Hurd et al., 2009). They continue, "the chemical environment within the DBL differs from that in the mainstream seawater just micrometers away, with implications for both the dissolution of, and formation of, calcium carbonate (Borowitzka and Larkum, 1976; Ries et al., 2009)."

In a study employing the still-evolving ecomechanic approach, Hurd *et al.* used pH microelectrodes and oxygen micro-optodes to measure the DBL thickness at the surface of the coralline seaweed *Sporolithon durum*, the sea urchin *Evechinus chloroticus*, and the abalone *Haliotis iris*, at a range of seawater velocities (0–10 cm/sec) that reflected those found within a temperate reef in Southern New Zealand (45.38°S) that may be vulnerable to ocean acidification (OA). For *S. durum*, they also determined whether DBL thickness would be affected when mainstream seawater pH was reduced to 7.5, the projected worst-case scenario for the year 2215 as calculated by Caldeira and Wickett (2003). In addition, they measured pH fluctuations at the surface of *S. durum* on a timescale of hours at ambient seawater pH and pH 7.5 at two different flows (1.5 and 6.3 cm/sec), and for the invertebrates they measured surface pH fluctuations at ambient pH and a flow of 1.5 cm/sec.

The seven scientists determined coralline seaweeds encounter a wide range of pH values over each daily cycle, but they are able to increase their pH substantially due to photosynthesis and to withstand periods of very low pH (relative to the present day and comparable to values predicted for coming centuries) under low flows. As to sea urchins, the scientists found they are currently subjected to-and readily survive-very low pH values (7.5) at their surfaces in slow seawater flows, values equivalent to those predicted to occur in the future. And abalone, the researchers write, "have a very thin DBL and hence their outer surface is subjected to the pH in the mainstream seawater, in all flow conditions," yet they too persist, probably because they are "internal calcifiers" and "the reduced pH predicted for future oceans may not directly alter their rates of calcification."

Hurd *et al.* conclude their findings "support the view that although the role of chemistry on OA is well understood, the biological responses to OA will be complex," citing their own work and that of Fabry *et al.* (2008). They also note, "both the site of calcification and the ecomechanics of the biota, i.e., the interactions between their morphology, physiology and the surrounding hydrodynamic environment, must be considered." Their work suggests marine calcifiers are much more robust to OA than originally thought.

Findlay *et al.* (2011) provide further evidence of the importance of biology in controlling calcification. They note, "calcifying marine organisms such as molluscs and foraminifera, crustaceans, echinoderms, corals and coccolithophores are predicted to be most vulnerable to decreasing oceanic pH (ocean acidification)." They point out there is a possibility for "increased or maintained calcification under high carbon dioxide conditions," and their experiment demonstrates the reality of this phenomenon in different types of calcifying marine animals. Working with five calcifying organisms—two gastropods (the limpet *Patella vulgata* and the periwinkle *Littorina littorea*), a bivalve mussel (*Mytilus edulis*), one

crustacean (the cirripede *Semibalanus balanoides*), and one echinoderm (the brittlestar *Amphiura filiformis*)—Findlay *et al.* "measured either the calcium (Ca²⁺) concentration in the calcified structures or shell morphological parameters as a proxy for a net change in calcium carbonate in live individuals exposed to lowered pH," where the lower pH of the seawater employed was created by the bubbling of CO₂ into header tanks.

"Contrary to popular predictions," they write, the results indicated "the deposition of calcium carbonate can be maintained or even increased in acidified seawater." In fact, four of the five species they studied actually exhibited increased levels of calcium in low pH conditions. In the case of Littorina littorea, for example, all morphological shell parameterswidth, height, thickness, area, perimeter, aperture area, and aperture perimeter-"increased in low pH treatments compared to the control," and "there was ~67% more growth in shell height, ~30% more growth in shell width and ~40% more growth in shell thickness under low pH conditions compared to the control." They also observed a large amount of dissolution taking place on isolated shells and arms of the creatures they studied, but they found "the presence of a live animal within its calcium carbonate structure offset this dissolution."

Findlay et al. say their findings demonstrate "there is a great degree of biological control on calcification with complex links to other physiological processes," and "increasing evidence in the literature agrees with the results of [our] study," noting, "McDonald et al. (2009) showed calcification in another barnacle species (Amphibalaus amphitrite) to continue, and possibly even increase, under low pH conditions (pH 7.4); Arnold et al. (2009) demonstrated larval lobsters (Homarus gammarus) were able to lav down calcium carbonate structure in pH conditions 0.3 units below the control levels; Checkley et al. (2009) showed young fish have enhanced aragonite otolith growth when grown under elevated CO₂; Maier et al. (2009) showed that, although there was a decrease in calcification in coldwater corals, overall they showed a positive net calcification at aragonite saturation states below 1, and longer-term experiments suggest these corals may actually maintain or even increase calcification over longer timescales at low pH (Schubert et al., 2010)."

In what was at the time the most comprehensive analysis ever conducted of experimental studies that have explored the effects of rising atmospheric CO₂ concentrations on marine biota, Hendriks *et al.* (2010) assembled a database of 372 experimentally evaluated

responses of 44 marine species to lower ocean pH levels induced by equilibrating seawater with CO₂enriched air. They note, "warnings that ocean acidification is a major threat to marine biodiversity are largely based on the analysis of predicted changes in ocean chemical fields," which are derived from theoretical models that do not account for numerous biological phenomena and have only "limited experimental support."

Of the published reports they scrutinized, only 154 assessed the significance of responses relative to controls. Of those reports, 47 reported no significant response, so "only a minority of studies" demonstrated "significant responses to acidification." 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 lower seawater pH levels.

Since their analyses to this point had included some extremely high acidification treatments, they repeated their analyses for only those pH levels induced by atmospheric CO₂ concentrations of 2,000 ppm or less, as that concentration had 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 $33 \pm 4.5\%$ and fertility by $11 \pm 3.5\%$ across groups, whereas survival and growth showed no significant overall responses. When the upper limiting CO_2 concentrations were in the range of 731–759 ppm, just below the value predicted by IPCC (2007) for the end of the twenty-first century (790 ppm)calcification rate reductions of only 25% were observed.

The three researchers say 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 Widdicombe *et al.* (2008) and noting "these gradual changes take place on the scale of decades, permitting adaptation of organisms even including genetic selection."

Even this mitigating factor is not the end of the good news, for Hendriks *et al.* also write, "most experiments assessed organisms in isolation, rather than [within] whole communities," and the responses of other entities and processes within the community

may buffer the negative impacts of CO_2 -induced acidification. As an example, they note "sea-grass photosynthetic rates may increase by 50% 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."

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 note these fluctuations also "offer opportunities for adaptation to the organisms involved."

Hendriks *et al.* additionally state the models on 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" and "photosynthetic activity"—such as that of the zooxanthellae hosted by corals—"depletes pCO_2 and raises pH (Kuhl *et al.*, 1995) so that the pH actually experienced by organisms may differ greatly from that in the bulk water phase (Sand-Jensen *et al.*, 1985)."

Hendriks et al. also note "calcification is an active process where biota can regulate intracellular calcium concentrations," so "marine organisms, like calcifying coccolithophores (Brownlee and Taylor, 2004), actively expel Ca^{2+} through the ATPase pump to maintain low intracellular calcium concentrations (Corstiens et al., 2001: Yates and Robbins, 1999)." They note, "as one Ca^{2+} is pumped out of the cell in exchange for 2H⁺ pumped into the cell, the resulting pH and Ca²⁺ concentrations increase the CaCO₃ saturation state near extracellular membranes and appear to enhance calcification (Pomar and Hallock, 2008)"-so much so, in fact, that "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.* note 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," and thus this phenomenon "may not be the widespread problem conjured into the 21st century" by the world's climate alarmists, echoing a similar conclusion reached at the turn of the last millennium (Idso *et al.*, 2000). Hendriks *et al.* conclude, "biological processes can provide homeostasis against changes in pH in bulk waters of the range predicted during the 21st century."

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6.4 Freshwater "Acidification"

The vast majority of studies of the effects of lower pH levels examine the topic as it pertains to marine life. However, a growing body of research investigates its potential effects on aquatic species inhabiting the world's freshwater lakes, rivers, and streams. That research suggests there may be great benefits in store for such aquatic life as the air's CO_2 concentration continues to rise.

6.4.1 Algae

The studies reviewed in this section examine what scientists have learned about potential impacts of falling freshwater pH levels on algae. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

• A "doubled atmospheric CO₂ concentration would affect the growth of *C. pyrenoidosa* when it grows under bright solar radiation, and such an effect

would increase by a great extent when the cell density becomes high."

- The effects of lower freshwater pH levels on algal production could be such that a "doubling of atmospheric CO₂ may result in an increase of the productivity of more than 50%."
- "Contrary to the dominating hypotheses in the literature," lower freshwater pH levels may lead to "positive, bottom-up effects on secondary production in some stream food webs."
- Lower freshwater pH levels may prevent bloom development and ambient toxicity of certain harm-ful algae.

Xia and Gao (2003) cultured cells of the freshwater alga Chlorella pyrenoidosa in Bristol's solution within controlled environment chambers maintained at low and high light levels (50 and 200 μ mol/m²/s) during 12-hour light periods followed by 12-hour dark periods for a total of 13 days, while the solutions in which the cells grew were continuously aerated with air of either 350 or 700 ppm CO_2 . When they harvested the cells (in the exponential growth phase) at the conclusion of this period, they found the biomass (cell density) of the twice-ambient CO₂ treatment was 10.9% and 8.3% greater than that of the ambient-air treatment in the low- and high-light regimes, respectively, although only the high-light result was statistically significant. The two scientists conclude a "doubled atmospheric CO₂ concentration would affect the growth of C. pyrenoidosa when it grows under bright solar radiation, and such an effect would increase by a great extent when the cell density becomes high." Their data also suggest the same may happen, perhaps only to a lesser extent, when the alga grows under less-bright conditions.

Andersen and Andersen (2006) placed six 1.5-mdiameter flexible plastic cylinders in the littoral zone of Lake Hampen in central Jutland, Denmark. Three of the cylinders were maintained at the ambient CO_2 concentration of the air and three were enriched to 10 times ambient, and the researchers measured the CO_2 -induced growth response of a mixture of several species of filamentous freshwater algae dominated by *Zygnema* species but also containing some *Mougeotia* and *Spirogyra*. After one full growing season (May to November), they determined the biomass of the microalgal mixture in the CO_2 -enriched cylinders was increased by 220% in early July, by 90% in mid-August, and by 3,750% in mid-November. Schippers *et al.* (2004a) note "it is usually thought that unlike terrestrial plants, phytoplankton will not show a significant response to an increase of atmospheric CO₂," but "most analyses have not examined the full dynamic interaction between phytoplankton production and assimilation, carbonchemistry and the air-water flux of CO₂," and "the effect of photosynthesis on pH and the dissociation of carbon (C) species have been neglected in most studies."

Schippers *et al.* developed "an integrated model of phytoplankton growth, air-water exchange and C chemistry to analyze the potential increase of phytoplankton productivity due to an atmospheric CO_2 elevation." As a test of their model, they let the freshwater alga *Chlamydomonas reinhardtii* grow in 300 ml bottles filled with 150 ml of a nutrient-rich medium at enclosed atmospheric CO_2 concentrations of 350 and 700 ppm maintained at two air-water exchange rates characterized by CO_2 exchange coefficients of 2.1 and 5.1 m day⁻¹, as Shippers *et al.* (2004b) describe it, periodically measuring the biovolume of the solutions by means of an electronic particle counter.

The results of this effort, they write, "confirm the theoretical prediction that if algal effects on C chemistry are strong, increased phytoplankton productivity because of atmospheric CO_2 elevation should become proportional to the increased atmospheric CO_2 ," which suggests algal productivity "would double at the predicted increase of atmospheric CO_2 to 700 ppm." Although "strong algal effects (resulting in high pH levels) at which this occurs are rare under natural conditions," they predict effects on algal production in freshwater systems could be such that a "doubling of atmospheric CO_2 may result in an increase of the productivity of more than 50%."

Collins *et al.* (2006) propagated 10 replicate lines from each of two clones of *Chlamydomonas reinhardtii* within a phytotron by batch-culturing them in flasks through which air of 430 ppm CO₂ was continuously bubbled or air of gradually increasing CO_2 concentration was bubbled over the course of development of 600 generations of the microalga, when a concentration of 1,050 ppm was reached and maintained throughout the development of 400 more algal generations. They grew each of these sets of plants (low-CO₂-adapted and high-CO₂-adapted) for a short period of time at both 430 and 1,050 ppm CO₂ and determined their steady-state CO_2 uptake rates.

For the algae whose atmospheric CO_2 concentration had been continuously maintained at 430 ppm,

Collins et al. report abruptly increasing it to a value of 1,050 ppm led to a 143% increase in steady-state CO₂ uptake rate. For the algae that had experienced the gradual CO_2 increase from 430 to 1,050 ppm, there was a 550% increase in CO_2 uptake rate when the rate in the 1,050-ppm air was compared to the rate that prevailed when the air's CO₂ concentration was abruptly lowered to 430 ppm. For the algae experiencing the most realistic scenario-gradually going from a state of continuous 430-ppm CO₂ exposure to one of 1,050 ppm exposure over a period of 600 generations and then maintaining the higher CO₂ level for a further 400 generations, the increase in steadystate CO₂ uptake rate due to the long-term 620-ppm increase in atmospheric CO₂ concentration was a more modest 50%, which roughly translates to a 25% increase in growth for the more typical 300 ppm increase in atmospheric CO₂ concentration employed in numerous CO₂ enrichment studies of terrestrial plants.

If the results obtained by Collins et al. for the freshwater Chlamydomonas reinhardtii are typical of what to expect of marine microalgae-which Field et al. suggest may provide nearly half of the primary production of the planet-the totality of Earth's plant life may provide a significant brake upon the rate at which the air's CO₂ content may increase in the future, as well as the ultimate level to which it may rise. Collins et al. provide a rough indication of just how powerful this phenomenon may be when they note, "mathematical simulations have estimated that pre-industrial levels of CO₂ would have been as high as 460 ppm" without the operation of the well-known "biological pump" (Sarmiento and Toggweiler, 1984) by which dying phytoplankton sink carbon into deep ocean sediments, "whereas pre-industrial atmospheric CO₂ levels were [actually] around 280 ppm (Etheridge et al., 1996)," or 180 ppm less.

Logothetis *et al.* (2004) note "the function and structure of the photosynthetic apparatus of many algal species resembles that of higher plants (Plumley and Smidt, 1984; Brown, 1988; Plumley *et al.*, 1993)," and "unicellular green algae demonstrate responses to increased CO₂ similar to those of higher plants in terms of biomass increases (Muller *et al.*, 1993)." Noting "little is known about the changes to their photosynthetic apparatus during exposure to high CO₂," they grew batches of the unicellular green alga *Scenedesmus obliquus* (wild type strain D3) autotrophically in liquid culture medium for several days in a temperature-controlled water bath of 30°C at low (55 µmol m⁻² s⁻¹) and high (235 µmol m⁻² s⁻¹) light intensity while continuously aerating the water with air of either 300 or 100,000 ppm CO_2 . Exposure to the latter high CO_2 concentration produces a "reorganization of the photosynthetic apparatus" and "leads to enhanced photosynthetic rates, which … leads to an immense increase of biomass." After five days under low light conditions, the CO_2 -induced increase in biomass was approximately 300%, and under high light conditions it was approximately 600%.

Hargrave et al. (2009) "used free air CO₂ 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." They found the primary productivity of benthic algae inhabiting the streams "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." 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, implying a reduced availability of phosphorus, which would make the algae less nutritious and, therefore, less beneficial for its consumers.

However, the researchers observed eCO_2 "had positive effects on benthic invertebrates, significantly increasing chironomid density, biomass, and average size." Hargrave et al. state "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 aCO₂ 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," Hargrave et al. conclude " eCO_2 might have positive, bottom-up effects on secondary production in some stream food webs." They state their experimental findings and "the large literature from terrestrial and marine ecosystems suggests that future [i.e., higher] atmospheric CO₂ concentrations are likely to have broad reaching effects on autotrophs and consumers across terrestrial and aquatic biomes."

Joint *et al.* (2011) write "marine and freshwater assemblages have always experienced variable pH conditions," noting "phytoplankton blooms can rapidly reduce pCO₂, with a concomitant increase in pH," which subsequently declines as the blooms die out, demonstrating "pH is naturally variable and that marine organisms—particularly microbes—must already be capable of adapting to rapid and sometimes large changes in pH." They note "oceanic pH can change by up to 0.06 pH unit during the year even in the oligotrophic Central Pacific, which does not experience the dramatic phytoplankton blooms of temperate oceans."

In the case of freshwater ecosystems, Joint *et al.* report, "Maberly (1996) showed that diel variations in a lake can be as much as 2–3 pH units," and "Talling (2006) showed that in some English lakes, pH could change by >2.5 pH units over a depth of only 14 m." They note, "phytoplankton, bacteria, archaea and metazoans are all present in lakes, and appear to be able to accommodate large daily and seasonal changes in pH."

Noting the "the impacts of elevated atmospheric CO_2 on freshwater habitats are still poorly understood," Wu *et al.* (2012) isolated specimens of the freshwater N₂-fixing cyanobacterium *Cylindrospermopsis raciborskii* from a pond near Dianchi Lake in Kunming (China). They cultured them semi-continuously for 18 days at low and high inorganic phosphorus (Pi) levels (0.022 μ M and 22 μ M, respectively) in contact with air of either 380 or 1,000 ppm CO₂, while measuring several important physiological functions of the cyanobacterium.

In the case of light-saturated net photosynthesis, the 620-ppm increase in the air's CO₂ content resulted in 37% and 74% increases in the low and high Pi treatments, respectively. The CO₂ increase resulted in 26% and 23% increases in biomass in the low and high Pi treatments, respectively. And the CO₂ increase resulted in 36% and 14% increases in nitrogen fixation in the low and high Pi treatments, respectively. Wu et al. say the cyanobacterial growth increase they observed "confirms previous studies with other algae (Burkhardt and Riebesell, 1997; Burkhardt et al., 1999; Clark and Flynn, 2000; Kim et al., 2006: Posselt et al., 2009: Kranz et al., 2010)," as well as the finding of Chinnasamy et al. (2009) that "the nitrogenase activity of Anabaena fertilissima increased with increasing levels of CO2."

Prosser *et al.* (2012) write, "harmful algal blooms of *Prymnesium parvum* are global phenomena occurring in marine, estuarine and inland ecosystems," citing Moestrup (1994), Edvardsen and Paasche (1998), and Lundholm and Moestrup (2006). They note *P. parvum*, commonly known as "golden algae" or "Texas tide," is "a mixotrophic flagellated haptophyte known to produce toxins that may severely impact aquatic organisms," citing Brooks *et al.* (2010). Prosser *et al.* evaluated "whether pH influences *P. parvum* bloom development and ambient toxicity" by manipulating pH levels (7, 7.5, 8.5) of *in situ* experimental enclosures during 21-day pre-bloom development experiments in Lake Granbury, Texas (USA).

The 10 U.S. researchers report neutral pH levels preempted *P. parvum* bloom development, as "population densities never reached bloom proportions and no ambient toxicity to fish or cladocerans resulted." They found "higher pH (8.5) allowed bloom formation to occur" and "resulted in ambient toxicity," whereas at the other end of the pH spectrum, "reducing pH to 7 and 7.5 did not adversely affect phytoplankton or zooplankton biomass."

The results of the studies reviewed above are encouraging, suggesting the growth and productivity of freshwater algae may be enhanced as the air's CO_2 concentration rises and the pH levels of freshwater lakes, rivers, and streams decline, while also making it more difficult for blooms of some harmful algae to occur.

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6.4.2 Macrophytes

The studies reviewed in this section examine what scientists have learned about potential impacts of lower freshwater pH levels on macrophytes—aquatic plants. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- The ongoing rise in the air's CO₂ content will likely induce significant positive impacts on most freshwater macrophytes, including submersed, floating, and emergent species.
- The CO₂-induced growth enhancement of Corkscrew vallisneria (*Vallisneria tortifolia*) has been observed to increase linearly out to CO₂ concentrations 10 times the ambient value.
- Total biomass accumulation of *Vallisneria spinulosa* plants grown at an elevated CO₂ concentration of 1,000 ppm was "2.3 times that of plants grown in ambient CO₂, with biomass of leaves, roots, and rhizomes increasing by 106%, 183%, and 67%, respectively."
- A tenfold increase in aquatic CO₂ concentration enhanced the biomass production of *Littorella uniflora* by 78% across an entire growing season.
- A 300 ppm increase in CO₂ produced a 3.7-fold increase in total dry matter production in the water lily *Nymphaea marliac*.
- In a CO₂ enrichment study of the common water fern *Azolla pinnata*, "the debilitating effects of high temperatures were [found to be] reduced: in one case to a much less severe negative growth rate, in another case to merely a short period of zero growth rate, and in a third case to no discernible ill effects whatsoever—in spite of the fact that the ambient treatment plants in this instance all died."
- Elevated CO₂ and temperature—both singly and in combination—positively impacted root growth of water horsetail (*Equisetum fluviatile*).

Idso (1997) grew specimens of corkscrew vallisneria (*Vallisneria tortifolia*) for several multiweek periods in several 10- and 29-gallon glass tanks (containing 10-cm bottom-layers of common aquarium gravel) filled with tap water maintained within 0.5° C of either 18.2°C or 24.5°C. He maintained the semi-sealed air spaces above these "poor man's biospheres," as he named them, at a number of CO₂ concentrations. Upon harvesting the plants at the end of the study, he found the CO₂-induced growth enhancement was linear, and this linear relationship extended to the highest atmospheric CO₂ concentration studied: 2,100 ppm. In addition, he found the CO₂-induced growth increase of the plants in the higher of the two water

temperature treatments (a 128% increase in going from an atmospheric CO₂ concentration of 365 ppm to one of 2,100 ppm) was 3.5 times greater than that of the plants in the lower water temperature treatment. Idso reports Titus *et al.* (1990), who studied the closely related *Vallisneria americana*, "observed that the biomass of their experimental plants also rose linearly with the CO₂ content of the air above the water within which they grew, and that [it] did so from the value of the [then] current global mean (365 ppm) to a concentration fully ten times larger."

Yan et al. (2006) collected turions of Vallisneria spinulosa from Liangzi Lake, Hubei Province (China) and planted them in tanks containing 15-cm-deep layers of fertile lake sediments, topped with 40 cm of lake water, placed in two glasshouses-one maintained at the ambient atmospheric CO₂ concentration of 390 ppm and the other at an elevated concentration of 1,000 ppm. They allowed the plants to grow for 120 days, harvested them, and determined the dry weights of their various organs. They found the "total biomass accumulation of plants grown in the elevated CO_2 was 2.3 times that of plants grown in ambient CO₂, with biomass of leaves, roots, and rhizomes increasing by 106%, 183%, and 67%, respectively." They report, "turion biomass increased 4.5-fold," because "the mean turion numbers per ramet and mean biomass per turion in elevated CO₂ were 1.7-4.3 and 1.9-3.4 times those in ambient CO₂."

Andersen et al. (2006) studied small, slowgrowing evergreen perennials called isoetids that live submersed along the shores of numerous freshwater lakes. They obtained specimens of Littorella uniflora from sediment cores removed from Lake Hampen, Denmark, which they grew in 75-liter tanks with 10cm overburdens of filtered lake water for 53 days. They measured various plant, water, and sediment properties throughout the experiment's duration, and then the researchers destructively harvested the plants and measured their biomass. Throughout this period, half of the tanks had ambient air bubbled through their waters, while the other half were similarly exposed to a mixture of ambient air and pure CO₂ that produced a tenfold increase in the air's CO₂ concentration. This ultra-CO₂-enrichment led to a 30% increase in plant biomass and "higher O2 release to the sediment which is important for the cycling and retention of nutrients in sediments of oligotrophic softwater lakes." When the ultra-CO₂-enrichment was maintained for an entire growing season (May-November), Andersen and Andersen (2006a) report the tenfold increase in aquatic CO₂ concentration enhanced the biomass production of *Littorella uniflora* by 78%.

Andersen and Andersen (2006b) propagated Littorella uniflora under sterile conditions in the absence of symbiotic arbuscular mycorrhizal fungi (AMF), after which they re-infected half of the plants with AMF and allowed both groups to grow for 60 days in water of either high (150 μ M) or low (ambient, about 15 µM) CO₂ concentration in conditions where concentrations of NO₃- and PO_4^{3} were low enough to limit plant growth. Under this experimental setup, the authors report, "both in treatments with and without AMF, high CO₂ concentration resulted in a significantly higher total biomass of L. uniflora, and the same was observed for both shoots and roots," although "the biomass of roots increased more than the biomass of shoots." They report, "in treatments without AMF, increasing the CO₂ concentration 10 times resulted in a change from a slightly negative growth to a twofold increase in biomass over the 60-day period," and "in treatments with AMF, the increase in CO₂ concentration resulted in a fourfold increase in biomass."

The researchers' work also demonstrated "*L. uniflora*'s symbiosis with mycorrhiza improved the retention of N and P in the plants at very low nutrient concentrations in the water." Consequently, as they observed "hyphal infection increased fivefold under the raised CO_2 concentration," it is evident elevated aquatic CO_2 concentrations may also help isoetids by enhancing the magnitude and stability of their AMF symbiosis, which helps them retain vital nutrients.

Idso et al. (1990) studied an "in-between" type of plant-water lily (Nymphaea marliac)-which has submersed roots and rhizomes anchored in waterbody sediments but also has floating leaves on the surface of the water and emergent flowers that protrude above the water surface. The water lilies were grown for two consecutive years in sunken metal stock tanks located out-of-doors at Phoenix, Arizona (USA) and enclosed within clear-plastic-wall open-top chambers through which air of either 350 or 650 ppm CO_2 was continuously circulated. In addition to the leaves of the plants being larger in the CO₂enriched treatment, there were 75% more of them than in the ambient-air tanks at the conclusion of the initial five-month-long growing season, the scientists report. Each of the plants in the high-CO₂ tanks also produced twice as many flowers as the plants growing in ambient air, and the flowers that blossomed in the CO₂-enriched air were more substantial than those that bloomed in the air of ambient CO₂ concentration-they had more petals, the petals were

longer, and they had a greater percent dry matter content, so the flowers weighed on average about 50% more than those in the ambient-air treatment. In addition, the stems that supported the flowers were slightly longer in the CO₂-enriched tanks, and the percent dry matter contents of both the flower and leaf stems were greater, so the total dry matter in the flower and leaf stems in the CO₂-enriched tanks exceeded that of the flower and leaf stems in the ambient-air tanks by approximately 60%.

There were also noticeable differences just above the surface of the soil that covered the bottoms of the tanks. Plants in the CO₂-enriched tanks had more and bigger basal rosette leaves, which were attached to longer stems of greater percent dry matter content, which led to the total biomass of these portions of the plants being 2.9 times greater than the total biomass of the corresponding portions of the plants in the ambient-air tanks. In addition, plants in the CO₂enriched tanks had more than twice as many unopened basal rosette leaves.

The greatest differences of all, however, were within the soil that covered the bottoms of the stock tanks. When half of the plants were harvested at the conclusion of the first growing season, the number of new rhizomes produced over that period was 2.4 times greater in the CO₂-enriched tanks than in the ambient-air tanks, and the number of major roots produced there was 3.2 times greater. The percent dry matter contents of the new roots and rhizomes were also greater in the CO₂-enriched tanks. Overall, the total dry matter production within the submerged soils of the water lily ecosystems was 4.3 times greater in the CO₂-enriched tanks than in the ambient-air tanks, and the total dry matter production of all plant partsthose in the submerged soil, those in the free water, and those in the air above-was 3.7 times greater in the high-CO₂ enclosures.

Over the second growing season, the growth enhancement in the high- CO_2 tanks was somewhat less, but the plants in those tanks were so far ahead of the plants in the ambient-air tanks that in their first five months of growth they produced what it took the plants in the ambient-air tanks fully 21 months to produce.

Idso (1997) focused on an exclusively floating freshwater macrophyte, growing many batches of the common water fern (*Azolla pinnata*) over a wide range of atmospheric CO₂ concentrations at two water temperatures (18.2°C and 24.5°C) for periods of several weeks. A 900 ppm increase in the CO₂ concentration of the air above the tanks led to a 19% increase in the biomass production of the plants

floating in the cooler water, but a 66% biomass increase in the plants floating in the warmer water.

In another study of Azolla pinnata, Idso et al. (1989) conducted three separate two- to three-month experiments in which they grew batches of the floating fern out-of-doors in adequately fertilized water contained in sunken metal stock tanks located within clear-plastic-wall open-top chambers continuously maintained at atmospheric CO₂ concentrations of either 340 or 640 ppm. At weekly intervals, the researchers briefly removed the plants from the water and weighed them, and they measured their photosynthetic rates at hourly intervals from dawn to dusk on selected cloudless days. They found the photosynthetic and growth rates of the plants growing in ambient air "first decreased, then stagnated, and finally became negative when mean air temperature rose above 30°C." In the high CO₂ treatment, they found "the debilitating effects of high temperatures were reduced: in one case to a much less severe negative growth rate, in another case to merely a short period of zero growth rate, and in a third case to no discernible ill effects whatsoever-in spite of the fact that the ambient treatment plants in this instance all died "

Ojala *et al.* (2002) studied an emergent freshwater macrophyte, growing water horsetail (*Equisetum fluviatile*) plants at ambient and double-ambient atmospheric CO₂ concentrations and ambient and ambient + 3°C air temperatures for three years, although the plants were subjected to the doubleambient CO₂ condition only for approximately five months of each year. The increase in air temperature boosted maximum shoot biomass by 60%, but the elevated CO₂ had no effect on this aspect of plant growth. Elevated CO₂ and temperature—both singly and in combination—positively impacted root growth, which was enhanced by 10, 15, and 25% by elevated air temperature, CO₂, and the two factors together, respectively.

The experimental findings discussed here indicate the ongoing rise in the air's CO_2 content likely will have significant positive impacts on most freshwater macrophytes, including submersed, floating, and emergent species.

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6.5 Simultaneous Ocean Warming and "Acidification"

6.5.1 Effects on Marine Plants

The studies reviewed in this section examine what scientists have learned about potential impacts of rising ocean temperatures and lower ocean pH levels on various types of marine phytoplankton and macroalgae. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

• Strains of one phytoplankton species, and even of a single population, can yield responses opposite

to changes in temperature and CO₂, which can lead to contrasting predictions about the future.

- Laboratory experiments suggest increases in the air's temperature and CO₂ content may improve the productivity of two dominating filamentous cyanobacteria species of the Baltic Sea.
- Future ocean warming and acidification will significantly increase the biological extraction of nitrogen and carbon dioxide from the atmosphere by diazotrophic cyanobacteria.
- Atmospheric CO₂ enrichment and sea-surface warming likely will have a large positive influence on the growth of *Emiliania huxleyi*, based on findings of laboratory studies.
- Consistent with findings of laboratory experiments, over the past 220 years of warming and lower ocean pH levels, there has been a 40% increase in average *E. huxleyi* coccolith mass in the subpolar North Atlantic Ocean, based on analyses of real-world sediment-core data.
- Sediment cores taken from the Santa Barbara Basin on the North American Pacific margin indicate an approximate 33% increase in mean coccolith weight over the 87-year period 1917– 2004.
- Modern *Coccolithus* populations in the Southern Ocean are, on average, more heavily calcified than their fossil counterparts from the Last Glacial Maximum (21.6–19.9 ka), the Holocene (4.2– 3.1 ka), and the Transition between the two periods (16.2–15.6 ka).
- A literature review of experiments conducted on more than 100 marine macroalgae (macro-autotrophs) species finds "photosynthetic and growth rates of marine macro-autotrophs are likely to increase under elevated CO₂ similar to terrestrial C₃ species."

Fiorini *et al.* (2011) note coccolithophores "are considered to be the most productive calcifying organisms on the planet," and "they play a crucial role in the marine carbon cycle through calcification and photosynthetic carbon production (Rost and Riebesell, 2004)." They also note coccolithophores "contribute significantly to the flux of organic matter from the sea surface to deep waters and sediments

(Klaas and Archer, 2002)" and are "responsible for about half of the global surface ocean calcification."

Fiorini et al. (2011) examined the effects of the pCO_2 and temperature levels projected for the end of this century on photosynthesis, growth, and calcification during both life stages (haploid and diploid) of strain AC418 of the coccolithophore Syracosphaera pulchra, via a series of culture studies conducted in the laboratory, where they focused on both particulate inorganic carbon (PIC) and particulate organic carbon (POC). The three researchers report "neither the rate of calcification (production of particulate inorganic carbon) nor the PIC:POC ratio were significantly affected by elevated pCO_2 , temperature or their interaction." They further state, "our results confirm that the expected 3°C increase in the present seawater temperature will not strongly affect the physiology of this eurythermal species" and "the effect of an elevated pCO_2 in seawater will not be significant on calcification or on the PIC:POC ratio in either life stage."

Feng et al. (2008) grew Emiliania huxleyi, which they isolated from the Sargasso Sea, by semicontinuous culture methods at two light intensities (low 50 and high 400 µmol photons/m²/sec), two temperatures (low 20 and high 24°C), and two CO₂ concentrations (low 375 and high 750 ppm). They found in the low-light environment, the chlorophyll anormalized photosynthetic rates of the coccolithophores in all four temperature/CO2 treatments attained maximum values at an irradiance of approximately 200 μ mol photons/m²/sec. The maximum photosynthetic rate was lowest in the lowtemperature, low-CO₂ (ambient) treatment, but was significantly increased by elevated temperature alone (by 55%) and by elevated CO_2 alone (by 95%). In the high-temperature, high-CO₂ (greenhouse) treatment the maximum photosynthetic rate was increased by 150% relative to the ambient treatment.

In the high-light environment, the chlorophyll *a*normalized photosynthetic rates did not max out below the maximum irradiance tested (900 μ mol photons/m²/sec) for any but the ambient treatment. Consequently, the equations fit to the data of the other treatments were extrapolated to their respective photosynthetic maxima, which produced corresponding maximum photosynthetic rate increases of 58%, 67%, and 92% for the elevated temperature alone, elevated CO₂ alone, and greenhouse treatments, respectively.

In the high-light greenhouse treatment characteristic of the expected future condition of Earth, the maximum photosynthetic rate was 178% greater than in the low-light ambient treatment characteristic of the present. The seven researchers say their results indicate "future trends of CO_2 enrichment, sea-surface warming and exposure to higher mean irradiances from intensified [surface water] stratification will have a large influence on the growth of *Emiliania huxleyi*."

Another important group of phytoplankton are diatoms, which Sobrino et al. (2008) say "are responsible for almost 40% of the ocean primary productivity (Nelson et al., 1995)." According to Kremp et al. (2012), "most of the laboratory studies investigating the effects of climate stressors on phytoplankton have been performed on single strains," and "the significant effects often found in such experiments are contrasted by the general lack of clear responses in natural populations," citing Engel et al. (2008). They hypothesize the "contradictory responses to changed climate conditions sometimes observed within the same species might be partly attributable to strain variability between or within populations," citing Langer et al. (2009) and noting these observations emphasize "the need to consider variability in studies aiming to understand the effects of climate change on phytoplankton species."

Kremp et al. studied "the effects of increased temperature and CO₂ availability, as predicted consequences of global change, on 16 genetically different isolates of the diatom Skeletonema marinoi from the Adriatic Sea and the Skagerrak (North Sea), and on eight strains of the PST (paralytic shellfish dinoflagellate toxin)-producing Alexandrium ostenfeldii from the Baltic Sea." They assessed maximum growth rates of acclimated isolates grown in batch cultures for five to 10 generations in a factorial design at 20 and 24°C, and present-day and next-century atmospheric CO₂ concentrations (385 and 750 ppm), respectively. The seven scientists found strains of one species, and even of a single population, "can be impacted in very different ways by climate stressors," noting "a particularly wide response range was found in the population of S. marinoi from the NW Adriatic sea, where temperature and CO₂ caused positive, negative or no effect at all."

Kremp *et al.* conclude, "depending on the strain of choice," experiments using single isolates of the population they studied "could have given opposite response patterns," which likely would have led to "contrasting predictions" about the future. Therefore, they write, "responses observed in single strain experiments may not be representative" of the species or population in question, and predictions for specific species behavior under future climatic conditions must "be treated with caution."

Noting "cyanobacteria such as Synechococcus and Prochlorococcus have a major impact on the global carbon cycle and contribute up to 50% of fixed carbon in marine systems (Partensky et al., 1999)," Fu et al. (2007) studied "how CO₂ and temperature individually and together affect the physiology of these two species under identical growth conditions." They grew stock cultures of the two picocyanobacteria in one-liter bottles of autoclaved and filtered seawater maintained at temperatures of either 20 or 24°C in equilibrium with air of either 380 or 750 ppm CO₂. The five researchers discovered the growth rate and maximum photosynthetic rate in Synechococcus increased about 2.3-fold and 4-fold, respectively, in the high-temperature and high-CO₂ treatment relative to ambient conditions, but they remained unchanged in Prochlorococcus.

Fu *et al.* say their observations "could be taken to mean that in the future, rising temperature and CO₂ would stimulate growth or photosynthesis of [the] *Synechococcus* isolate but would have much less effect on [the] Procholrococcus strain," and such a result could "potentially influence competition between particular *Synechococcus* and *Prochlorococcus* ecotypes." However, they add, "we need to be very cautious about inferring ecosystem-scale shifts in broad taxonomic groups like picocyanobacteria from studies using only two isolates." They report stimulation of algal growth rates by elevated CO₂ also has been observed by Burkhardt and Riebesell (1997), Burkhardt *et al.* (1999), Yang and Gao (2003), Beardall and Raven (2004), and Kim *et al.* (2006).

Hutchins *et al.* (2007) note *Trichodesmium* species and other diazotrophic cyanobacteria support a large fraction of the total biological productivity of Earth's tropical and subtropical seas, and they exert a significant influence on the planet's carbon cycle by supplying much of the nitrogen that enables marine phytoplankton to maintain a level of productivity that removes vast amounts of CO_2 from the atmosphere. They hypothesized that if an increase in the air's CO_2 content or its temperature led to an increase in oceanic N₂ fixation, it also could lead to the biological extraction of more CO_2 greenhouse effect via this negative feedback process.

To explore this possibility, the eight researchers grew cultures of Pacific and Atlantic Ocean isolates of *Trichodesmium* ecotypes across a range of atmospheric CO_2 concentrations characteristic of Earth's past (150 ppm), its current state (380 ppm), and possible future conditions (750, 1,250, and 1,500 ppm) at two temperatures (25 and 29°C) and at sufficient and limiting phosphorus concentrations (20 and 0.2 μ mol L⁻¹ of phosphate, respectively), in situations where the carbonate buffer system parameters in their artificial seawater culture media were "virtually identical to those found in natural seawater across the relevant range of CO₂ values."

Hutchins et al. found, at atmospheric CO₂ concentrations projected for the year 2100 (750 ppm), "N2 fixation rates of Pacific and Atlantic isolates increased 35-100%, and CO₂ fixation rates increased 15-128% relative to present day CO₂ conditions (380 ppm)." In what they call one of their "most striking results," they found "increased CO₂ enhanced N₂ and CO₂ fixation and growth rates even under severely phosphorus-limited steady-state growth conditions." They also report "neither isolate could grow at 150 ppm CO₂," but "N₂ and CO₂ fixation rates, growth rates, and nitrogen:phosophorus ratios all increased significantly between 380 and 1500 ppm," and, "in contrast, these parameters were affected only minimally or not at all by a 4°C temperature change."

Hutchins et al. note current global estimates of N₂ fixation by *Trichodesmium* are about 60×10^9 kg N yr⁻¹, and if their experimental results can be extrapolated to the world's oceans, by 2100 this amount could increase to 81–120 x 10⁹ kg N yr⁻¹. "If these estimates are coupled with modeling predictions of a 27% warming-induced expansion of suitable habitat (Boyd and Doney, 2002), calculations suggest that global N₂ fixation by Trichodesmium alone could range from $103-152 \times 10^9$ kg N yr⁻¹ by the end of this century," which is to be compared to recent estimates for total pelagic N₂ fixation of 100–200 x 10⁹ kg N yr⁻ ¹ (Galloway et al., 2004). They also note free-living unicellular cvano-bacteria in the ocean are believed to fix at least as much nitrogen as Trichodesmium (Montoya et al., 2004), and endosymbiotic cyanobacteria also con-tribute substantially to N₂ fixation. Hence they conclude, "if N₂ fixation rates in these groups show commensurate increases with rising CO₂, the cumulative effect on the global nitrogen cycle could be considerably larger (e.g., a doubling)." In addition, they state their results indicate "like N₂ fixation, CO₂ fixation by Trichodesmium should also increase dramatically in the future because of CO₂ enrichment."

Hutchins *et al.* conclude, "many of our current concepts describing the interactions between oceanic nitrogen fixation, atmospheric CO₂, nutrient biogeochemistry, and global climate may need re-evaluation

to take into account these previously unrecognized feedback mechanisms between atmospheric composition and ocean biology."

Karlberg and Wulff (2013) investigated the ramifications of potential future increases in the air's CO₂ content on the productivity of two dominating filamentous cyanobacteria species of the Baltic Sea (Nodularia spumigena and a mix of Aphanizomenon sp.) during the summer bloom of the Baltic Proper. The pair of researchers set out to experimentally determine the response of these two species to changes in that region's environment predicted to occur in response to IPCC's business-as-usual A1FI scenario described by Meehl et al. (2007): a temperature increase of 4° C, an atmospheric pCO₂ increase from 380 to 960 ppm, and a reduction in salinity from 7 to 4. Working in the laboratory, Karlberg and Wulff measured numerous responses of the two species of cyanobacteria, growing both separately and together, to different combinations of these environmental changes.

The two researchers report "increased temperature, from 12 to 16°C, had a positive effect on the biovolume and photosynthetic activity of both species," and "compared when growing separately, the biovolume of each species was lower when grown together." They also note "decreased salinity, from 7 to 4, and elevated levels of pCO_2 , from 380 to 960 ppm, had no effect on the biovolume, but on [the photosynthetic activity] (Fv/Fm) of N. spumigena with higher Fv/Fm in salinity 7." Karlberg and Wulff say their results suggest "the projected A1FI scenario might be beneficial for the two species dominating the extensive summer blooms in the Baltic Proper." They caution their results "further stress the importance of studying interactions between species." They conclude, "long-term studies together with multifactorial and mesocosm/field experiments are needed to elucidate the future impact of climate change effects on Baltic filamentous cyanobacteria."

Grelaud *et al.* (2009) 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 ocean-ographic global changes." They analyzed 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." They found "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." Specifically, they note "a >33% increase in mean coccolith weight was determined for the order Isochrysidales over 87 years from ~1917 until 2004."

The three researchers note "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. They note those concerned about lower ocean pH levels predicted such conditions will "result in reduced coccolithophore carbonate mass and a concomitant decrease in size and weight of coccoliths." They discovered just the opposite appears to have occurred in the real world, even in places where the predicted calcification reductions were expected to be greatest.

Iglesias-Rodriguez et al. (2008) grew several batch incubations of the coccolithophore species Emiliania huxleyi in the laboratory, bubbling air of a number of different atmospheric CO₂ concentrations through the culture medium and determining the amounts of particulate inorganic carbon (PIC) and particulate organic carbon (POC) produced by the coccolithophores within the CO₂ treatments. In addition, they determined the change in average coccolithophore mass of Emiliania huxleyi over the past 220 years in the real world of nature, based on data they obtained from a sediment core extracted from the subpolar North Atlantic Ocean, over which period of time temperatures increased and the air's CO₂ concentration rose by approximately 90 ppm. The 13 researchers from the United Kingdom, France, and United States observed an approximate doubling of both PIC and POC between the culture media in equilibrium with air of today's CO₂ concentration and air of 750 ppm CO₂. They report the field evidence obtained from the deep-ocean sediment core they studied "is consistent with these laboratory conclusions, indicating that over the past 220 years there has been a 40% increase in average coccolith mass."

Cubillos *et al.* (2012) set out to adapt "an existing method to estimate coccolith calcite weight using birefringence (Beaufort, 2005)," which they decided was needed "to suit the large coccoliths of *Coccolithus pelagicus*," focusing "only on the central area, which is the thickest and most robust part of the coccolith." They applied this technique "to fossil and sediment trap material from the South Tasman Rise area of the Southern Ocean," based on three sediment samples each from the Last Glacial Maximum (21.6–19.9 ka), the Holocene (4.2–3.1 ka), and the

Transition between the two periods (16.2–15.6 ka), as well as modern-day trap samples. "Most strikingly," the five researchers report, "it appears that modern *Coccolithus* populations in the Southern Ocean are, on average, more heavily calcified than their fossil counterparts," a positive and encouraging finding. Cubillos *et al.* say their work reveals "substantial nonlinearity and independency of variations (plasticity) in coccolith size, shape and volumetric weight between the investigated time intervals." They say they hope to study these phenomena "in more detail" in order to "unravel what environmental conditions are related to intra-specific phenotypic variability in ancient and modern coccolithophores."

Koch *et al.* (2013) write, "although seagrasses and marine macroalgae (macro-autotrophs) play critical ecological roles in reef, lagoon, coastal and open-water ecosystems, their response to ocean acidification (OA) and climate change is not well understood." They reviewed the scientific literature on these subjects, examining "marine macroautotroph biochemistry and physiology relevant to their response to elevated dissolved inorganic carbon (DIC), carbon dioxide (CO₂), and lower carbonate (CO_3^{2-}) and pH," and also exploring "the effects of increasing temperature under climate change and the interactions of elevated temperature and CO₂."

The four researchers determined their "literature review of >100 species revealed marine macroautotroph photosynthesis is overwhelmingly C₃ (>=85%) with most species capable of utilizing HCO₃⁻," and "most are not saturated at current ocean DIC." They conclude, "photosynthetic and growth rates of marine macro-autotrophs are likely to increase under elevated CO₂ similar to terrestrial C₃ species." In addition, as "the photosynthesis of the majority of the species examined was not saturated at the current levels of DIC in the ocean and responded to an increase in CO₂," they conclude seagrasses and many marine macroalgae have the potential to respond positively, in terms of photosynthesis and growth, under elevated ocean CO₂ and OA.

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6.5.2 Effects on Marine Animals

6.5.2.1 Corals

6.5.2.1.1 Review Papers

Few studies have investigated the interactive effects of lower ocean pH levels and rising temperature. This section examines what scientists have learned from such studies, focusing on the impacts of these variables on coral reefs as reported in review papers on the topic. The key findings, all of which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- "Neither climate nor sea-level nor chemical changes in the oceans can elucidate the waxing and waning of reefs" throughout their history on Earth. The "boom and bust pattern" observed through geologic time is "impossible to explain by linear responses to physicochemical changes."
- Shallow water tropical reef organisms existed throughout the entire 540 million years of the Phanerozoic, which included times when sea surface temperatures were more than 7°C higher than those of today and the air's CO₂ concentration was as much as 6,000 ppm higher.
- Although the Paleocene-Eocene Thermal Maximum, some 55.8 million years ago, was "characterized by rapid sea surface temperature rise and a similar order of magnitude of CO₂ increase as present," there is evidence "reef assemblages in at least one oceanic setting were

unaffected." Other reefs also have shown "greater resilience to past rapid warming and acidification than previously thought."

• Emerging evidence indicates there is variability in the coral calcification response to lower seawater pH levels, geographical variation in bleaching susceptibility and recovery, and potential adaptation to rapid warming and declining pH, supporting "an alternative scenario in which reef degradation occurs with greater temporal and spatial heterogeneity than current projections suggest."

Kiessling (2009), from the Museum fur Naturkunde of the Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University in Berlin, reviewed the state of knowledge of the long-term effects of changes in ocean temperature and the atmosphere's CO₂ concentration on the vigor of the planet's coral reefs as of 2009. With respect to global warming, Kiessling 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). He also 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."

Regarding lower ocean pH levels, the German researcher reports, "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).

In light 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 writes, "ecologically complex reef systems have been around for hundreds of millions if not billions of years," and "geologic models of CO₂ concentrations in the atmosphere suggest that these were much greater during most of Earth's history than today." This further suggests something other than CO₂-induced global warming and lower ocean pH levels must have been responsible for their prior "boom and bust" pattern of behavior.

In a major review article published in *Science*, Pandolfi *et al.* (2011) summarize "the most recent evidence for past, present and predicted future responses of coral reefs to environmental change, with emphasis on rapid increases in temperature and lower ocean pH levels and their effects on reefbuilding corals." They note, "many physiological responses in present-day coral reefs to climate change are interpreted as consistent with the imminent disappearance of modern reefs globally because of annual mass bleaching events, carbonate dissolution and insufficient time for substantial evolutionary responses." All of these interpretations, they demonstrate, may be incorrect.

The four researchers report shallow water tropical reef organisms existed throughout the entire 540 million years of the Phanerozoic, which included times when sea surface temperatures (SSTs) were more than 7°C higher than those of today and the air's CO_2 concentration was as much as 6,000 ppm higher. As to what they call "the most recent reef crisis," they report "the Paleocene-Eocene Thermal Maximum (PETM; 55.8 million years ago), was characterized by rapid SST rise and a similar order of magnitude of CO_2 increase as present," yet there is evidence "reef assemblages in at least one oceanic setting were unaffected (Robinson, 2011)" and other reefs also have shown "greater resilience to past rapid warming and acidification than previously thought."

More recently, during the Holocene, Pandolfi *et al.* state, "evidence from high-resolution proxy records suggests that tropical SSTs had the potential to repeatedly warm over centennial to millennial time scales (Rosenthal *et al.*, 2003; Schmidt *et al.*, 2004)." In one location, they report, SSTs rose "at rates comparable to those projected for the coming century (Lea *et al.*, 2003)," yet "none of these post-Last Glacial Maximum warming episodes appear to have interrupted reef growth."

As for current coral responses to SST increases, the four scientists note "numerous characteristics of coral hosts have the potential to confer differences in bleaching susceptibility," and "these characteristics vary substantially within and among coral species (Baird *et al.*, 2009a; Csaszar *et al.*, 2010)." They note "some coral species also harbor multiple strains of zooxanthellae, which confer differential susceptibility of their hosts to bleaching (Rowan, 2004)." They note there is also "substantial variation in reef recovery in the aftermath of bleaching events (Baker *et al.*, 2008)."

The story is much the same regarding coral responses to lower ocean pH levels. Pandolfi et al. note, for example, studies have shown calcification has "increased under moderately elevated partial pressure of CO₂ (Rodolfo-Metalpa et al., 2010; Jury et al., 2010; Reynaud et al., 2003), as has also been observed for some coralline algae, crustacea and echinoderms (Ries et al., 2009)." They also note sensitivity of calcification to lower ocean pH levels "appears to be reduced when (i) studies are conducted over weeks or months (Ries et al., 2009; Rodolfo-Metalpa et al., 2010; Marubini et al., 2001; Revnaud et al., 2003) as opposed to less than one day (Langdon and Atkinson, 2005; Ohde and Hossain, 2004) or (ii) corals are reared under nutritionally replete conditions by feeding or elevating inorganic nutrient concentrations (Langdon and Atkinson, 2005; Ries et al., 2009)."

The four researchers write, "because bleachingsusceptible species often have faster rates of recovery from disturbances, their relative abundances will not necessarily decline" in the future. They continue, "such species could potentially increase in abundance, depending on how demographic characteristics and competitive ability are correlated with thermal tolerance and on the response of other benthic taxa, such as algae." They further note "the shorter generation times typical of more-susceptible species (Baird *et al.*, 2009b) may also confer faster rates of evolution of bleaching thresholds, which would further facilitate maintenance of, or increases to, the relative abundance of thermally sensitive but faster-evolving species (Baskett *et al.*, 2009)."

Pandolfi *et al.* state emerging evidence for variability in the coral calcification response to lower ocean pH levels, geographical variation in bleaching susceptibility and recovery, responses to past climate change, and potential rates of adaptation to rapid warming "supports an alternative scenario in which reef degradation occurs with greater temporal and spatial heterogeneity than current projections suggest." Further noting "non-climate-related threats already confronting coral reefs are likely to reduce the capacity of coral reefs to cope with climate change," they conclude "the best and most achievable thing we can do for coral reefs currently to deal with climate change is to seek to manage them well" by reducing more direct anthropogenic impacts such as fishing, pollution, and habitat destruction, which fragment populations or decrease population sizes and reduce the potential of coral reefs to adapt to warmer, lower pH conditions.

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6.5.2.1.2 A Model-based Study

This section reviews one model-based study that focuses on the impact of lower ocean pH levels in combination with higher temperatures on coral reefs.

Couce *et al.* (2013) note "there is concern that the growing frequency and severity of mass bleaching episodes may lead to species composition shifts and functional collapse in coral reefs in the near future." They also note global warming "has the potential to improve currently marginal environmental conditions and extend the range of tropical coral reefs into higher latitudes," as is "demonstrated in the fossil record in response to warmer geological periods (e.g., Lighty *et al.*, 1978; Veron, 1992; Precht and Aronson, 2004; Greenstein and Pandolfi, 2008; Woodroffe *et al.*, 2010; Kiessling *et al.*, 2012)." Less is known about the interacting effects of global warming and lower ocean pH levels, although these phenomena are projected to occur concurrently.

Couce *et al.* employed "a suite of statistical models based on the environmental factors thought to be limiting to the present equilibrium distribution of shallow-water coral reefs, perturbing them with Earth System Model projected future sea surface temperatures and aragonite saturation changes (the simulations used in Turley *et al.*, 2010)," while considering "a range of potential future CO_2 emissions scenarios" but focusing on "the consequences of the 'A2' scenario (characterized by regionally oriented economic development and high population growth, expecting ca. 850 ppm CO_2 by 2100)."

The three UK researchers write of their modelbased results, "contrary to expectations, the combined impact of ocean surface temperature rise and acidification leads to little, if any, degradation in future habitat suitability across much of the Atlantic and areas currently considered 'marginal' for tropical corals, such as the eastern Equatorial Pacific." They note, "these results are consistent with fossil evidence of range expansions during past warm periods." Such findings, Couce *et al.* conclude, "present important implications for future coral reef management, as they suggest that more emphasis should be placed on conservation efforts on marginal reefs as they are not necessarily a 'lost cause'."

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6.5.2.1.3 Laboratory Studies

Several laboratory studies have focused on the combined impacts of rising temperatures and falling ocean pH levels on coral reefs.. The key findings, all of which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- The "enhanced kinetics of calcification owing to higher temperatures has the potential to counter the effects of ocean acidification."
- The conventional belief that calcification rates will be affected by lower ocean pH levels may be unfounded for temperate zone corals.
- The study of a Mediterranean zooxanthellate coral, *Cladocora caespitosa*, revealed "an increase in CO₂, alone or in combination with elevated

temperature, had no significant effect on photosynthesis, photosynthetic efficiency and calcification."

- Lower seawater pH due to atmospheric CO₂ enrichment and increased temperature (but short of reaching the bleaching level) "will both enhance active biotic calcification" of *Agaricia agaricites* corals.
- "The immediate effects of rising seawater temperature and ocean acidification may be tolerable for some species," possibly because the increased availability of $CO_{2(aq)}$ under ocean acidification conditions may enhance algal productivity, especially in *Symbiodinium* phylotypes with less efficient carbon-concentrating mechanisms that rely to a greater extent on the passive, diffusive uptake of $CO_{2(aq)}$ and its fertilization effect.

In a paper published in *Nature Climate Change*, McCulloch et al. (2012) describe how biogenic calcification occurs within an extracellular calcifying fluid located in the semi-isolated space between a coral's skeleton and its calicoblastic ectoderm, where during active calcification the pH of the calcifying fluid (pH_{cf}) is often increased relative to ambient seawater pH. At a typical seawater pH of ~8.1, for example, the pH of aragonitic corals shows a speciesdependent range of 8.4 to 8.7, representing a systematic increase in pH_{cf} relative to ambient sea water (ΔpH) of ~0.3–0.6 units. They report in situ measurements of pH within the calcifying medium of live coral polyps using microelectrodes (Al-Horani et al., 2003; Ries, 2011a) and pH-sensitive dyes (Venn et al., 2011) have registered enhanced pH_{cf} values between 0.6 and 1.2-and sometimes up to 2-pH units above seawater during the day, when both net production and calcification are highest.

Using a model of pH regulation combined with abiotic calcification, McCulloch *et al.* show "the enhanced kinetics of calcification owing to higher temperatures has the potential to counter the effects of ocean acidification," and "the extra energy required to up-regulate pH is minor, only <1% of that generated by photosynthesis," which highlights the importance of maintaining the zooxanthellae-coral symbiosis for sustaining calcification. They further note their model predicts "a ~15% increase in calcification rates from the Last Glacial Maximum to the late Holocene," an increase they describe as being "consistent with the expansion of tropical habitats that occurred during

this time despite P_{CO2} increasing."

Projecting into the future with their experimentally verified model, the four researchers assess the response of coral reefs "to both global warming, with mean tropical sea surface temperatures $\sim 2^{\circ}$ C higher, and with P_{CO2} increasing from presentday levels to \sim 1,000 ppm by the year 2100." For this scenario, they report their model predicts "either unchanged or only minimal effects on calcification rates." Thus, from a strictly chemical and kinetic perspective, their model indicates "ocean acidification combined with rising ocean temperatures should have only minimal effects on coral calcification," which they describe as "a direct outcome" of corals' ability to up-regulate pH at the site of calcification.

Rodolfo-Metalpa et al. (2010) collected three live colonies of the Mediterranean zooxanthellate coral Cladocora caespitosa in the Bay of Villefranche (Ligurian Sea, France) at about 25 meters depth in July 2006, plus three other colonies in February 2007. They divided the colonies into fragments and removed single polyps they attached to PVC plates and randomly assigned to aquariums continuously supplied with unfiltered seawater maintained at ambient or elevated water temperature (T or $T + 3^{\circ}C$) in equilibrium with air of ambient or elevated CO₂ concentration (400 or 700 ppm). They subjected the polyps 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."

They found "an increase in CO_2 , in the range predicted for 2100, does not reduce [the coral's] 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." They report a 3°C rise in temperature in winter resulted in a 72% increase in gross photosynthesis and a significant increase in daytime calcification rate.

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 Ries et al. (2009) have reported the calcification rate of the temperate coral Oculina arbuscula is also unaffected by an increase in atmospheric CO₂ concentration of up to 840 ppm, and a large decrease in calcification was found only at a CO₂ 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)." They note 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 CO₂ expected in 2100."

In a study designed to explore what controls calcification in corals, Sandeman (2012) suspendedby means of a torsion microbalance (as per Kesling and Crafts, 1962)-small pieces of coral he carefully removed from the edges of thin plates of Agaricia agaricites corals and lowered into gently stirred temperature-controlled seawater, after which he used the microbalance to measure coral net calcification rates over a range of seawater temperature and pH. He reported calcification rates of live A. agaricites coral increased by 15-17.7% per °C as seawater temperature rose from 27 to 29.5°C, and in his experiments in which the pH of the seawater was reduced from an average of 8.2 to 7.6, he observed calcification in living corals increased significantly. Similar experiments conducted with small portions of dead coral skeleton revealed "when the average pH was reduced from 8.2 to 7.5, calcification rate decreased." He determined the difference between calcification rates in going from seawater of pH 8.2 to seawater of pH 7.8 ranged from +30% for coral with no dead areas to -21.5% for coral with 30% dead exposed surface area.

The Trent University researcher from Peterborough, Ontario (Canada) says his findings suggest lower seawater pH due to atmospheric CO_2 enrichment and increased temperature (but short of reaching the bleaching level) "will both enhance active biotic calcification." He states the wide range of results between his and other scientists' studies of calcification rate and carbon dioxide "may be explainable in terms of the ratio of 'live' to 'dead' areas of coral," as is also suggested by the work of Rodolfo-Metalpa *et al.* (2011) and Ries (2011b), all of which leads him to conclude coral species that typically have smaller areas of exposed dead surface "may have a better chance of survival as pH levels drop."

Schoepf *et al.* (2013) note "since scleractinian corals are calcifying organisms that already live close

to their upper thermal tolerance limits, both ocean warming and acidification severely threaten their survival and role as reef ecosystem engineers." They observe "no studies to date have measured energy reserve pools (i.e., lipid, protein, and carbohydrate) together with calcification under ocean acidification conditions under different temperature scenarios." Schoepf et al. studied the single and interactive effects of pCO₂ (382, 607, and 741 ppm) and temperature (26.5 and 29.0°C) on coral calcification, energy reserves (i.e., lipid, protein, and carbohydrate), chlorophyll a, and endosymbiont concentrations in four species of Pacific coral having different growth morphologies (Acropora millepora, Pocillopora damicornis, Montipora monasteriata, and Turbinaria reniformis).

The 13 researchers found coral energy reserves were largely not metabolized "in order to sustain calcification under elevated pCO_2 and temperature," as "maintenance of energy reserves has been shown to be associated with higher resistance to coral bleaching and to promote recovery from bleaching (Rodrigues and Grottoli, 2007; Anthony et al., 2009)." They report lipid concentrations increased under lower ocean pH levels conditions in both A. millepora and P. damicornis and "were fully maintained in M. monasteriata and T. reniformis." Protein, carbohydrate, and tissue biomass also were "overall maintained under ocean acidification conditions in all species." Thus "only one of the four corals species studied [Acropora millepora] decreased calcification in response to average ocean acidification levels expected by the second half of this century (741 ppm), even when combined with elevated temperature (+2.5°C)."

Schoepf *et al.* conclude "some corals could be more resistant to combined ocean acidification and warming expected by the end of this century than previously thought," so "the immediate effects of rising seawater temperature and ocean acidification may be tolerable for some species," possibly because the increased availability of $CO_{2(aq)}$ under lower ocean pH levels conditions may enhance algal productivity, especially in *Symbiodinium* phylotypes with less efficient carbon-concentrating mechanisms that rely to a greater extent on the passive, diffusive uptake of $CO_{2(aq)}$ and its fertilization effect, citing Herfort *et al.* (2008) and Brading *et al.* (2011).

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6.5.2.1.4 Field Studies

Several field studies have focused on the combined effects of lower ocean pH levels and higher temperatures. The key findings of these studies are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Over the period 1937–1996, *Montastraea faveolata* colonies located in the upper Florida Keys maintained rates of extension and calcification in spite of the combination of local environmental and climatic changes.
- A nearly three-century-long history of coral calcification in the South China Sea reveals an 11% increase between 1716 and 2005.
- Between 1900 and 2010, increases in *Porites* coral calcification on reefs in the southeast Indian Ocean ranged from small, non-significant positive trends, to increases as high as 23% per decade. In these regions, "the rate of change in the thermal environment of coral reefs is currently the primary driver of change in coral calcification rates," and "the large-scale phenomenon of ocean acidification is not currently limiting calcification on coral reefs uniformly at a global scale."
- Flexibility in community composition observed along latitudinal environmental gradients across the Great Barrier Reef "indicates that climate change is likely to result in a re-assortment of coral reef taxa rather than wholesale loss of entire reef ecosystems."

According to Cantin *et al.* (2009), "zooxanthellae (symbiotic dinoflagellates of the genus *Symbiodinium*) are critical to the survival of reef-building corals, providing a major source of energy from photosynthesis for cell maintenance, growth and reproduction of their coral hosts," and these services include the energetically expensive process of calcification (Idso *et al.*, 2000). Cantin *et al.* studied the amount of photosynthetic "rent" paid by two clades of *Symbiodinium* (C1 and D) to their coral hosts (juvenile *Acropora millepora*) for the privilege of living within the latter's calcareous "houses." This was done by measuring the "financial transfer" to nine-month-old corals developed "from crosses involving the same parent corals." This "planned parenthood" minimized any host genetic differences that otherwise might have influenced the physiology of the host-symbiont "lease agreement."

They found "Symbiodinium C1 exhibited a 121% greater capacity for translocation of photosynthate to A. millepora juveniles along with 87% greater relative electron transport through photosystem II under identical environmental conditions." In addition, the five researchers note "A. tenuis and A. millepora juveniles in a previous study exhibited 2 to 3 times growth rates when associated faster with Symbiodinium C1 compared to those associated with Symbiodinium D (Little et al., 2004) at the same field site where juveniles were reared in the present study."

Cantin et al. conclude "the differences in carbonbased energy transfer between symbiont types may provide a competitive advantage to corals associating with Symbiodinium C1, particularly during their early life histories, when greater energy investment into rapid tissue and skeletal growth can prevent overgrowth of juveniles by competitors and mortality from grazers." They write, "as the community structure of coral reefs shift in response to global climate change and water quality impacts, opportunistic corals harboring symbionts that enable maximum rates of growth may similarly gain a competitive advantage." Consequently, in the economy of nature ample provision evidently has been made for corals to weather all sorts of environmental challenges that may come their way, including those IPCC contends will be driven by rising atmospheric CO₂ concentrations.

In studying coral calcification rates on Australia's Great Barrier Reef, De'ath *et al.* (2009) report there was a 14% drop in *Porites* calcification rate from 1990 to 2005 (although a graphical view of their data indicates the decline began around 1970) and this decline "is unprecedented in at least the past 400 years," which is indeed what their data show. Such statements, however, do not reveal the full story.

If, for example, their calcification history is followed 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 it is today and, therefore, was supposedly so much healthier for corals (according to the ocean "acidification" hypothesis)—it shows the coral calcification rate at that earlier time was approximately 21% lower than it was at its twentieth century peak.

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 increased by about 27% as the atmospheric CO_2 concentration and air temperature rose concurrently. After 1970, calcification rates declined, but by a much smaller 14%, even as air temperature and CO_2 concentrations continued to increase, further obscuring the issue. De'ath *et al.* note, "the causes for the [1990 to 2005] Great Barrier Reef-wide decline in coral calcification of massive *Porites* remain unknown."

Three years later, the work of another research team provided a possible answer. Uthicke et al. (2012) state, "tropical coral reefs are currently under threat by a variety of regional and global stressors," with examples of the former being "land runoff and overfishing (e.g., Pandolfi et al., 2003; Fabricius, 2005)," and examples of the latter "sea temperature increase and ocean acidification (Hoegh-Guldberg et al., 2007; Fabricius et al., 2011)." To determine which set of stressors is the most significant threat, Uthicke et al. analyzed sediment cores collected from inshore fringing coral reefs in the Whitsunday area of the Great Barrier Reef (GBR) of Australia. They collected these cores from three locations: inner nearshore reefs with low coral cover and high macroalgal abundance, intermediate reefs, and reefs at outer islands with low algal and high coral cover. They chose these three locations because inner near-shore reefs are typically the first to produce evidence of regional human impacts; reefs at outer islands are the last to experience the negative effects of human influence, as well as the most likely to exhibit evidence of global stressors; and intermediate reefs often show evidence of both.

The three researchers report benthic foraminiferal assemblages found in the cores of outer-island reefs unaffected by increased land runoff have been "naturally highly persistent over long (>2000 years) timescales." In both of the other zones, assemblages were also persistent, but only until 150 years ago, and assemblages less than 55 years old from inner near-shore and intermediate reefs were significantly different from older assemblages.

Uthicke *et al.* conclude they found support for the likelihood "increased land runoff since the start of land clearing and agriculture in the catchment of the Whitsunday Region of the GBR has left a signature in the foraminiferal assemblages of inner and intermediate areas of the study area," when previously the assemblages of these areas had been "persistent for at least several thousand years." In addition, and based on the fact "no changes were observed on outer reefs located away from land runoff," they propose "changes observed on inner and intermediate reefs were mainly driven by enhanced agricultural runoff after European settlement." And finally, they affirm

"the hypothesis that global forcing, such as sea temperature increase or ocean acidification, altered the foraminiferal community found little support."

Browne (2012) writes "local stressors erode reef resilience, and therefore increase their vulnerability to global stressors that include ocean warming, [which is] predicted to increase the severity and intensity of coral bleaching events (Hoegh-Guldberg, 1999). ocean acidification, [which is] predicted to reduce calcification rates and reef growth (Kleypas et al., 1999), and increased storm and cyclone activity, [which is] predicted to reduce coral framework complexity and stability (Puotinen, 2004)." In a study designed to assess the overall impact of these several reef stressors, Browne describes how "coral growth rates (linear extension, density, calcification rates) of three fast-growing corals (Acropora, Montipora, Turbinaria) were studied in situ on Middle Reef, an inshore reef located on the central Great Barrier Reef (GBR)," in order to "assess the influence of changing environmental conditions on coral condition and reef growth."

Browne found "despite local anthropogenic pressures and global climate change, Middle Reef has a robust and resilient coral community," and "Acropora linear extension rates were comparable with rates observed at similar depths and sea surface temperatures on mid to offshore reefs on the GBR, and in the Caribbean." In addition, "Montipora and Turbinaria are abundant on inshore turbid reefs due to their adaptive capacities and are therefore an important source of carbonate for reef growth and development." Browne writes, "Montipora linear extension was greater than current estimates available, and Turbinaria, although characterized by slow linear extension, had a dense skeleton and hence may be more resilient to physical damage as ocean pH falls." Although both species "may be more susceptible during the warmer months due to multiple stressors, they were able to rapidly recover during the cooler months," Browne writes. "In summary," Browne concludes, "corals on Middle Reef are robust and resilient to their marginal environmental conditions."

Helmle *et al.* (2011) collected coral cores in May 1997 and June 1998 from seven *Montastraea faveolata* colonies located in the upper Florida Keys (USA), where they "were drilled at the location of maximum vertical growth of the colony." The scientists constructed chronologies from the annual density bands found in the cores and determined all of them had a 60-year common period from 1937 to 1996. For these cores the scientists obtained and analyzed annual extension, density, and calcification rates, to see how they varied over this period of intensifying warming and acidification of the global ocean.

The five U.S. scientists report their data show "no evidence of significant age effects" over the 1937-1996 period for extension, density, or calcification. Helmle *et al.* say their findings demonstrate "the measured corals have historically been able to maintain rates of extension and calcification over the 60-year period from 1937 to 1996 under the combination of local environmental and climatic changes." They also note calcification rates were positively related to sea surface temperature, "similar to results for Porites corals from Tahiti (Bessat and Buigues, 2001) and the Great Barrier Reef (Lough and Barnes, 1997)," but they say the Florida results explained only about 7% of the annual calcification variability as opposed to $\sim 30\%$ at the Pacific locations.

As for why the Florida Keys corals have fared so well, Helmle *et al.* suggest the answer could be "massive reef-building corals are not as susceptible to declines in Ω_{arag} [aragonite saturation state] as demonstrated by laboratory experiments; local processes, such as high seasonal variation in Ω_{arag} in the Florida Keys, may be temporarily enabling these corals to maintain their historical rates of calcification; the role of Ω_{arag} in controlling calcification is masked amidst considerable natural inter-annual variability; or the actual *in situ* reef-site carbonate chemistry is decoupled from the oceanic values, which could occur as a result of shifts in benthic community metabolism, mineral buffering and/or coastal biogeochemical processes."

Shi *et al.* (2012) state "rising atmospheric CO_2 and global warming are regarded as fatal threats to coral reefs," noting "IPCC has reported that by the end of this century, coral reefs will be the first ecological system that will become extinct," citing Wilkinson (2004). They write, "others contend that rising seawater temperature is conducive to enhanced coral calcification, and increased calcification will be higher than the decline caused by rising CO_2 ," so "coral calcification will increase by about 35% beyond pre-industrial levels by 2100, and no extinction of coral reefs will occur in the future," citing McNeil *et al.* (2004).

In late May of 2004 and 2007 Shi *et al.* extracted core samples of coral skeletons from several massive live and dead *Porites lutea* colonies comprising part of the Meiji Reef in the southern South China Sea, after which they analyzed their skeletal calcification

rates by means of X-ray photography, which enabled them to construct a nearly three-century-long history of coral calcification rate for the period 1716–2005. The results of the six scientists' efforts are depicted in Figure 6.5.2.1.3.1.

As best as can be determined from the Chinese scientists' graph, over the period of time depicted when IPCC claims the world warmed at a rate unprecedented over the past millennium or two, and when the atmosphere's CO_2 concentration rose to values not seen for millions of years—the two "fatal threats to coral reefs," even acting together, did not prevent coral calcification rates on Meiji Reef from rising by about 11% over the past three centuries.



Figure 6.5.2.1.3.1. The long-term history of coral calcification rate on Meiji Reef. Adapted from Shi *et al.* (2012).

Cooper *et al.* (2012) studied coral reefs spanning an 11° latitudinal range in the southeast Indian Ocean, collecting 27 long cores from massive *Porites* coral colonies at six locations covering a north-south distance of about 1,000 km off the coast of Western Australia. From these cores they developed 1900– 2010 histories of "annual extension (linear distance between adjacent density minima, cm/year), skeletal density (g/cm³), and calcification rate (the product of skeletal density and annual extension, g/cm²/year)," based on gamma densitometry data.

Cooper *et al.* report calcification rates at the Houtman Abrolhos Islands, where a relatively large sea surface temperature (SST) increase had occurred (0.10° C/decade), rose by 23.5%, and at Coral Bay and Tantabiddi, SST increases of 0.8 and 0.6°C/decade were associated with 8.7 and 4.9% increases in decadal calcification rates, respectively. They found smaller and non-significant positive trends in

calcification rates at Clerke and Imperieuse Reefs, where the increase in SST was only 0.2°C/decade.

The three Australian researchers say their latter non-significant findings are consistent with those of Helmle et al. (2011), who they say "found a similar non-correlation for the massive coral Montastraea faveolata in the Florida Keys between 1937 and 1996, when there was no significant SST warming." Regarding the large increases in calcification rates they documented at the rapidly warming Houtman Abrolhos Islands, they write, "Lough and Barnes (2000) documented a similar positive correlation, suggesting that calcification rates may, at least initially, increase with global warming." They conclude "the rate of change in the thermal environment of coral reefs is currently the primary driver of change in coral calcification rates," driving them ever-higher as temperatures continue to rise, and "the large-scale phenomenon of ocean acidification is not currently limiting calcification on coral reefs uniformly at a global scale."

Hughes *et al.* (2012) note, "contemporary research on how climate change affects coral reefs has matured beyond the simplistic 'canary in the coal mine' concept to a more nuanced recognition that climate-related pressures such as bleaching (due to the loss of symbiotic zooxanthellae) and ocean acidification do not affect all species equally." And "in this context," they note, "a critical issue for the future status of reefs will be their ability to maintain functional capacity in the face of the changes in species composition that are already underway due to multiple anthropogenic impacts."

Hughes et al. applied a "rigorous quantitative approach to examine large-scale spatial variation in the species composition and abundance of corals on mid-shelf reefs along the length of Australia's Great Barrier Reef, a biogeographic region where species richness is high and relatively homogeneous." They used "a hierarchical, nested sampling design to quantify scale-dependent patterns of coral abundances [for] five regions of the Great Barrier Reef [they] sampled from north to south, each 250-500 km apart." They thus identified and measured a total of 35,428 coral colonies on 33 reefs, categorizing each colony they encountered (including the majority of species that are too rare to analyze individually) into "ecologically relevant groups depending on their physiology, morphology and life history."

The seven scientists report the diverse pool of species they examined along the latitudinal gradient of the Great Barrier Reef "can assemble in markedly different configurations across a wide range of contemporary environments." Regarding temperature, for example, they indicate "the geographic ranges of 93% of the 416 coral species found on the Great Barrier Reef extend northwards toward the equator (e.g., to Papua New Guinea, the Solomon Islands, and/or the Indonesian archipelago)," whereas "46% are also found in colder conditions further to the south." As for lower ocean pH levels, they write, "globally, ocean surface pH has decreased by 0.1 unit since 1750 due to the uptake of atmospheric CO_2 , with a smaller 0.06 decline recorded for the tropics," citing Kleypas et al. (2006). In contrast, they report contemporary variation in pH among various reef habitats on the Great Barrier Reef, as well as differences among short-term replicate measurements, span a range of 0.39 unit, from 8.37 to 7.98, citing Gagliano et al. (2010). And they note this short-term and habitat-scale variability literally swamps that of latitudinal trends.

Hughes *et al.* say their real-world observations "all point to a surprisingly resilient response by some elements of coral assemblages to spatial and temporal shifts in climatic conditions." They conclude, "the flexibility in community composition that we document along latitudinal environmental gradients indicates that climate change is likely to result in a reassortment of coral reef taxa rather than wholesale loss of entire reef ecosystems." This clearly deflates the catastrophic prognostications put forth by IPCC with regard to the future of the planet's corals.

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6.5.2.2 Echinoderms

This section examines what scientists have learned from studies focusing on the impacts of higher temperatures and lower seawater pH levels on echinoderms. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

• The relative growth of juvenile sea stars increased linearly with temperature from 5°C to 21°C, while also responding positively to atmospheric CO₂ enrichment.

- Serpent starfish were able to successfully cope with the physiological changes brought about by a modest temperature increase and/or pH decline.
- The intertidal seastar *Parvulastra exigua* was shown to be resilient to elevated temperature and reduced pH, and "may possess scope for adaptation (evolutionary change) and/or acclimation via phenotypic plasticity" to withstand future changes in temperature and pH.
- The negative effects of a 0.35 to 0.55 CO₂-induced decline in seawater pH on the growth and calcification of the sea urchin *Tripneustes gratilla* can be largely overcome by an accompanying 3°C increase in water temperature.
- No significant effect of ocean warming and lower seawater pH levels on the percentage of egg fertilization in four intertidal and shallow subtidal echinoids was found, possibly reflecting adaptation to the large temperature and pH fluctuations that characterize their shallow water coastal habitats.
- In a combined pH decline/temperature increase study on the sea urchin *Psammechinus miliaris*, it was determined "current ocean pH levels are suboptimal for *P. miliaris* sperm-swimming speed and that reproductive success for certain marine species may benefit from a reduced pH ocean."
- Fertilization and embryonic development of the ecologically important sea urchin *Sterechinus neumayeri* to the blastula stage was "robust to levels of temperature and pH change predicted over coming decades."
- The ecologically important sea urchin *Centrostephanus rodgersii* displays a genetic variation in tolerance affirming its ability to successfully adapt to ocean warming and falling ocean pH levels..

Gooding *et al.* (2009) measured growth and feeding rates of juvenile sea stars (*Pisaster ochraceus*) maintained in 246-liter aquaria filled with recirculating natural seawater maintained at temperatures ranging from 5 to 21°C and constantly bubbled with ambient air of 380 ppm CO₂ or CO₂-enriched air of 780 ppm CO₂. They found "the relative growth (change in wet mass/initial wet mass) of juvenile *P. ochraceus* increased linearly with temperature from 5°C to 21°C," and it also responded positively to atmospheric CO₂ enrichment. The authors state "relative to control treatments, high CO₂ alone increased relative growth by ~67% over 10 weeks, while a 3°C increase in temperature alone increased relative growth by 110%." They also state increased CO₂ "had a positive but non-significant effect on sea star feeding rates, suggesting CO₂ may be acting directly at the physiological level to increase growth rates." Their data show the percentage of calcified mass in the sea stars dropped from approximately 12% to 11% in response to atmospheric CO₂ enrichment at 12°C, but it did not decline further in response to a subsequent 3°C warming at either ambient or elevated CO2. The three Canadian researchers say their findings demonstrate "increased CO₂ will not have direct negative effects on all marine invertebrates, suggesting that predictions of biotic responses to climate should consider how different types of organisms will respond to changing climatic variables." They state, "responses to anthropogenic climate change, including ocean acidification, will not always be negative."

Wood *et al.* (2010) studied the serpent starfish (*Ophiura ophiura*), collecting 96 individuals with a disc diameter between 10 and 15 mm from Cawsand Bay, Plymouth Sound ($50^{\circ}09.77^{\circ}$ N, $4^{\circ}11.50^{\circ}$ W). They exposed the brittlestars to three pH treatments (pH of 8.0, 7.7, or 7.3) and two temperature treatments (10.5° C or 15° C) for 40 days. They measured metabolism, calcification, mortality, motility, arm structure, and arm regeneration; the latter parameter was studied by removing either 10, 20, 30, or 40 mm of arm length on one of the animals' arms.

The researchers found survival was "100% at both temperatures and across all pH treatments"; metabolic rate increased as pH decreased in the low temperature treatment, but there was no significant difference across the different pH treatments in the high temperature regime; muscle appearance and density did not change over either the temperature or pH treatment ranges in established or regenerated arms; and a faster response time in movement (motility) was observed at low temperature and low pH. They also found brittlestars across "all treatments had the same net calcification throughout the experiment"; arm regeneration rate within the low temperature treatment was "unaffected by the length of arm lost and the rate was similar between all pH treatments"; and arm regeneration rate was significantly faster at higher temperatures than lower temperatures. Taken as a whole, the findings indicate the serpent starfish should be able to cope

successfully with the physiological changes brought about by any modest temperature increase and/or pH decline likely to occur in the future.

McElroy et al. (2012) measured the metabolic rates of adult specimens of the intertidal seastar Parvulastra exigua collected from Little Bay, Sydney (Australia) at conditions characteristic of high tide (ca. 18°C and pH 8.2), as well as at 3 and 6°C warmer conditions and at additional pH values of 7.8 and 7.6 "in all combinations." The measurements revealed "the metabolic response of P. exigua to increased temperature ($+3^{\circ}C$ and $+6^{\circ}C$) at control pH [8.2] indicates that this species is resilient to periods of warming as probably often currently experienced by this species in the field." They also report they "did not observe a negative effect of acidification on rate of oxygen consumption at control temperature, a combination of stressors that this species currently experiences at night time low tide."

Although the metabolic response of *P. exigua* is resilient to current levels of extreme temperature and pH stress—which are equivalent to mean conditions predicted for the end of the twenty-first century-it is possible the extreme seawater temperatures and pH levels at that future time (if IPCC predictions prove true) will be greater than the extreme levels of today, which could prove to be a real challenge for the seastars. McElroy et al. point out, in the concluding paragraph of their report, "species such as P. exigua with a broad distribution from warm to cold temperate latitudes may possess scope for adaptation (evolutionary change) and/or acclimation via phenotypic plasticity (Visser, 2008), as suggested for sympatric echinoid and ophiuroid species (Byrne et al., 2011; Christensen et al., 2011)."

Brennand *et al.* (2010) reared embryos of the sea urchin *Tripneustes gratilla* in flow-through chambers filled with filtered seawater maintained at all combinations of three temperatures (24, 27, and 30°C) and three 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, they assessed the growth and development of the larvae.

Brennand *et al.* found "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 CO₂," 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, "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 projected maximum decline in seawater pH is somewhere in the range of 0.1 to 0.18 in the vicinity of AD 2100, there is 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 well suited for production by aquaculture (Lawrence and Agatsuma, 2007; Juinio-Menez *et al.*, 1998; Dworjanyn *et al.* 2007).

Byrne *et al.* (2009) investigated the effects of lower ocean pH levels (pH values of 8.2-7.6, corresponding to atmospheric CO₂ concentrations of 230–690 ppm) and seawater temperature (20–26°C, where 20°C represents the recent thermal history of indigenous adults) on the fertilization of sea urchin (*Heliocidaris erythrogramma*) eggs and their subsequent development in what they call "the eastern Australia climate change hot spot," located near Sydney.

According to the authors, over the ranges of seawater pH and temperature they studied, there was "no effect of pH" and "no interaction between temperature and pH" on sea urchin egg fertilization. Seawater pH also had no effect on the longer-term development of fertilized sea urchin eggs; but the six scientists say warming led to "developmental failure at the upper warming (+4 to +6°C) level, regardless of pH." Even here, however, they appear quite hopeful, stating "it is not known whether gametes from H. erythrogramma adults acclimated to 24°C would have successful development in a +4°C treatment." noting their study "highlights the potentiality that adaptive phenotypic plasticity may help buffer the negative effects of warming, as suggested for corals." They write, "single stressor studies of thermotolerance in a diverse suite of tropical and temperate sea urchins show that fertilization and early development are robust to temperature well above ambient and the increases expected from climate change," citing Farmanfarmaian and Giese (1963), Chen and Chen (1992), and Roller and Stickle (1993).

Byrne *et al.* (2010a) examined the interactive effects of near-future (ca. AD 2070–2100) ocean warming (temperature increases of 2–6°C) and lower ocean pH levels (pH reductions of 0.2–0.6) on fer-tilization in four intertidal and shallow subtidal

echinoids (*Heliocidaris erythrogramma, Heliocidaris Tuberculata, Tripneustes gratilla, Centrostephanus rodgersii*), an asteroid (*Patiriella regularis*), and an abalone (*Haliotis coccoradiata*), working with batches of eggs they collected from multiple females fertilized by sperm obtained from multiple males, all of which species were maintained in all combinations of three temperature and three pH treatments.

The eight researchers found "no significant effect of warming and acidification on the percentage of fertilization." Byrne *et al.* say their results indicate "fertilization in these species is robust to temperature and pH/PCO₂ fluctuation," and their findings "may reflect adaptation to the marked fluctuation in temperature and pH that characterizes their shallow water coastal habitats."

Byrne et al. (2010b) investigated the effects of projected near-future oceanic warming and acidification of the sea urchin *Heliocidaris erythrogramma* for conditions 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. Byrne et al. conducted multifactorial 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). They found "across all treatments there was a highly significant effect of sperm density, but no significant effect of temperature or interaction between factors." 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." They write, "a number of ecotoxicology and climate change studies, where pH was manipulated with CO₂ 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 CO₂)," citing Bay et al. (1993), Carr et al. (2006), and Kurihara and Shirayama (2004). Because neither seawater warming nor seawater acidification (caused by contact with CO₂-enriched air) had either a positive or a negative effect on sea urchin fertilization, the five scientists conclude "sea urchin fertilization is robust to climate change stressors."

According to Caldwell *et al.* (2011), "the reproductive processes and early life-stages of both calcifying and non-calcifying animals are believed to be particularly vulnerable to a reduced pH environment," but "there is as yet no clear and reliable predictor for the impacts of ocean acidification on marine animal reproduction." Caldwell *et al.* "investigated the combined effect of

pH (8.06-7.67) and temperature (14-20°C) on percent sperm motility and swimming speed in the sea urchin Psammechinus miliaris using computer assisted sperm analysis (CASA)," working with specimens they collected from the Isle of Cumbrae (Scotland). "Surprisingly," the six scientists write, "sperm swimming performance benefited greatly from a reduced pH environment," as "both percent motility and swimming speeds were significantly enhanced at pHs below current levels." In light of the additional fact that sperm-activating peptides-which are believed to have evolved some 70 million years ago during a period of high atmospheric CO_2 concentration-are fully functional from pH 6.6 to 8.0 (Hirohashi and Vacquier, 2002), they state "the combined data on motility, swimming speed and SAP function at reduced pH indicates that sperm are sufficiently robust to allow functionality at pHs that would have been experienced in the paleo-ocean (ca pH 7.4-7.6) and which are within projections for near-future climate change scenarios." The UK researchers conclude "current ocean pH levels are suboptimal for P. miliaris sperm-swimming speed and ... reproductive success for certain marine species may benefit from a reduced pH ocean."

Ericson *et al.* (2012) "examined the interactive effects of warming and acidification on fertilization and embryonic development of the ecologically important sea urchin *Sterechinus neumayeri* reared from fertilization in elevated temperature (+1.5°C and 3°C) and decreased pH (-0.3 and -0.5 pH units)." They found "fertilization using gametes from multiple males and females, to represent populations of spawners, was resilient to acidification at ambient temperature (0°C)," and development to the blastula stage was "robust to levels of temperature and pH change predicted over coming decades." The sea urchins the seven scientists studied thus appear wellequipped to deal with IPCC-predicted near-future increases in seawater temperature and acidification.

Ho *et al.* (2013) report, "the impact of increased temperature (2–4°C above ambient) and decreased pH (0.2–0.4 pH units below ambient) on fertilization in the Antarctic echinoid *Sterechinus neumayeri* across a range of sperm concentrations was investigated in cross-factorial experiments," where "gametes from multiple males and females in replicate experiments were used to reflect the multiple spawner scenario in nature." They examined this species because "polar marine organisms are among the most stenothermal in the world due to the stability of their environment over evolutionary time (Clarke, 1983)," which suggests they may be "sensitive to the slightest of

environmental perturbations, particularly [in] early life history stages (Barnes and Peck, 2008)."

The five researchers' work confirmed "the importance of considering both ocean warming and acidification," and they note "decreased pH did not affect fertilization." Warming, however, "enhanced fertilization ... likely through stimulation of sperm motility and reduced water viscosity." In the concluding sentence of their paper's abstract, Ho *et al.* state their results indicate "fertilization in *S. neumayeri*, even at low sperm levels potentially found in nature, is resilient to near-future ocean warming and acidification."

Foo *et al.* (2012) write, "selection by stressful conditions will only result in adaptation if [1] variation in stress tolerance exists within a population, if [2] tolerance of stressors is heritable, and if [3] changes in tolerance traits are not constrained by negative genetic correlations with other fitness traits," citing references both old and recent: Darwin (1859) and Blows and Hoffmann (2005).

Foo et al. "quantified genetic variation in tolerance of early development of the ecologically important sea urchin Centrostephanus rodgersii to near-future (2100) ocean conditions projected for the southeast Australian global change hot spot," in which "multiple dam-sire crosses were used to quantify the interactive effects of warming $(+2-4^{\circ}C)$ and acidification (-0.3-0.5 pH units) across twentyseven family lines" of the species. The four Australian researchers report, "significant genotype by environment interactions for both stressors [warming and acidification] at gastrulation indicated the presence of heritable variation in thermal tolerance and the ability of embryos to respond to changing environments." They say "positive genetic correlations for gastrulation indicated that genotypes that did well at lower pH also did well in higher temperatures." Thus, Foo et al. conclude "the presence of tolerant genotypes, and the lack of a trade-off between tolerance to pH and tolerance to warming contribute to the potential of C. rodgersii to adapt to concurrent ocean warming and acidification, adding to the resilience of this ecologically important species in a changing ocean."

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6.5.2.3 Other Marine Species

This section examines what scientists have learned in studies , focusing on the impacts of changing seawater temperature and pH levels on marine species not discussed in prior sections. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- A high tolerance to pH decline and rising temperature was observed during the larval growth stage of the Portuguese oyster.
- The often complex and severe spatial and temporal variability of environmental conditions in coastal ecosystems suggests organisms living there are preconditioned to be tolerant of lower ocean pH levels and warming.
- There is no evidence that predator-prey interactions among green crabs and periwinkles will change in the future under lower ocean pH levels and warming.
- Analyses of tube mineralogy, ultrastructure, and mechanical properties of the serpulid tubeworm *Hydroides elegans* reveal "predicted coastal warming may not hinder *H. elegans* ability to build normal tubes even in the face of projected near-future decreases in pH or salinity."
- Norway lobster (*Nephrops norvegicus*) "would benefit from global warming and be able to

withstand the predicted decrease in ocean pH in the next century during their earliest life stages."

- Baltic cod (*Gadus morhua*), which live in sea waters naturally high in pCO₂ "may be adapted to conditions predicted in ocean acidification scenarios for centuries to come," as "no effect on hatching, survival, development, and otolith size was found at any stage in the development of Baltic cod" under projected future ocean pH levels and temperature scenarios.
- Polyps of the moon jellyfish have been shown to be tolerant of low pH and warmer temperatures, surviving and reproducing asexually. Yet analyses of "all available long-term datasets on changes in jellyfish abundance across multiple coastal stations" reveal there is no compelling evidence to support the view that the global abundance of jellyfish is increasing as a result of lower ocean pH levels and warming.
- Lower ocean pH levels and temperature increases were found to negatively impact the growth and survival of juvenile anemone fish. The negative effects were absent or reversed when the parents of the juveniles also experienced lower ocean pH levels and warming, revealing "conditions experienced by adults can have significant carryover effects on the performance of their offspring ... leading to improved capacity to cope with environmental stress."
- In a study of copepods, "higher production temperature induced a positive maternal effect resulting in faster hatching and indicating that the mothers can invest more in their eggs, and therefore produce better quality eggs."

Thiyagarajan and Ko (2012) conducted a number of laboratory studies designed to see how the larval growth stage of the Portuguese oyster responds to various "climate change stressors," investigating the effects of low pH (7.9, 7.6, 7.4) at ambient salinity (34 ppt) and low salinity (27 ppt), while "the combined effect of pH (8.1, 7.6), salinity (24 and 34 ppt) and temperature (24°C and 30°C) was examined using factorial experimental design." The two researchers write, "surprisingly, the early growth phase from hatching to 5-day-old veliger stage showed high tolerance to pH 7.9 and pH 7.6 at both 34 ppt and 27 ppt," and "larval shell area was significantly smaller at pH 7.4 only in low-salinity."

In the three-factor experiment (see Figure 6.5.2.3.1), they observed "shell area was affected by salinity and the interaction between salinity and temperature but not by other combinations." They also discovered "larvae produced the largest shell at the elevated temperature in low-salinity, regardless of pH."



Figure 6.5.2.3.1. Mean shell area of the Portuguese oyster larvae exposed to a low-pH or elevated carbon dioxide treatment for five days at two levels of salinity (ambient and low-salinity) and temperature (ambient and elevated). Each bar represents the mean \pm S.D. of four replicate cultures. Adapted from Thiyagarajan and Ko (2012).

Thiyagarajan and Ko conclude "the growth of the Portuguese oyster larvae appears to be robust to nearfuture pH level (>7.6) when combined with projected elevated temperature and low-salinity in the coastal aquaculture zones of [the] South China Sea."

Pansch *et al.* (2012) note to date "most studies have focused on ocean acidification (OA) effects in fully marine environments, while little attention has been devoted to more variable coastal ecosystems, such as the Western Baltic Sea." Since "natural spatial and temporal variability of environmental conditions such as salinity, temperature or CO_2 impose more complex stresses upon organisms inhabiting these habitats, species [living there] can be expected to be more tolerant to OA (or warming) than fully marine taxa."

Pansch *et al.* acquired data on the variability of temperature and pH within the inner Kiel Fjord of Schleswig-Holstein, Germany, and on "the responses of the barnacle *Amphibalanus improvisus* from this habitat to simulated warming and OA during its early development." They exposed *A. improvisus* nauplii

(the first larval stage of many crustaceans) and cyprids (the second larval stage of barnacles) to different temperatures (12, 20, and 27° C) and CO₂ (nominally 400, 1,250, and 3,250 ppm) treatments for eight and four weeks, respectively," while "survival, larval duration and settlement success were monitored."

The four researchers found a prolongation of the nauplius phase, which they acknowledge could "lead to a mismatch of the larvae with their phytoplankton prey." However, they note the predicted increase in seawater temperature would likely "accelerate nauplii development and, thus, may buffer OA effects." Such results, they write, have been observed "in sea urchin larvae and oysters, where higher temperatures mitigated negative effects of OA," citing Brennand *et al.* (2010) and Waldbusser *et al.* (2011). In their own study, however, they found just the opposite, saying "warming negatively impacted cyprid survival" but "OA counteracted these negative effects."

"It should also be stressed," they continue, "that only the most severe OA level applied herein (3,250 ppm CO₂) had occasional effects, whereas the OA conditions as predicted by the end of this century $(1,250 \text{ ppm CO}_2)$ in most cases did not affect A. improvisus larvae." In addition, and "interestingly," they report, "the major release of larvae and thus, development, settlement and first intense calcification in A. improvisus occurs during early summer when pH is lowest." They add, "A. improvisus is also found in stands of the brown macroalga Fucus spp. where 2,500 ppm CO_2 (pH 7.4) can be measured," and they note "another barnacle species, Chthamalus stellatus, was shown to survive and grow at extremely low mean pH of 6.6 in the vicinity of volcanic CO₂ vents in Ischia, Italy (Hall-Spencer et al., 2008)."

Pansch *et al.* write, "given their present wide tolerance and the possibility to adapt to shifting environmental conditions over many generations, barnacles (*A. improvisus*) from the Western Baltic Sea might be able to overcome OA as predicted by the end of this century." And, "supporting this," they note Parker *et al.* (2011) have shown "selectively bred lines of the estuarine oyster *Saccostrea glomerata* to be more resilient to OA than wild populations."

Pansch *et al.* (2013) again collected juvenile barnacles (*Amphibalanus improvisus*) from Kiel Fjord in the western Baltic Sea and distributed them to different temperature and pH treatment combinations in a laboratory setting: seawater of two temperatures (20 and 24°C) and three pH levels (mean pCO_2 values of 700, 1,000, and 2,140 µatm). They fed the barnacles a mix of two marine diatoms every other day until day 24, after which they added specified amounts of brine shrimp until the end of the experiment, on day 62. The four German scientists observed "reduced growth rates as well as weakening of barnacle shells only under very high pCO₂ (>1930 µatm)." They state "even under these highly acidified conditions, and corroborating other recent investigations on barnacles (e.g., McDonald et al., 2009; Findlay et al., 2010a,b), these impacts were subtle and sub-lethal." And "furthermore," they write, "ocean warming as expected to occur in the future (IPCC, 2007) has the potential to mitigate the negative effects of ocean acidification (Brennand et al., 2010; Waldbusser, 2011; present study)." The findings of Pansch et al., as well as those of the other researchers they cite, indicate juvenile barnacles of the species they studied are already equipped to meet the challenges of a significantly warmed and acidified ocean should such challenges occur.

Landes and Zimmer (2012) state, "both ocean warming and acidification have been demonstrated to affect the growth, performance and reproductive success of calcifying invertebrates." However, they write, "relatively little is known regarding how such environmental change may affect interspecific interactions." They separately treated green crabs (Carcinus maenas, the predators) and periwinkles (Littorina littorea, their prey) under conditions that mimicked either ambient conditions (control) or warming and acidification (both separately and in combination), for five months, after which they assessed the predators, their prey, and the predatorprey interaction for CO₂- and warming-induced changes in response to the environmental perturbations imposed on them.

They found "acidification negatively affected the closer-muscle length of the crusher chela and correspondingly the claw-strength increment in *C. maenas*," and "the effects of warming and/or acidification on *L. littorea* were less consistent but indicated weaker shells in response to acidification." As might have been expected on the basis of these individual species responses to lower ocean pH levels and warming (weaker claw strength in the predator, but weaker shells in the prey), Landes and Zimmer say "on the community level," they "found no evidence that predator-prey interactions will change in the future."

Chan *et al.* (2013) write, "the majority of marine benthic invertebrates protect themselves from predators by producing calcareous tubes or shells that have remarkable mechanical strength," but "an elevation of CO_2 or a decrease in pH in the environment can reduce intracellular pH at the site of calcification and thus interfere with the animal's ability to accrete CaCO₃," which "may result in the animal producing severely damaged and mechanically weak tubes." They investigated how the interaction of environmental drivers affects the production of calcareous tubes by the serpulid tubeworm, *Hydroides elegans*, in a factorial manipulative experiment in which they analyzed the effects of pH (8.1 and 7.8), salinity (34 and 27%), and temperature (23 and 29°C) on the biomineral composition, ultrastructure, and mechanical properties of the tubeworm's tubes.

The five researchers report, "at an elevated temperature of 29°C, the tube calcite/aragonite ratio and Mg/Ca ratio were both increased, the Sr/Ca ratio was decreased, and the amorphous CaCO₃ content was reduced." And "notably," they emphasize, at elevated temperature with decreased pH and reduced salinity, "the constructed tubes had a more compact ultrastructure with enhanced hardness and elasticity compared to decreased pH at ambient temperature." Chan *et al.* conclude their "results from the analyses of tube mineralogy, ultrastructure and mechanical properties showed that predicted coastal warming may not hinder *H. elegans* ability to build normal tubes even in the face of projected near-future decreases in pH or salinity."

The Norway lobster (Nephrops norvegicus) is a decapod crustacean found on the continental shelf and slope throughout the northeastern Atlantic Ocean and the Mediterranean Sea. Styf et al. (2013) exposed berried Norway lobsters (females carrying fertilized eggs on the undersides of their abdomens) to four months of "the combination of six ecologically relevant temperatures (5-18°C) and reduced pH (by 0.4 units)," studying embryonic development of the species "by quantifying proxies for development rate and fitness including: % volk consumption, mean heart rate, rate of oxygen consumption, and oxidative stress." The three Swedish scientists report "the rate of volk consumption per day, as a measure of embryonic development rate, significantly increased with temperature," and lower pH "had no effect on development rate." They also found "pH had no effect on heart rate" and "there was no interaction between pH and temperature." Further, "there was no significant effect of temperature on oxidative stress when analyzed independent of embryonic age," but "there was a significantly higher level of oxidative stress in the control embryos compared with the embryos developed in low pH." They "observed no mortality nor abnormalities."

The three researchers conclude "this species

would benefit from global warming and be able to withstand the predicted decrease in ocean pH in the next century during their earliest life stages," a significant expression of optimism regarding a species considered the most important crustacean in all Europe (Nofima, 2012).

Winans and Purcell (2010) tested the ability of jellvfish to respond to changes in water temperature and pH during the 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 comprised of 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 researchers found "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," 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 write, "statolith size was significantly smaller in ephyrae released from polyps reared at low pH."

Winans and Purcell conclude "A. labiata polyps are quite tolerant of low pH, surviving and reproducing asexually even at the lowest tested pH." Nevertheless, the authors note "the effects of small statoliths on ephyra fitness are unknown," which means the phenomenon could bode poorly for jellyfish. Winans and Purcell acknowledge many organisms "may be able to acclimate or adapt to slowly changing pH conditions." They report 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," and "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."

That the findings of Winans and Purcell should not be considered as evidence of future jellyfish blooms is made clear by the study of Condon *et al.* (2013), who note there is "concern about the deterioration of the world's oceans," and that one line of evidence for this concern is "an increasing incidence of jellyfish blooms." They say this "perception," as they describe it, is "largely based on reports of increases in a few disparate regions (Condon *et al.*, 2012)" and on "an analysis of media reports and perceptions of scientific experts and fishers (Brotz et al., 2012)."

Condon *et al.* set out to analyze "all available long-term datasets on changes in jellyfish abundance across multiple coastal stations, using linear and logistic mixed models and effect-size analysis," in order "to test the null hypothesis that jellyfish population sizes and the occurrence of blooms have not significantly increased in the world's oceans."

The 22 researchers, from Argentina, Australia, Canada, Japan, Norway, Peru, Slovenia, Spain, the United Kingdom, and the United States, found "no robust evidence for a global increase in jellyfish." Although they acknowledge "there has been a small linear increase in jellyfish since the 1970s," they say "this trend was unsubstantiated by effect-size analysis that showed no difference in the proportion of increasing vs. decreasing jellyfish populations over all time periods examined." Instead, they report, "the strongest non-random trend indicated jellyfish populations undergo larger, worldwide oscillations with an approximate 20-year periodicity, including a rising phase during the 1990s that contributed to the perception of a global increase in jellyfish abundance." They conclude their research points normal "recurrent phases of rise and fall in jellyfish populations that society should be prepared to face."

Miller *et al.* (2012) note "a major limitation to predicting the effects of increasing [atmospheric] CO_2 concentrations on marine species and ecosystems is the lack of information on acclimation or adaptation to increased CO_2 over timescales relevant to climate change predictions," and "there is increasing evidence that the capacity for acclimation to environmental stress may depend on the history of previous life stages (Marshall and Morgan, 2011; Parker *et al.*, 2012)."

Miller *et al.* conditioned adult anemone fish, *Amphiprion melanopus*, to present-day (430 ppm), moderate (581 ppm), and high (1,032 ppm) CO₂ treatments—"consistent with projections for CO₂ concentrations in the atmosphere and ocean over the next 50–100 years." They allowed the fish to spawn naturally, after which juvenile fish from control parents were reared at either the control CO₂ or transferred to high CO₂ at each of three temperatures (28.5, 30.0, and 31.5°C), while "juveniles from parents in the moderate- and high-CO₂ treatments were reared in similar CO₂ conditions as their parents at each of the three temperatures."

They found "ocean conditions projected for the end of the century (approximately 1,000 ppm CO_2 and a temperature rise of 1.5–3.0°C) cause an increase in metabolic rate and decreases in length, weight, condition and survival of juvenile fish." But the five Australian researchers found "these effects are absent or reversed when parents also experience high CO2 concentrations," indicating "conditions experienced by adults can have significant carry-over effects on the performance of their offspring (Bonduriansky and Day, 2009; Marshall and Morgan, 2011; Donelson et al., 2012), often leading to improved capacity to cope with environmental stress (Bernardo, 1996; Donelson et al., 2009)." Miller et al. conclude "parental effects prepare juveniles for similar conditions to those experienced in the parental generation," and, therefore, they suggest "non-genetic parental effects can dramatically alter the response of marine organisms to increasing CO₂ and demonstrate that some species have more capacity to acclimate to ocean acidification than previously thought."

Vehmaa *et al.* (2012) state "maternal effects are defined as cross-generation phenotypic plasticity, implying the capability of a mother to adjust the phenotype of her offspring [in] response to environmental cues that her offspring will encounter, in a manner that enhances offspring fitness (Parker and Begon, 1986; Lacey, 1998)," stating as an example, "Sydney rock oyster larvae are larger and develop faster in higher CO₂ conditions, if the adults also have been incubated in high CO₂ conditions (Parker *et al.*, 2012)."

Vehmaa *et al.* "tested the reproductive response of *Acartia* sp. calanoid copepods and the importance of maternal effects in determining the offspring quality in a changing environment according to a 2100 climate scenario of a pH decline by 0.4 unit and a temperature elevation of 3°C." They monitored the egg production of copepods incubated in four pH and temperature conditions for five consecutive days, and on days one, three, and five they divided the eggs and allowed them to hatch in conditions either the same as or different from those in which they were produced.

The three Finnish researchers report, "higher production temperature induced a positive maternal effect resulting in faster hatching and indicating that the mothers can invest more in their eggs, and therefore produce better quality eggs." They note the similar studies of Karell *et al.* (2008) and Jonasdottir *et al.* (2009) showed how "the egg quality in terms of maternal immunological or nutritional provisioning improved," and they suggest this phenomenon may explain "the declining effect of pH difference on egg hatching." Vehmaa *et al.* conclude maternal effects "are an important mechanism in the face of environmental change."

Frommel et al. (2013) provide evidence for the

adaptive capacity of fish to overcome the potential threat of lower ocean pH levels as well. In spite of its predicted detrimental effects on calcifying organisms, studies of possible impacts of ocean acidification [OA] on fish "remain scarce," the research team found. And although "adults will most likely remain relatively unaffected by changes in seawater pH," they state the "early life-history stages are potentially more sensitive, due to the lack of gills with specialized ion-regulatory mechanisms." They studied the egg and early larval stages of Baltic cod (Gadus morhua), which they describe as "the commercially most important fish stock in the Baltic Sea." They examined the effects of lower ocean pH levels on a number of egg and larval properties of G. morhua "over the range of CO₂ concentrations predicted in future scenarios for the Baltic Sea (from current values of 380 µatm up to 3,200 µatm CO₂ water)," both "with and without the combination of increasing temperature."

They report "no effect on hatching, survival, development, and otolith size was found at any stage in the development of Baltic cod," where "in situ levels of pCO_2 are already at levels of 1,100 µatm with a pH of 7.2." Their data showed "the eggs and early larval stages of Baltic cod seem to be robust to even higher levels of OA (3,200 µatm), indicating an adaptational response to CO_2 ." Frommel *et al.* conclude, "since the Baltic Sea is naturally high in pCO_2 , its fish stocks may be adapted to conditions predicted in ocean acidification scenarios for centuries to come."

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