

EFFECTS OF OCEAN ACIDIFICATION ON MARINE ECOSYSTEMS

Submitted by:

Dr. Craig Idso and Robert E. H. Ferguson

*Comments related to EPA's April 15, 2009 Notice of Data Availability (NODA) on
Ocean Acidification and Marine pH Water Quality Criteria.*



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To: OW-Docket@epa.gov

Re: Docket ID No. EPA-HQ-OW-2009-0224

Please find the following comments related to EPA's April 15, 2009 Notice of Data Availability (NODA) on Ocean Acidification and Marine pH Water Quality Criteria.

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Summary

The EPA's Notice of Data Availability (NODA), Docket ID No. EPA-HQ-OW-2009-0224, solicited public comment on available scientific information pertaining to the effects of ocean acidification on marine ecosystems. This document, submitted as a public comment, reviews numerous peer-reviewed research papers that have investigated the phenomenon of ocean acidification. The key findings are as follows:

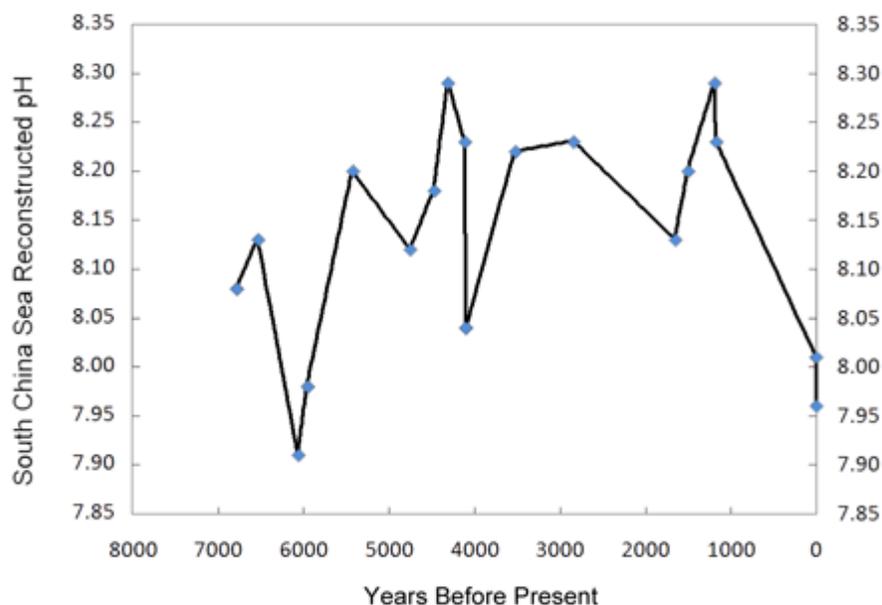
- There is nothing unnatural or unprecedented about current measurements of ocean water pH. Model-derived estimates of a CO₂-induced 0.1 pH unit decline since the start of the Industrial Revolution cannot be validated in the historical record.
- Coral calcification is a biologically-driven process that will likely overcome physical-chemical limitations, which in the absence of life would not be possible.
- Observational data overwhelmingly demonstrate that rates of coral calcification have *increased* over the past century and beyond as temperatures and atmospheric CO₂ concentrations have risen.
- Potential future declines in oceanic pH will likely not prove to be a major detriment to corals and other sea life. For many such organisms, the future rise in pCO₂ will yield growth *benefits*.

Such findings contrast with statements made by the EPA in the NODA (see Part II. Background on Ocean Acidification), which consider the impact of ocean acidification on marine organisms to largely be negative.

Historic Trends in Oceanic pH

There is considerable current concern that the ongoing rise in the air's CO₂ content is causing a significant drop in the pH of the world's oceans in response to their absorption of a large fraction of each year's anthropogenic CO₂ emissions. It has been estimated, for example, that the globe's seawater has been *acidified* (actually made *less basic*) by about 0.1 pH unit relative to what it was in pre-industrial times; and model calculations imply an additional 0.7-unit drop by the year 2300 (Caldeira and Wickett, 2003), which decline is hypothesized to cause great harm to calcifying marine life such as corals.

According to Liu *et al.* (2009), "the history of ocean pH variation during the current interglacial (Holocene) remains largely unknown." Using eighteen samples of fossil and modern *Porites* corals recovered from the South China Sea, therefore, the nine researchers employed ¹⁴C dating using the *liquid scintillation counting* method, along with *positive thermal ionization mass spectrometry* to generate high precision δ¹¹B (boron) data to reconstruct a paleo-pH record of the past 7000 years, which record "would provide critical insights on the possible impact of acidification on marine ecosystems."

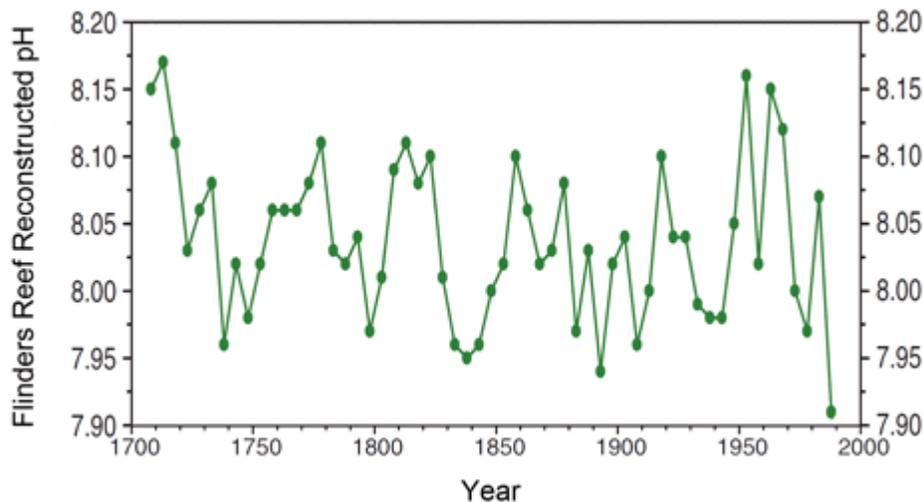


Reconstructed pH history of the South China Sea. Created from Table 1 of Liu et al. (2009).

As can be seen in their proxy pH reproduction above, there is nothing *unusual*, *unnatural* or *unprecedented* about the two most recent pH values. They are neither the lowest of the record, nor is the decline rate that led to them the greatest of the record. There is also no compelling reason to believe these last two values were influenced in any way by the nearly 40% increase in the air's CO₂ concentration that has occurred to date over the course of the Industrial

Revolution, as there clearly were much greater oscillations in pH prior to that time when the air's CO₂ concentration varied by only a few parts per million. Furthermore, with regard to the pre-Industrial Revolution portion of the record, Liu *et al.* note that there is "no correlation between the atmospheric CO₂ concentration record from Antarctica ice cores and $\delta^{11}\text{B}$ -reconstructed paleo-pH over the mid-late Holocene up to the Industrial Revolution."

Additional enlightenment on the subject 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 the figure below), based on $\delta^{11}\text{B}$ data obtained from a massive *Porites* coral from Flinders Reef in the western Coral Sea of the southwestern Pacific. According to these researchers, "there is no notable trend toward lower $\delta^{11}\text{B}$ values." Instead, they discovered that "the dominant feature of the coral $\delta^{11}\text{B}$ record is a clear interdecadal oscillation of pH, with $\delta^{11}\text{B}$ 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."

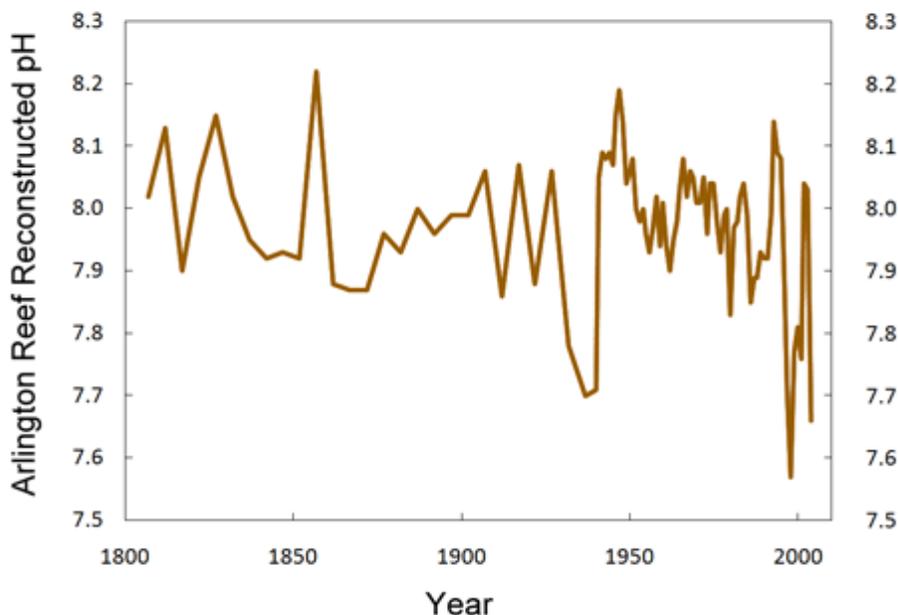


Reconstructed pH history of Flinders Reef of the Western Coral Sea of the Southwestern Pacific. Adapted from Pelejero et al. (2005).

Most recently, Wei *et al.* (2009) derived the pH history of Arlington Reef (off the north-east coast of Australia) that is depicted in the figure below. As can be seen there, there was a pH minimum centered at about 1935 and a shorter more variable minimum at the end of the record, neither of which could have been CO₂-induced given the rapidity of the drop and ensuing rise; and apart from these two non-CO₂-related exceptions, the majority of the data once again fall within a band that exhibits no long-term trend, which observation is opposite what is projected to have occurred if the gradual increase in atmospheric CO₂ concentration since the inception of the Industrial Revolution were truly making the global ocean less basic.

In considering the results of all three of these independent publications, it is clear that natural oscillations have dominated trends in oceanic pH over the past several thousand years, and

there is no compelling evidence to validate the model-based claim of a 0.1 pH unit decline since the start of the Industrial Revolution.



Reconstructed pH history of Arlington Reef off the northeast coast of Australia. Adapted from Wei et al. (2009).

Ocean Acidification

The rate of deposition of calcium carbonate on coral reefs, or coral calcification rate, is controlled at the cellular level by the saturation state of calcium carbonate in seawater; and oceanic surface waters have likely been saturated or supersaturated in this regard – providing a good environment for coral reef growth – since early Precambrian times (Holland, 1984). Currently, however, as the air's CO₂ content rises in response to ever-increasing anthropogenic CO₂ emissions, and as more and more carbon dioxide therefore dissolves in the surface waters of the world's oceans, pH values of the planet's oceanic waters are, or should be, gradually dropping, leading to a reduction in the calcium carbonate saturation state of seawater.

This phenomenon has been theorized to be leading to a corresponding reduction in coral calcification rates (Smith and Buddemeier, 1992; Buddemeier, 1994; Buddemeier and Fautin, 1996a,b; Holligan and Robertson, 1996; Gattuso *et al.*, 1998; Buddemeier and Smith, 1999; IPCC, 2007a,b; De'ath *et al.*, 2009), which reduction has been hypothesized to be rendering corals more susceptible to a number of other environmental stresses, including “sea-level rise, extreme temperatures, human damage (from mining, dredging, fishing and tourism), and changes in salinity and pollutant concentrations (nutrients, pesticides, herbicides and particulates), and in ocean currents, ENSO, and storm damage” (Pittock, 1999). Kleypas *et al.*

(1999), for example, have calculated that calcification rates of tropical corals should already have declined by 6 to 11% or more since 1880, as a result of the concomitant increase in atmospheric CO₂ concentration; and they predict that the reductions could reach 17 to 35% by 2100, as a result of expected increases in the air's CO₂ content over the coming century. Likewise, Langdon *et al.* (2000) calculated a decrease in coral calcification rate of up to 40% between 1880 and 2065.

The ocean chemistry aspect of this theory is rather straightforward; but it is not as solid as model projections make it out to be. In evaluating global seawater impacts of (1) model-predicted global warming and (2) direct seawater chemical consequences of a doubling of the air's CO₂ content, Loaiciga (2006), for example, used a mass-balance approach to (1) "estimate the change in average seawater salinity caused by the melting of terrestrial ice and permanent snow in a warming earth," and he (2) applied "a chemical equilibrium model for the concentration of carbonate species in seawater open to the atmosphere" in order to "estimate the effect of changes in atmospheric CO₂ on the acidity of seawater." Assuming that the rise in the planet's mean surface air temperature continues unabated, and that it eventually causes the melting of all terrestrial ice and permanent snow, Loaiciga calculated that "the average seawater salinity would be lowered not more than 0.61‰ from its current 35‰." He also reports that across the range of seawater temperature considered (0 to 30°C), "a doubling of CO₂ from 380 ppm to 760 ppm increases the seawater acidity [lowers its pH] approximately 0.19 pH units." He thus concludes that "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."

Furthermore, with more CO₂ in the air, additional weathering of terrestrial carbonates is likely to occur, which would increase delivery of Ca²⁺ to the oceans and partly compensate for the CO₂-induced decrease in oceanic calcium carbonate saturation state (Riding, 1996). And as with all phenomena involving living organisms, the introduction of life into the ocean acidification picture greatly complicates things. A suite of interrelated biological phenomena, for example, should also be considered, and when they are, it makes it much more difficult to draw such sweeping negative conclusions. In fact, as demonstrated in the following paragraphs, they even suggest that the rising CO₂ content of earth's atmosphere may well be a positive phenomenon, enhancing the growth rates of coral reefs and helping them to better withstand the many environmental stresses that truly are inimical to their well-being.

Over half a century ago, Kawaguti and Sakumoto (1948) illustrated the important role played by photosynthesis in the construction of coral reefs. Specifically, they analyzed numerous data sets recorded in several earlier publications, demonstrating that coral calcification rates are considerably higher in the daylight (when photosynthesis by coral symbionts occurs) than they are in the dark (when the symbionts lose carbon via respiration). A number of more modern studies have also demonstrated that symbiont photosynthesis enhances coral calcification (Barnes and Chalker, 1990; Yamashiro, 1995); and they have further demonstrated that long-term reef calcification rates generally rise in direct proportion to increases in rates of reef primary production (Frankignoulle *et al.*, 1996; Gattuso *et al.*, 1996, 1999). In fact, the work of

Muscatine (1990) suggests that “the photosynthetic activity of zooxanthellae is the chief source of energy for the energetically expensive process of calcification” (Hoegh-Guldberg, 1999). Consequently, if an anthropogenic-induced increase in the transfer of CO₂ from the atmosphere to the world’s oceans, i.e., hydrospheric CO₂ enrichment, were to lead to increases in coral symbiont photosynthesis – as atmospheric CO₂ enrichment does for essentially all terrestrial plants (Kimball, 1983; Idso, 1992) – it is likely that increases in coral calcification rates would occur as well.

There are several reasons for expecting a positive coral calcification response to CO₂-enhanced symbiont photosynthesis. One mechanism is the opposite of the phenomenon that has been proffered as a cause of future declines in coral calcification rates. This reverse phenomenon is the decrease in extracellular CO₂ partial pressure in coral tissues that is driven by the drawdown of aqueous CO₂ caused by the photosynthetic process. With CO₂ being removed from the water in intimate contact with the coral host via its fixation by photosynthesis (which CO₂ drawdown is of far greater significance to the coral than the increase in the CO₂ content of the surrounding bulk water that is affected by the ongoing rise in the air’s CO₂ content), the pH and calcium carbonate saturation state of the water immediately surrounding the coral host should rise (Goreau, 1959), enhancing the coral’s calcification rate (Gattuso *et al.*, 1999). And if hydrospheric CO₂ enrichment stimulates zooxanthellae photosynthesis to the same degree that atmospheric CO₂ enrichment stimulates photosynthesis in terrestrial plants, i.e., by 30 to 50% for a 300 ppm increase in CO₂ concentration (Kimball, 1983; Idso 1992, Idso and Idso, 1994), this phenomenon alone would more than compensate for the drop in the calcium carbonate saturation state of the bulk-water of the world’s oceans produced by the ongoing rise in the air’s CO₂ content, which Gattuso *et al.* (1999) have calculated could lead to a 15% reduction in coral calcification rate for a doubling of the pre-industrial atmospheric CO₂ concentration.

Another reason why coral calcification may proceed at a higher rate in the presence of CO₂-stimulated symbiont photosynthesis is that, while growing more robustly, the zooxanthellae may take up more of the metabolic waste products of the coral host, which, if present in too great quantities, can prove detrimental to the health of the host, as well as the health of the entire coral plant-animal assemblage (Yonge, 1968; Crossland and Barnes, 1974). There are also a number of other substances that are known to directly interfere with calcium carbonate precipitation; and they too can be actively removed from the water by coral symbionts in much the same way that symbionts remove host waste products (Simkiss, 1964). More importantly, perhaps, a greater amount of symbiont-produced photosynthates may provide more fuel for the active transport processes involved in coral calcification (Chalker and Taylor, 1975), as well as more raw materials for the synthesis of the coral organic matrix (Wainwright, 1963; Muscatine, 1967; Battey and Patton, 1984). Finally, the photosynthetic process helps to maintain a healthy aerobic or oxic environment for the optimal growth of the coral animals (Rinkevich and Loya, 1984; Rands *et al.*, 1992); and greater CO₂-induced rates of symbiont photosynthesis would enhance this important “environmental protection activity.”

With ever more CO₂ going into the air, driving ever more CO₂ into the oceans, increasingly greater rates of coral symbiont photosynthesis should be seen, due to the photosynthesis-

stimulating effect of hydrospheric CO₂ enrichment. And this phenomenon, in turn, should increasingly enhance all of the many positive photosynthetic-dependent phenomena described previously and thereby increase coral calcification rates. Furthermore, it could increase these rates well beyond the point of overpowering the modest negative effect of the purely chemical consequences of elevated dissolved CO₂ on ocean pH and calcium carbonate saturation state. However, arriving at these conclusions is not as simple as it sounds. For one thing, although many types of marine plant life do indeed respond to hydrospheric CO₂ enrichment (Raven *et al.*, 1985) – including seagrasses (Zimmerman *et al.*, 1997), certain diatoms (Riebesell *et al.*, 1993; Chen and Gao, 2004; Sobrino *et al.*, 2008), macroalgae (Borowitzka and Larkum, 1976; Gao *et al.*, 1993), and microalgae or phytoplankton (Raven, 1991; Nimer and Merrett, 1993) – the photosynthesis of many marine autotrophs is normally not considered to be carbon-limited, because of the large supply of bicarbonate in the world's oceans (Raven, 1997). However, as Gattuso *et al.* (1999) explain, this situation is only true for autotrophs that possess an effective carbon-concentrating mechanism; but to swing once again in the other direction, it is also believed that many coral symbionts are of this type (Burriss *et al.*, 1983; Al-Moghrabi *et al.*, 1996; Goiran *et al.*, 1996).

Nevertheless, Gattuso *et al.* (1999) reported that coral zooxanthellae – in another grand example of adaptation – are able to change their mechanism of carbon supply in response to various environmental stimuli. Furthermore, Beardall *et al.* (1998) suggest that an increased concentration of dissolved CO₂, together with an increase in the rate of CO₂ generation by bicarbonate dehydration in host cells, may favor a transition to the diffusional mode of carbon supply, which is sensitive to hydrospheric CO₂ concentration. Consequently, if such a change in mode of carbon supply were to occur – prompted, perhaps, by hydrospheric CO₂ enrichment itself – this shift in CO₂ fixation strategy would indeed allow the several biological mechanisms described above to operate to enhance reef calcification rates in response to a rise in the air's CO₂ content.

In one final example that demonstrates the importance of biology in driving the physical-chemical process of coral calcification, Muscatine *et al.* (2005) note that the "photosynthetic activity of zooxanthellae is the chief source of energy for the energetically-expensive process of calcification," and that long-term reef calcification rates have generally been observed to rise in direct proportion to increases in rates of reef primary production, which they say may well be enhanced by increases in the air's CO₂ concentration.

Muscatine *et al.* begin the report of their investigation of the subject by stating much the same thing, i.e., that endosymbiotic algae "release products of photosynthesis to animal cells ... and augment the rate of skeletal calcification." Then, noting that the "natural abundance of stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) has answered paleobiological and modern questions about the effect of photosymbiosis on sources of carbon and oxygen in coral skeletal calcium carbonate," they go on to investigate the natural abundance of these isotopes in another coral skeletal compartment - the skeletal organic matrix (OM) - in 17 species of modern scleractinian corals, after which they compare the results for symbiotic and nonsymbiotic forms to determine the role played by algae in OM development.

The significance of this study, in the words of Muscatine *et al.*, is because "the scleractinian coral skeleton is a two-phase composite structure consisting of fiber-like crystals of aragonitic calcium carbonate intimately associated with an intrinsic OM," and although the OM generally comprises less than 0.1% of the total weight of the coral skeleton, it is, in their words, "believed to initiate nucleation of calcium carbonate and provide a framework for crystallographic orientation and species-specific architecture." In fact, they say that inhibition of OM synthesis "brings coral calcification to a halt."

In commenting on what was learned from their experiments, the authors say their "most striking observation is the significant difference in mean OM $\delta^{15}\text{N}$ between symbiotic and nonsymbiotic corals," which makes OM $\delta^{15}\text{N}$ an important proxy for photosymbiosis. As an example of its usefulness, they applied the technique to a fossil coral (*Pachytheclis major*) from the Triassic (which prevailed some 240 million years ago), finding that the ancient coral was indeed photosymbiotic. Even more importantly, however, they conclude in the final sentence of their paper that "it now seems that symbiotic algae may control calcification by both modification of physico-chemical parameters within the coral polyps (Gautret *et al.*, 1997; Cuif *et al.*, 1999) and augmenting the synthesis of OM (Allemand *et al.*, 1998)."

Although lacking the research to absolutely identify the "what" and definitively describe the "how" of the hypothesis of hydrospheric CO_2 enhancement of coral calcification, it is likely that something of the nature described above can indeed act to overcome the negative effect of the high- CO_2 -induced decrease in calcium carbonate saturation state on coral calcification rate. It has been clearly demonstrated, for example, that corals can grow quite well in aquariums containing water of very high dissolved CO_2 concentration (Atkinson *et al.*, 1995); and Carlson (1999) has stated that the fact that corals often thrive in such water "seems to contradict conclusions ... that high CO_2 may inhibit calcification." And there are numerous other examples of such phenomena in the real world of nature, which are examined next.

Coral Calcification Measurements

Many are the predictions that rates of coral calcification, as well as 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 in the years, decades and centuries to come. As ever more pertinent evidence accumulates, however, the true story appears to be just the opposite of these predictions.

Herfort *et al.* (2008), for example, note that an increase in atmospheric CO_2 will cause an increase in the abundance of HCO_3^- (bicarbonate) ions and dissolved CO_2 , and report that several studies on marine plants have observed "increased photosynthesis with higher than ambient DIC [dissolved inorganic carbon] concentrations," citing the works of 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).

To further explore this subject, and to see what it might imply for coral calcification, 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." This work revealed that additions of HCO_3^- to synthetic seawater continued to increase the calcification rate of *Porites porites* until the bicarbonate concentration exceeded three times that of seawater, while 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 that calcification and photosynthetic rates in these corals were enhanced to an even greater extent, with calcification continuing to increase above a quadrupling of the HCO_3^- concentration and photosynthesis saturating at triple the concentration of seawater. In addition, they monitored calcification rates of the *Acropora* sp. in the dark, and, in their words, "although these were lower than in the light for a given HCO_3^- concentration, they still increased dramatically with HCO_3^- addition, showing that calcification in this coral is light stimulated but not light dependent."

In discussing the significance of their findings, Herfort *et al.* suggest that "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 that come courtesy of the ongoing rise in the air's CO_2 content. As for the real-world implications of their work, the three researchers note that over the next century the predicted increase in atmospheric CO_2 concentration "will result in about a 15% increase in oceanic HCO_3^- ," and they say that this development "could stimulate photosynthesis and calcification in a wide variety of hermatypic corals."

In another study, Pelejero *et al.* (2005) developed a reconstruction of seawater pH spanning the period 1708-1988, based on the boron isotopic composition ($\delta^{11}\text{B}$) of a long-lived massive coral (*Porites*) from Flinders Reef in the western Coral Sea of the southwestern Pacific. Results indicated that "there [was] no notable trend toward lower $\delta^{11}\text{B}$ values" over the 300-year period investigated. Instead, they say that "the dominant feature of the coral $\delta^{11}\text{B}$ record is a clear interdecadal oscillation of pH, with $\delta^{11}\text{B}$ values ranging between 23 and 25 per mil (7.9 and 8.2 pH units)," which "is synchronous with the Interdecadal Pacific Oscillation." Furthermore, they calculated changes in aragonite saturation state from the Flinders pH record that varied between ~3 and 4.5, which values encompass "the lower and upper limits of aragonite saturation state within which corals can survive." Despite this fact, they report that "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 that historical anthropogenic CO_2 emissions have already resulted in a significant decline in ocean water pH and aragonite saturation state, Pelejero *et al.*'s 300-year record of these parameters (which, in their words, began "well before the start of the Industrial Revolution") provides no evidence of such a decline. What is more, and also contrary to claims of how sensitive coral calcification rate is to changes in pH and aragonite saturation state, they

found that huge 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, such that a 1°C increase in mean annual water temperature increased mean annual coral calcification rate by about 3.5%. Nevertheless, they report there were "declines in calcification in *Porites* on the Great Barrier Reef over recent decades." They point out, however, that their data depict several extended periods of time when coral growth rates were either above or below the long-term mean, cautioning that "it would be unwise to rely on short-term values (say averages over less than 30 years) to assess mean conditions."

As an example of this fact, they report that "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 CO₂ emissions made much of an impact on the air's CO₂ concentration. In fact, over the entire expanse of their data set, Lough and Barnes say "the 20th century has witnessed the second highest period of above average calcification in the past 237 years," which is not exactly what one would expect in light of (1) how dangerous high water temperatures are often said to be for corals, (2) the claim that earth is currently warmer than it has been at any other time during the entire past millennium, and (3) the fact that the air's CO₂ content is currently much higher than it has been for far longer than a mere thousand years.

Similar findings were reported by Bessat and Buigues (2001), who derived a history of coral calcification rates from a core extracted from a massive *Porites* coral head on the French Polynesian island of Moorea that covered the period 1801-1990. They performed this work, they say, because "recent coral-growth models highlight the enhanced greenhouse effect on the decrease of calcification rate," and rather than relying on theoretical calculations, they wanted to work with real-world data, stating that 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."

Results indicated that a 1°C increase in water temperature increased coral calcification rate at the site they studied by 4.5%. Then, they found that "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, which were 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 that their results "do not confirm those predicted by the Kleypas *et al.* (1999) model."

Additional observation evidence contrary to the Kleypas *et al.* model was provided by the work of Lough and Barnes (2000), who 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), which 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), thereby extending the latitudinal range of the expanded data set to 20° and the annual average SST range to 23-29°C.

This analysis revealed that the GBR calcification data were linearly related to the average annual SST data, such that "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 data set; Lough and Barnes report that "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 0.001)," noting that "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."

With respect to the significance of their findings, Lough and Barnes say they "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 that "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." What is more, the authors report that between the two 20-year periods 1903-1922 and 1979-1998, "the SST-associated 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 ~50%) to the south of the GBR."

In light of these real-world observations, Lough and Barnes concluded that coral calcification rates "may have already significantly increased along the GBR in response to global climate change." Yet in spite of this compelling evidence, as well as the similar findings of others, claims of impending coral demise caused by rising air temperatures and CO₂ concentrations continue to surface, including the study of Caldeira and Wickett (2003).

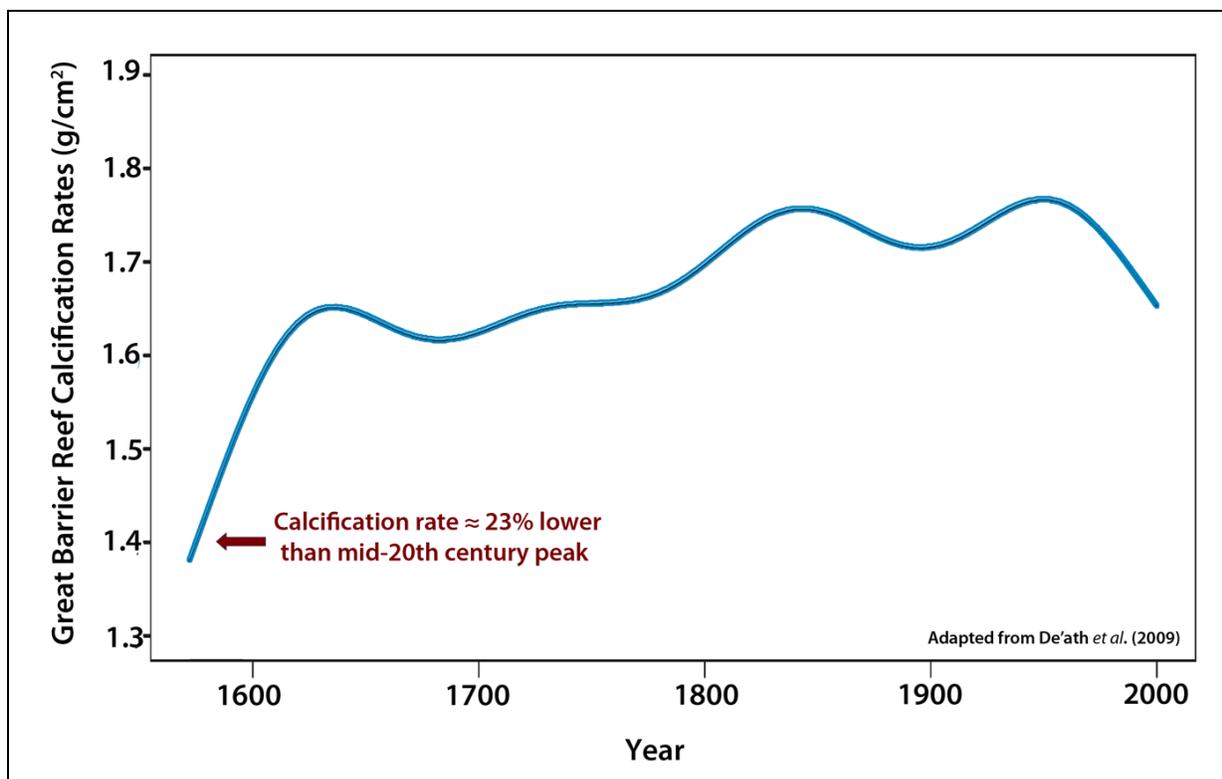
Based on a geochemical model, an ocean general-circulation model, an IPCC CO₂ emissions scenario for the 21st century, and a logistic function for the burning of earth's post-21st century fossil-fuel reserves, they calculated three important numbers: the maximum level to which the air's CO₂ concentration might rise, the point in time when that might happen, and the related decline that might be expected to occur in ocean-surface pH. These calculations indicated that earth's atmospheric CO₂ concentration could approach 2000 ppm around the year 2300, leading to an ocean-surface pH reduction of 0.7 unit, a change described by Caldeira and Wickett as being much more rapid and considerably greater "than any experienced in the past 300 million years," which proves deadly for earth's corals in their scenario.

The following year, similar concerns were raised in a report prepared for the Pew Center on Global Climate Change, which was released to the public on 13 February 2004 at the annual meeting of the *American Association for the Advancement of Science*. In that document,

Buddemeier *et al.* (2004) claimed that the projected increase in the air's CO₂ content and the simulated decline in ocean-surface pH would dramatically decrease coral calcification rates, which were predicted to lead to "a slow-down or reversal of reef-building and the potential loss of reef structures."

Nevertheless, and because of all the contrary evidence, much of which we have cited above, Buddemeier *et al.* (2004) acknowledged that "calcification rates of large heads of the massive coral *Porites* increased rather than decreased over the latter half of the 20th century," further noting that "temperature and calcification rates are correlated, and these corals have so far responded more to increases in water temperature (growing faster through increased metabolism and the increased photosynthetic rates of their zooxanthellae) than to decreases in carbonate ion concentration."

The most recent claims of impending coral demise derive from the 2009 study of De'ath *et al.*, who examined coral calcification rates on the Great Barrier Reef over the past 400 years. Results of their analysis indicate there was a 14% decline in *Porites* calcification rate between 1990 and 2005, which they claimed to be "unprecedented in at least the past 400 years." But if De'ath *et al.*'s calcification history is followed back in time a mere 33 more years, from 1605 to 1572, that claim is no longer true, because the coral calcification rate during that earlier time was approximately 23% lower than what it was at its 20th-century peak, when the air's CO₂ concentration was more than 100 ppm less than what it is today and, therefore, supposedly so much more healthier for corals.



Another way of looking at De'ath *et al.*'s data is to realize that from 1572 to the 20th century peak, *Porites* calcification rates on the Great Barrier Reef rose by about 29%, as the atmospheric CO₂ concentration and air temperature rose concurrently, after which calcification rates declined, but by a smaller 14%, as these same air temperature and CO₂ trends continued, further obfuscating the issue. With respect to the cause of the recent decline, De'ath *et al.* state that "the causes for the Great Barrier Reef-wide decline in coral calcification of massive *Porites* remain unknown."

Another reason why the ongoing rise in the air's CO₂ content may not lead to reduced oceanic pH and, therefore, lower calcification rates in the world's coral reefs, is that 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); and 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.*, 2001; Hansen, 2002) as well as to significantly enhance the surface water pH of areas as large as the North Sea (Brussaard *et al.*, 1996).

In one example, 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, reporting that, in line with what one would expect if photosynthesis tends to increase surface-water pH, (1) "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, that (2) "diurnal measurements at the most exposed site showed significantly higher pH during the day than during the night," reaching values that sometimes exceeded 9 during daylight hours but that typically dipped below 8 at night, and (3) that "diurnal variations were largest in the shallow water and decreased with increasing water depth."

In addition to their own findings, Middelboe and Hansen cite those of (1) Pearson *et al.* (1998), who found that pH averaged about 9 during the summer in populations of *Fucus vesiculosus* in the Baltic Sea, (2) Menendez *et al.* (2001), who found that maximum pH was 9 to 9.5 in dense floating macroalgae in a brackish coastal lagoon in the Ebro River Delta, and (3) Bjork *et al.* (2004), who found pH values as high as 9.8 to 10.1 in isolated rock pools in Sweden. Noting that "pH in the sea is usually considered to be stable at around 8 to 8.2," the two Danish researchers thus concluded that "pH is higher in natural shallow-water habitats than previously thought."

In a more recent example of this phenomena, 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 marine meadows. This feat was accomplished by measuring rates 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.

Results indicated that “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 5.8-fold for *Hydrolithon* sp. and 1.6-fold for the other 2 species,” while “the rETRs of all algae largely followed the irradiance throughout the day and were (in *Mesophyllum* sp.) significantly higher in the presence of seagrasses.” Thus, the three researchers concluded that “algal calcification within 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.” In fact, they note that the high pH values that were created by seagrass photosynthesis are what actually *caused* the elevated calcification rates of the macroalgae; and this observation supports the thesis that the lowering of seawater pH caused by higher atmospheric CO₂ concentrations may well be *counteracted* by CO₂-induced increases in the photosynthetic activity of the symbiotic zooxanthellae of earth’s corals, which phenomenon may boost the pH of seawater *in intimate contact with the coral host*, allowing the host to actually *increase* its calcification rate in CO₂-enriched seawater (or to at least not suffer a major reduction in calcification), which end result is what has generally been observed in the real world over the course of the increase in the air’s CO₂ concentration that has been experienced since the inception of the Industrial Revolution.

Returning back to calcification studies, Reynaud *et al.* (2004) grew nubbins of the branching zooxanthellate scleractinian coral *Acropora verweyi* in aquariums maintained at 20, 25 and 29°C, while weighing them once a week over a period of four weeks. This exercise revealed that coral calcification rates increased in nearly perfect linear fashion with increasing water temperature, yielding values of 0.06, 0.22 and 0.35% per day at 20, 25 and 29°C, respectively. These data reveal an approximate 480% increase in calcification rate in response to a 9°C increase in water temperature and a 160% increase in response to a 3°C increase in temperature, the latter of which temperature increases is somewhere in the low to midrange of global warming that the IPCC claims will result from a 300 ppm increase in the air’s CO₂ concentration; and this positive temperature effect far outweighs the negative effect of rising CO₂ concentrations on coral calcification via ocean acidification.

Working in the ocean, Carricart-Ganivet (2004) developed relationships between coral calcification rate and annual average SST based on data collected from colonies of the reef-building coral *Montastraea annularis* at twelve localities in the Gulf of Mexico and the Caribbean Sea, finding that calcification rate in the Gulf of Mexico increased 0.55 g cm⁻² year⁻¹ for each 1°C increase, while in the Caribbean Sea it increased 0.58 g cm⁻² year⁻¹ for each 1°C increase. Pooling these data with those of *M. annularis* and *M. faveolata* growing to a depth of 10 m at Carrie Bow Cay, Belize, those from reefs at St. Croix in the US Virgin Islands, and those of *M. faveolata* growing to a depth of 10 m at Curacao, Antilles, Carricart-Ganivet reports he obtained a mean increase in calcification rate of ~0.5 g cm⁻² year⁻¹ for each 1°C increase in annual average SST, which is even greater than what was found by Lough and Barnes for *Porites* corals.

Some new and updated real-world assessments of coral growth were also provided by Lough (2008), who reported that "average linear extension and calcification rates in Indo-Pacific *Porites* are linearly [and positively] related to average water temperatures through 23 to 30°C," based on data obtained from 49 different reefs. She also reports, however, that "coral growth characteristics at 2 of 3 reefs in the central Great Barrier Reef provide evidence of a recent decline," but she adds that "the exact causes of these declines cannot be identified at present nor can they, at present, be directly related to lower aragonite saturation state."

In another study, McNeil *et al.* (2004) used a coupled atmosphere-ice-ocean carbon cycle model to calculate annual mean SST increases within the world's current coral reef habitat from 1995 to 2100 for increases in the air's CO₂ concentration specified by the IPCC's IS92a scenario, after which concomitant changes in coral reef calcification rates were estimated by combining the output of the climate model with empirical relationships between coral calcification rate and (1) aragonite saturation state (the negative CO₂ effect) and (2) annual SST (the positive temperature effect). Their choice for the first of these two relationships was that derived by Langdon *et al.* (2000), which leads to an even greater reduction in calcification than was predicted in the study of Kleypas *et al.* Their choice for the second relationship was that derived by Lough and Barnes (2000), which leads to an increase in calcification that is only half as large as that derived by Carricart-Ganivet (2004). As a result, the net result of the two phenomena was doubly weighted in favor of reduced coral calcification. Nevertheless, McNeil *et al.* found that the increase in coral reef calcification associated with ocean warming far outweighed the decrease associated with the CO₂-induced decrease in aragonite saturation state. In fact, they calculated that coral calcification in 2100 would be 35% higher than what it was in pre-industrial times at the very least. And, they found that the area of coral reef habitat expands in association with the projected ocean warming.

In a study devoted to corals that involves a much longer period of time than all of the others previously discussed, another research team (Crabbe *et al.*, 2006) determined the original growth rates of long-dead Quaternary corals found in limestone deposits of islands in the Wakatobi Marine National Park of Indonesia, after which they compared them to the growth rates of present-day corals of the same genera living in the same area. This work revealed that the Quaternary corals grew "in a comparable environment to modern reefs" -- except for the air's CO₂ concentration, which is currently higher than it has been at any other time throughout the entire Quaternary, which spans the past 1.8 million years. Their measurements indicated that the radial growth rates of the modern corals were 31% greater than those of their ancient predecessors in the case of *Porites* species, and 34% greater in the case of *Favites* species.

Many other papers also depict increasing rates of coral calcification in the face of rising temperatures and atmospheric CO₂ concentrations (Clausen and Roth, 1975; Coles and Jokiel, 1977; Kajiwarra *et al.*, 1995; Nie *et al.*, 1997; Reynaud-Vaganay *et al.*, 1999; Reynaud *et al.*, 2007). Such observations indicate that the net impact of 20th-century increases in atmospheric CO₂ and temperature has not been anywhere near as catastrophically disruptive to earth's corals as theoretical calculations suggest it should have been. Rather, observational data

suggest that the temperature and CO₂ increases appear to have been helpful, perhaps evidencing the fact that coral calcification is a biologically-driven process that can overcome physical-chemical limitations, which in the absence of life would not be possible.

Ocean Acidification Effects on Other Marine Organisms

Kurihara *et al.* (2007) extracted sedimentary mud containing meiofauna (small benthic invertebrates that can pass through a 0.5 - 1 mm mesh but are retained by a 30 - 45 µm mesh) from the seafloor of Tanabe Bay on the Kii Peninsula of Japan and incubated it in marine microcosms that were continuously aerated for 56 days with air of either 360 or 2,360 ppm CO₂ -- the latter of which concentrations has been predicted by some to be characteristic of the real world in the year 2300 -- while they periodically measured the abundance and biomass of different members of the meiobenthic community contained in the sediments.

Observations revealed "no significant differences in the abundance of total meiofauna, nematodes, harpacticoid copepods (including adults and copepodites) and nauplii by the end of the experiment." In addition, they say there "may have been successful recruitments under elevated CO₂ conditions," and, therefore, that "elevated CO₂ had not impacted the reproduction of nematodes and harpacticoid copepods." Thus, the three researchers concluded that "these results suggest that the projected atmospheric CO₂ concentration in the year 2300 does not have acute effects on the meiofauna."

In another paper, Kranz *et al.* (2009) write that "marine phytoplankton contribute up to 50% of global primary production (Falkowski *et al.*, 1998) and influence earth's climate by altering various biogeochemical cycles (Schlesinger, 2005)." They also note, with respect to the latter subject and, more specifically, the marine nitrogen (N) cycle, that among diazotrophic cyanobacteria (dinitrogen-fixers), the species *Trichodesmium* "contributes 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, 2007)." Thus, to see how the ongoing and projected increase in the air's CO₂ concentration may impact one of the global ocean's most important diazotrophic cyanobacteria (*Trichodesmium erythraeum* IMS101), Kranz *et al.* (2009) grew the ubiquitous marine N₂-fixer in semicontinuous batch cultures through which they bubbled air with CO₂ concentrations of either 370 or 1000 ppm. After the cultures were acclimated to their respective CO₂ concentrations for at least 14 days (more than 5 generations), they then measured rates of particulate organic carbon (POC) and particulate organic nitrogen (PON) fixation.

Results indicated there was "a strong increase in photosynthesis and N₂ fixation under elevated CO₂ levels," such that POC and PON production rates rose "by almost 40%." In discussing the generality of their results, the German scientists noted that -- working with the same *Trichodesmium* species -- "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% over the respective CO₂ range." And in discussing the significance of

these similar findings, they state that “the observed increase in photosynthesis and N₂ fixation could have potential [global] biogeochemical implications, as it may stimulate productivity in N-limited oligotrophic regions and thus provide a negative feedback on rising atmospheric CO₂ levels,” slowing the rate of CO₂ rise and reducing the degree of CO₂-induced global warming.

In a similar vein, employing semi-continuous culturing methods that used filtered, microwave-sterilized surface Sargasso seawater that was enriched with phosphate and trace nutrients, Fu *et al.* (2008) “examined the physiological responses of steady-state iron (Fe)-replete and Fe-limited cultures of the biogeochemically critical marine unicellular diazotrophic cyanobacterium *Crocospaera [watsonii]* at glacial (190 ppm), current (380 ppm), and projected year 2100 (750 ppm) CO₂ levels.”

Results of their experiment indicated that when the seawater was *replete* with iron, daily primary production at 750 ppm CO₂ was 21% greater than it was at 380 ppm, while at 190 ppm CO₂ it was 38% lower than it was at 380 ppm. When the seawater was *iron-limited*, however, daily primary production at 750 ppm CO₂ was 150% greater than it was at 380 ppm, while at 190 ppm CO₂ it was 22% lower than it was at 380 ppm. With respect to N₂ fixation, rates varied little among the three CO₂ treatments when the seawater was *iron-limited*; but when the seawater was *replete* with iron, N₂ fixation at 750 ppm CO₂ was 60% greater than it was at 380 ppm, while at 190 ppm CO₂ it was 33% lower than it was at 380 ppm.

In discussing their findings, Fu *et al.* note that “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 they say their data “extend these findings to encompass the marine unicellular N₂-fixing cyanobacterium *Crocospaera*,” which group, they add, “is now recognized as being perhaps equally as important as *Trichodesmium* to the ocean nitrogen cycle (Montoya *et al.*, 2004).” Consequently, they conclude that “anthropogenic CO₂ enrichment could substantially increase global oceanic N₂ and CO₂ fixation,” which two-pronged phenomenon would be a tremendous boon to the marine biosphere.

In another study, Bernhard *et al.* (2009) grew the marine foraminiferal protist *Allogromia laticollaris* -- which they describe 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, while examining its response to a number of super-high atmospheric CO₂ concentrations to which the tubes were exposed: 15,000, 30,000, 60,000, 90,000 and 200,000 ppm, which values were compared to the study’s atmospheric control concentration of 375 ppm CO₂.

Results indicated that the protist “is able to survive 10-14-day exposure to elevated CO₂ as high as 200,000 ppm.” In fact, they say that “both ATP [Adenosine Triphosphate, an indicator of cellular energy] data and microscopic examination indicate 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.” And they found that “at least three

specimens reproduced during exposure to either 90,000 ppm or 200,000 ppm CO₂,” while “such reproduction was observed only once in an atmospheric [375-ppm CO₂] treatment.”

With respect to the significance of their findings, the four researchers first note that “*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.” Hence, they go on to say their results indicate that “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.” And, last of all, they say that *A. laticollaris* will also tolerate CO₂ values that are one to two orders of magnitude greater than those predicted to occur for the “extreme case” of burning all fossil fuels in the crust of the earth.

In a review of what is known about the effects of a CO₂-enriched atmosphere on micro- and macro-algae living in the world’s oceans, Wu *et al.* (2008) write that “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],” adding that “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 light-limiting conditions,” because “at higher CO₂ levels, less light energy is required to drive CCM.” In addition, they report that enhanced CO₂ levels have been found to enhance the activity of nitrogen reductase in several marine plants, and that this phenomenon “would support enhanced growth rate by providing adequate nitrogen required for the metabolism under the high CO₂ level.” Last of all, they say that “altered physiological performances under high-CO₂ conditions may cause genetic alteration in view of adaptation over long time scales,” and that “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.”

The findings described by the three researchers represent good news for the biosphere, since “marine phytoplankton contribute to about half of the global primary productivity,” and this phenomenon, in their words, “promotes the absorption of CO₂ from the atmosphere.” Consequently, both the micro- and macro-algae of the world’s oceans should be able to do an even more robust job of performing these vital functions in a CO₂-enriched world of the future.

In another study, Vogt *et al.* (2008) examined the effects of atmospheric CO₂ enrichment on various marine microorganisms in nine marine mesocosms in a fjord adjacent to the Large-Scale Facilities of the Biological Station of the University of Bergen in Espesgrend, Norway. Three of the mesocosms were maintained at ambient levels of CO₂ (~375 ppm), three were maintained at levels expected to prevail at the end of the current century (760 ppm or 2x CO₂), and three were maintained at levels predicted for the middle of the next century (1150 ppm or 3x CO₂), while measurements of numerous ecosystem parameters were made over a period of 24 days.

Results of the analysis showed no significant phytoplankton species shifts between treatments, and that "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," citing in support of this statement the work of Riebesell *et al.* (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). With respect to their many findings, the eight researchers say their observations suggest that "the system under study was surprisingly resilient to abrupt and large pH changes."

In another study, Langer *et al.* (2006) conducted batch-culture experiments on two coccolithophores, *Calcidiscus leptoporus* and *Coccolithus pelagicus*, in which they observed a "deterioration of coccolith production above as well as below present-day CO₂ concentrations in *C. leptoporus*," and a "lack of a CO₂ sensitivity of calcification in *C. pelagicus*" over an atmospheric CO₂ concentration range of 98-915 ppm. Both of these observations, in their words, "refute the notion of a linear relationship of calcification with the carbonate ion concentration and carbonate saturation state." In an apparent negative finding, however, particularly in the case of *C. leptoporus*, Langer *et al.* observed that although their experiments revealed that "at 360 ppm CO₂ most coccoliths show normal morphology," at both "higher and lower CO₂ concentrations the proportion of coccoliths showing incomplete growth and malformation increases notably."

To determine if such deleterious responses might have also occurred in the real world at different times in the past, the researchers studied coccolith morphologies in six sediment cores obtained along a range of latitudes in the Atlantic Ocean. As they describe it, this work revealed that changes in coccolith morphology similar to those "occurring in response to the abrupt CO₂ perturbation applied in experimental treatments are not mirrored in the sedimentary record." This finding indicates, as they suggest, that "in the natural environment *C. leptoporus* has adjusted to the 80-ppm CO₂ and 180-ppm CO₂ difference between present [and] preindustrial and glacial times, respectively."

In further discussing these observations, Langer *et al.* say "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 that "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 that 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," which leads them to conclude that such populations "may be able to evolve so that the optimal CO₂ level for calcification of the species tracks the environmental value." With respect to the future, therefore, Langer *et al.* end by stating that "genetic diversity, both between and within species, may allow calcifying organisms to prevail in a high CO₂ ocean."

Focusing on another coccolithophore species, Riebesell (2004) notes that "a moderate increase in CO₂ facilitates photosynthetic carbon fixation of some phytoplankton groups," including "the coccolithophorids *Emiliana huxleyi* and *Gephyrocapsa oceanica*." Hence, in a major challenge to the claim that atmospheric CO₂ enrichment will definitely harm such marine organisms, Riebesell suggests that "CO₂-sensitive taxa, such as the calcifying coccolithophorids, should therefore benefit more from the present increase in atmospheric CO₂ compared to the non-calcifying diatoms."

In support of this suggestion, Riebesell describes the results of some CO₂ perturbation experiments conducted south of Bergen, Norway, where nine 11-m³ enclosures moored to a floating raft were aerated in triplicate with CO₂-depleted, normal and CO₂-enriched air to achieve CO₂ levels of 190, 370 and 710 ppm, simulating glacial, present-day and predicted conditions for the end of the century, respectively. In the course of the study, a bloom consisting of a mixed phytoplankton community developed, and, in Riebesell's words, "significantly higher net community production was observed under elevated CO₂ levels during the build-up of the bloom." He further reports that "CO₂-related differences in primary production continued after nutrient exhaustion, leading to higher production of transparent exopolymer particles under high CO₂ conditions," something that has also been observed by Engel (2002) in a natural plankton assemblage and by Heemann (2002) in monospecific cultures of both diatoms and coccolithophores.

Another significant finding of this experiment was that the community that developed under the high CO₂ conditions expected for the end of this century was dominated by *Emiliana huxleyi*. Consequently, Riebesell finds even more reason to believe that "coccolithophores may benefit from the present increase in atmospheric CO₂ and related changes in seawater carbonate chemistry," in contrast to the many negative predictions that have been made about rising atmospheric CO₂ concentrations in this regard. Finally, in further commentary on the topic, Riebesell states that "increasing CO₂ availability may improve the overall resource utilization of *E. huxleyi* and possibly of other fast-growing coccolithophore species," concluding that "if this provides an ecological advantage for coccolithophores, rising atmospheric CO₂ could potentially increase the contribution of calcifying phytoplankton to overall primary production." In fact, noting that "a moderate increase in CO₂ facilitates photosynthetic carbon fixation of some phytoplankton groups," including "the coccolithophorids *Emiliana huxleyi* and *Gephyrocapsa oceanica*" - and in a major challenge to the claim that atmospheric CO₂ enrichment will harm such marine organisms - Riebesell suggests that "CO₂-sensitive taxa, such as the calcifying coccolithophorids, should therefore benefit more from the present increase in atmospheric CO₂ compared to the non-calcifying diatoms."

Support for Riebesell's findings was provided by an international team of thirteen researchers (Iglesias-Rodriguez *et al.*, 2008), who bubbled air of a number of different atmospheric CO₂ concentrations through culture media containing the phytoplanktonic coccolithophore species *Emiliana huxleyi*, while determining the amounts of particulate organic and inorganic carbon they produced. In addition, they determined the real-world change in average coccolithophore mass over the past 220 years in the subpolar North Atlantic Ocean, based on data obtained

from a sediment core, over which period of time the atmosphere's CO₂ concentration rose by approximately 90 ppm and the earth emerged from the frigid depths of the Little Ice Age to experience the supposedly unprecedented high temperatures of the Current Warm Period.

Results of their analysis revealed an approximate doubling of both particulate organic and inorganic carbon between the culture media in equilibrium with air of today's CO₂ concentration and the culture media in equilibrium with air of 750 ppm CO₂. In addition, they say the field evidence they obtained from the deep-ocean sediment core they studied "is consistent with these laboratory conclusions," and that it indicates that "over the past 220 years there has been a 40% increase in average coccolith mass."

Focusing more on the future, a third independent team of seven scientists (Feng *et al.*, 2008) studied *Emiliania huxleyi* coccoliths that they isolated from the Sargasso Sea, and which they grew in semi-continuous culture media at low and high light intensities, low and high temperatures (20 and 24°C), and low and high CO₂ concentrations (375 and 750 ppm). This work revealed that in the low-light environment, the maximum photosynthetic rate was lowest in the low-temperature, low-CO₂ or ambient treatment, but was increased by 55% by elevated temperature alone and by 95% by elevated CO₂ alone, while in the high-temperature, high-CO₂ or greenhouse treatment it was increased by 150% relative to the ambient treatment. Likewise, in the high-light environment, there were maximum photosynthetic rate increases of 58%, 67% and 92% for the elevated temperature alone, elevated CO₂ alone and greenhouse treatments, respectively. Consequently, the researchers concluded, in their words, that "future trends of CO₂ enrichment, sea-surface warming and exposure to higher mean irradiances from intensified stratification will have a large influence on the growth of *Emiliania huxleyi*," and that large influence will be *positive*.

In addressing the impacts of ocean acidification on fish, Ishimatsu *et al.* (2005) note that "fish are important members of both freshwater and marine ecosystems and constitute a major protein source in many countries." Hence, they say 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." In response to this concern, Ishimatsu *et al.* conducted a survey of the scientific literature with respect to the potential negative consequences of atmospheric CO₂ enrichment on the health of fish that could arise from continued anthropogenic CO₂ emissions, finding a number of *possible* dire consequences.

Focusing on hypercapnia - a condition characterized by an excessive amount of CO₂ in the blood that typically results in acidosis, a serious and sometimes fatal condition characterized in humans by headache, nausea and visual disturbances - they say their survey revealed that "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 conclusion sounds dire indeed, it represents an egregious flight of the imagination in terms of what could realistically be expected to happen *anytime* in earth's future. Ishimatsu *et al.* report, for example, that "predicted future CO₂ concentrations in the atmosphere are lower than the known lethal concentrations for fish," noting that "the expected peak value is about 1.4 torr [just under 1850 ppm] around the year 2300 according to Caldeira and Wickett (2003)."

With regard to just how far below the lethal CO₂ concentration for fish 1.4 torr is, in the case of *short-term* exposures on the order of a few days, the authors cite a number of studies that yield median lethal concentrations ranging from 37 to 50 torr, which values are *26 and 36 times greater than the maximum CO₂ concentration expected some 300 years from now!* In the case of long-term exposures, to cite just a few examples, the authors report that Fivelstad *et al.* (1999) observed only 5 and 8% mortality at the end of 62 days of exposure to CO₂ concentrations of 5 and 9 torr, respectively, for freshwater Atlantic salmon smolts, while mere 1 and 5% mortalities were found for seawater postsmolts of the same species at 12 and 20 torr after 43 days (Fivelstad *et al.*, 1998). In addition, they say that Smart *et al.* (1979) found little difference in mortality for freshwater rainbow trout reared for 275 days at 4 to 17 torr, and that 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, however, are often more vulnerable to environmental stresses than are adult fish. Yet even here, the authors report that the 24-hour median lethal concentration of CO₂ on both 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 *over seven times greater* than the CO₂ concentration expected 300 years from now. Lastly, Ishimatsu *et al.*'s review reveals growth reductions of 24 to 48%; but, again, the CO₂ concentrations needed to induce these growth reductions ranged from 17 to 20 torr, or 12 to 14 times more than the CO₂ concentration expected 300 years from now. Clearly, the scientific literature review of Ishimatsu *et al.* suggests that earth's fish, both freshwater and marine, will likely *never* experience any discomfort or ill effects from the direct consequences of the elevated atmospheric CO₂ concentrations caused by human activities.

In another study examining ocean acidification on fish, Melzner *et al.* (2009) write with respect to earth's 30,000 species of *teleost fish*, which include virtually all of the world's important sport and commercial fishes, that several of them have previously been shown to be able to "fully compensate extra cellular fluid pH," as well as "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)," but they note that there have been no studies of these phenomena that have lasted for more than a few days. To rectify this situation, Melzner *et al.* maintained a group of Atlantic Cod (*Gadus morhua*) for four months in a re-circulating aquaculture system of 15 cubic meters volume at an atmospheric CO₂ partial pressure of 0.3 kPa (~3,000 ppm) and another group for twelve months at a CO₂ partial pressure of 0.6 kPa (~6,000 ppm), after which the fishes' swimming metabolism was investigated in a swim-tunnel respirometer, and tissue samples of their gills were taken for

various chemical analyses, including gill Na^+/K^+ -ATPase capacity, which serves “as a general indicator for ion regulatory effort.”

At the conclusion of the study, the six German scientists reported that “motor activity in adult Atlantic Cod is not compromised by long-term exposure to water P_{CO_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 (Calderia and Wickett, 2003).” In light of what they learned from their study, therefore, Melzner *et al.* concluded that “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 prospected scenarios of global climate change,” even those far beyond what could likely be produced by the burning of all fossil fuels in the crust of the earth.

In a separate paper, Kurihara (2008) focused on “the effects of ocean acidification on early developmental and reproductive stages of calcifiers, both of which are believed to be the most vulnerable stages to environmental change within a life cycle.” In doing so, he notes that certain laboratory experiments suggest that “ocean acidification has negative impacts on the fertilization, cleavage, larva, settlement and reproductive stages of several marine calcifiers, including echinoderm, bivalve, coral and crustacean species,” and he concludes that “future changes in ocean acidity will potentially impact the population size and dynamics, as well as the community structure of calcifiers, and will therefore have negative impacts on marine ecosystems.”

However, most of the studies Kurihara cited did not observe statistically-significant negative effects of atmospheric CO_2 enrichment until very large increases in the air's CO_2 content were employed. In studies of sea urchins, for example, statistically-significant reductions in egg fertilization rates did not occur in *Echinometra mathaei* until the atmospheric CO_2 concentration was raised a full 5,000 ppm above that of the ambient air; and in *Hemicentrotus pulcherrimus*, even a 10,000 ppm increase in the air's CO_2 concentration was insufficient to elicit a statistically-significant decline in egg fertilization rate. In addition, Kurihara himself suggests that the great degree of scatter in the data may reflect “a degree of genetic variation for CO_2 tolerance within populations,” which may allow the species to readily adapt to a long-term upward trend in the air's CO_2 content. And in the conclusion to his review, he acknowledges that “recent research has revealed that organisms could evolve within decades in response to strong pressures, which Stockwell *et al.* (2003) termed 'contemporary evolution',” citing the work of Collins and Bell (2004), to which can also be added the studies of Collins and Bell (2006) and Collins *et al.* (2006).

In another study, Gooding *et al.* (2009) measured growth rates and feeding rates of juvenile sea stars (*Pisaster ochraceus*) maintained in 246-liter aquaria that were filled with re-circulating natural sea water maintained at temperatures ranging from 5 to 21°C, and which were constantly bubbled with either ambient air of 380 ppm CO_2 or CO_2 -enriched air of 780 ppm CO_2 . The study indicated that “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 that it also responded positively to atmospheric CO_2 enrichment. More specifically, the authors stated that “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 that 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.” Last of all, their data show that 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 that it did not decline further in response to a subsequent 3°C warming at either ambient or elevated CO₂. Based on these findings, the three Canadian researchers say that “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.”

Byrne *et al.* (2009) investigated the effects of ocean acidification state (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,” which is located near Sydney. Results indicated that 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. In addition, they report that “comparative data on the effect of increased CO₂ and decreased pH as a single stressor on sea urchin fertilization and development are available for five species,” and that “these studies show that sea urchin fertilization and early development are only affected by pH < 7.4 (above 1000 ppm CO₂),” citing the work of Bay *et al.* (1993), Kurihara and Shirayama (2004) and Carr *et al.* (2006).

Seawater pH also had no effect on the longer-term development of fertilized sea urchin eggs; but the six scientists say that 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 that “it is not known whether gametes from *H. erythrogramma* adults acclimated to 24°C would have successful development in a +4°C treatment,” stating that their study “highlights the potentiality that adaptive phenotypic plasticity may help buffer the negative effects of warming, as suggested for corals.” In fact, they note that “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 the work of Farmanfarmanian and Giese (1963), Chen and Chen (1992) and Roller and Stickle (1993). Thus, all things considered, it would appear that sea urchins may be well equipped to deal with the challenges of projected ocean acidification and global warming, *and then some*, even if they were to occur simultaneously.

Citing a drop of 0.1 pH unit in the global ocean since the start of the Industrial Revolution, Richardson and Gibbons (2008) acknowledge that “such acidification of the ocean may make calcification more difficult for calcareous organisms,” resulting in the “opening [of] ecological space for non-calcifying species.” In line with this thinking, they report that Attrill *et al.* (2007) have argued that “jellyfish may take advantage of the vacant niches made available by the

negative effects of acidification on calcifying plankton," causing jellyfish to become more abundant; and they note that the latter researchers provided some evidence for this effect in the west-central North Sea over the period 1971-1995. Hence, they undertook a study to see if Attrill *et al.*'s findings (which were claimed to be the first of their kind) could be replicated on a much larger scale.

Working with data from a larger portion of the North Sea, as well as throughout most of the much vaster Northeast Atlantic Ocean, Richardson and Gibbons used coelenterate (jellyfish) records from the Continuous Plankton Recorder (CPR) and pH data from the International Council for the Exploration of the Sea (ICES) for the period 1946-2003 to explore the possibility of a relationship between jellyfish abundance and acidic ocean conditions. This work revealed that there were, as they describe it, "no significant relationships between jellyfish abundance and acidic conditions in any of the regions investigated."

In harmony with their findings, the two researchers note that "no observed declines in the abundance of calcifiers with lowering pH have yet been reported." In addition, they write that the "larvae of sea urchins form skeletal parts comprising magnesium-bearing calcite, which is 30 times more soluble than calcite without magnesium," and, therefore, that "lower ocean pH should drastically inhibit the formation of these soluble calcite precursors." Yet they report that "there is no observable negative effect of pH." In fact, they say that echinoderm larvae in the North Sea have actually exhibited "a 10-fold increase in recent times," which they say has been "linked predominantly to warming (Kirby *et al.*, 2007)." In light of this body of real-world evidence, Richardson and Gibbons concluded that "the role of pH in structuring zooplankton communities in the North Sea and further afield at present is tenuous."

Gutowska *et al.* (2008) studied the cephalopod mollusk *Sepia officinalis* and found that it "is capable of not only maintaining calcification, but also growth rates and metabolism when exposed to elevated partial pressures of carbon dioxide." Over a six-week test period, for example, they found that "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 over 500%. These findings thus led them to specifically conclude that "active cephalopods possess a certain level of pre-adaptation to long-term increments in carbon dioxide levels," and to generally conclude that our "understanding of the mechanistic processes that limit calcification must improve before we can begin to predict what effects future ocean acidification will have on calcifying marine invertebrates."

In another study, Berge *et al.* (2006) continuously supplied five 5-liter aquariums with low-food-content sea water that was extracted from the top meter of the Oslofjord outside the Marine Research Station Solbergstrand in Norway, while CO₂ was continuously added to the waters of the aquaria so as to maintain them at five different pH values (means of 8.1, 7.6, 7.4, 7.1 and 6.7) for a period of 44 days. Prior to the start of the study, blue mussels (*Mytilus edulis*) of two different size classes (mean lengths of either 11 or 21 mm) were collected from the outer part of the Oslofjord, and 50 of each size class were introduced into each aquarium, where they

were examined close to daily for any deaths that may have occurred, after which 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. Simultaneously, water temperature rose slowly from 16 to 19°C during the initial 23 days of the experiment, but then declined slightly to day 31, after which it rose rapidly to attain a maximum value of 24°C on day 39.

A lack of mortality during the first 23 days of the study showed, in the words of the researchers, that "the increased concentration of CO₂ in the water and the correspondingly reduced pH had no acute effects on the mussels." Thereafter, however, some mortality was observed in the highest CO₂ (lowest pH) treatment from day 23 to day 37, after which deaths could also be observed in some of the other treatments, which mortality Berge *et al.* attributed to the rapid increase in water temperature that occurred between days 31 and 39.

With respect to growth, the Norwegian researchers report that "mean increments of shell length were much lower for the two largest CO₂ 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 (small shells at pH = 7.6)," such that there were "no significant differences between the three aquaria within the pH range 7.4-8.1."

Berge *et al.* say their results "indicate that future reductions in pH caused by increased concentrations of anthropogenic CO₂ in the sea may have an impact on blue mussels," but that "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." Indeed, Caldeira and Wickett's calculation of the maximum level to which the air's CO₂ concentration might rise yields a value that approaches 2000 ppm around the year 2300, representing a surface oceanic pH reduction of 0.7 unit, which only drops the pH to the upper limit of the "threshold for negative effects on growth of blue mussels" found by Berge *et al.*, i.e., 7.4. Consequently, blue mussels will likely not be affected by the tendency for atmospheric CO₂ enrichment to lower oceanic pH values.

In another paper dealing with mussels, Tunnicliffe *et al.* (2009) discovered "dense clusters of the vent mussel *Bathymodiulus brevior* 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," which they studied 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." Accordingly, the authors identified four-decade-old mussels that had learned to cope with the extreme acidity of these hellish conditions, although their shell thickness and daily shell growth increments were "only about half those recorded from mussels living in water with pH > 7.8." Nevertheless, the mussels were alive and doing well in such conditions. And the six researchers note that the mussels were accompanied by "many other associated species," as reported in the study of Limen and Juniper (2006).

These several findings, according to Tunnicliffe *et al.*, attest to "the extent to which long-term adaptation can develop tolerance to extreme conditions." And just how extreme were the conditions in which the mussels lived? Referring back to the study of Caldeira and Wickett (2003) who calculated a 0.7 unit pH decline from 8.1 to 7.4 by the year 2300, considering the much *lower* pH range in which the mussels studied by Tunnicliffe *et al.* and the many species studied by Limen and Juniper were living (5.36 to 7.29), there is ample reason to believe that even *the worst case atmospheric CO₂-induced acidification scenario that can possibly be conceived* would not prove a major detriment to most calcifying sea life. Consequently, what will likely happen in the *real* world should be no problem at all.

Consequently, based on the observations presented above, claims of impending marine species extinctions due to increases in temperature and atmospheric CO₂ concentration do not appear to be supported by real-world evidence. In fact, they are typically refuted by it.

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