CO_2, GLOBAL WARMING AND CORAL REEFS: PROSPECTS FOR THE FUTURE

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Summary for Policy Makers

One of the long-recognized potential consequences of the ongoing rise in the air's CO_2 content is CO_2-induced global warming, which has been predicted to pose a number of problems for both natural and managed ecosystems in the years ahead. Of newer concern, in this regard, are the effects that the ongoing rise in the air's CO_2 content may have on coral reefs. It has been suggested, for example, that CO_2-induced global warming will do great damage to corals by magnifying the intensity, frequency, and duration of a number of environmental stresses to which they are exposed. The predicted consequences of such phenomena include ever more cases of coral disease, bleaching, and death.

Increases in the atmosphere's CO_2 content have also been postulated to possess the potential to harm coral reefs *directly*. By inducing changes in ocean water chemistry that can lead to reductions in the calcium carbonate saturation state of seawater, it has been predicted that elevated levels of atmospheric CO_2 may reduce rates of coral calcification, possibly leading to slower-growing – and, therefore, weaker – coral skeletons, and in some cases, death.

Because of these many concerns, and the logical desire of individuals and governments to do something about what they perceive to be bona fide threats to the well-being of the biosphere, it is important to have a correct understanding of the scientific basis for the potential problems that have been predicted. Hence, in the following pages we review the scientific literature on CO_2, global warming and coral reefs, in an effort to determine if the ongoing rise in the air's CO_2 content does indeed pose a threat to these incomparable underwater ecosystems. The key findings of this review are as follows:

- There is no simple linkage between high temperatures and coral bleaching.

- As living entities, corals are not only acted upon by the various elements of their environment, they also *react* or *respond* to them. And when changes in environmental factors pose a challenge to their continued existence, they sometimes take major defensive or adaptive actions to insure their survival.

- A particularly ingenious way by which almost any adaptive response to any type of environmental stress may be enhanced in the face of the occurrence of that stress would be to replace the zooxanthellae expelled by the coral host during a stress-induced bleaching episode by one or more varieties of zooxanthellae that are more tolerant of the stress that caused the bleaching.

- The persistence of coral reefs through geologic time – when temperatures were as much as 10-15°C warmer than at present, and atmospheric CO_2 concentrations were 2 to 7 times higher than they are currently – provides substantive evidence that these marine entities can successfully adapt to a dramatically changing global environment.

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Thus, the recent die-off of many corals cannot be due solely, or even mostly, to global warming or the modest rise in atmospheric CO_2 concentration over the course of the Industrial Revolution.

- The 18- to 59-cm warming-induced sea level rise that is predicted for the coming century by the IPCC – which could be greatly exaggerated if predictions of CO_2-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 year during the Holocene and can be more than double that value in certain branching corals. Rising sea levels should therefore present no difficulties for coral reefs. In fact, rising sea levels may actually have a *positive* effect on reefs, permitting increased coral growth in areas that have already reached the upward limit imposed by current sea levels.

- The rising CO_2 content of the atmosphere may induce changes in ocean chemistry (pH) that could slightly reduce coral calcification rates; but potential positive effects of hydrospheric CO_2 enrichment may more than compensate for this modest negative phenomenon.

- Theoretical predictions indicate that coral calcification rates should decline as a result of increasing atmospheric CO_2 concentrations by as much as 40% by 2100. However, real-world observations indicate that elevated CO_2 and elevated temperatures are having just the *opposite* effect.

In light of the above observations, and in conjunction with all of the material presented in this review, it is clear that climate-alarmist claims of impending marine species extinctions due to increases in both temperature and atmospheric CO_2 concentration are not only *not supported* by real-world evidence, they are actually *refuted* by it.

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Part 1: Indirect Threats

Coral bleaching ranks as probably the most frequently cited indirect negative consequence believed to result from CO_2-induced global warming. It is a phenomenon that is characterized by a loss of color in certain reef-building corals that occurs when the 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. However, if the stress is prolonged, or extreme, the corals eventually die, being deprived of their primary food source.

We begin our review of the subject by discussing, in Section 1 below, the many suspected causes of coral bleaching, almost all of which have been attributed, in one way or another, to CO_2-induced global warming. Then, in Section 2, we examine the possibility that corals can adapt to the various environmental threats they face, after which we explore in section 3 whether or not the widespread bleaching events seen in recent decades are indeed caused by global warming, or if there might be other factors at play that may be of equal or even greater importance. Lastly, in section 4, we conclude our discussion of the major indirect threats facing modern coral reefs by examining the threat of rising sea levels, which the Intergovernmental Panel on Climate Change predicts will occur over the course of the 21st Century.

1. Coral Bleaching

1.1. Temperature Effects

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 1982-83, in which widespread bleaching was reported in corals exposed to unusually high surface water temperatures (Glynn, 1988). Since that time, 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 that elevated seawater temperatures can indeed induce bleaching in corals (Hoegh-Guldberg and Smith, 1989; Jokiel and Coles, 1990; Glynn and D'Croz, 1990).

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However, just as anomalously *high* seawater temperatures have been found to be correlated with coral reef bleaching events, so too have anomalously *low* seawater temperatures been identified with this phenomenon (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); and these observations suggest that 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. Winter *et al*. (1998), for example, studied relationships between coral bleaching and nine different temperature indices, concluding that although "prolonged heat stress may be an important precondition for bleaching to occur," *sharp* temperature changes act as the "immediate trigger."

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In a related study, 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 the brief period of eight-days. Likewise, Kobluk and Lysenko (1994) observed severe coral bleaching following an 18-hour *decline* of 3°C in seawater temperature. Because the corals they studied had experienced massive bleaching two years earlier as a result of an anomalous 4°C *increase* in water temperature, the authors concluded that coral bleaching is more a function of corals not being able to adapt to the *rapidity* of a temperature change than it is of the absolute magnitude or *sign* of the change, i.e., heating or cooling.

Further evidence that high or low seawater temperatures *per se* are not the critical factors in producing coral bleaching is provided by Podesta and Glynn (1997), who examined a number of temperature-related indices of surface waters in the vicinity of Panama over the period 1970-1994. Their analysis revealed that for the two years of highest maximum monthly sea surface temperature, 1972 and 1983, coral bleaching was only reported in 1983, while 1972 produced no bleaching whatsoever, in spite of the fact that water temperatures that year were just as high as they were in 1983.

1.2. Solar Radiation Effects

The link between solar radiation and coral reef bleaching goes back over a century to when MacMunn (1903) postulated that ultraviolet radiation could be potentially damaging to corals. It wasn't until half a century later, however, that scientists began to confirm this suspicion (Catala-Stucki, 1959; Siebeck, 1988; Gleason and Wellington, 1995).

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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 that the shielded corals experienced less bleaching than the unshielded corals, and that 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. Likewise, 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; and 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, however, Glynn (1996) notes that artificially *reduced* light levels have also 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 been a difficult task. Fitt and Warner (1995), for example, reported that 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), while 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*., 1994a).

1.3. Solar Radiation-Temperature Interaction

As additional studies provided evidence for a solar-induced mechanism of coral reef bleaching (Brown *et al*., 1994b; Williams *et al*., 1997; Lyons *et al*., 1998), some also provided evidence for a solar radiation-temperature stress synergism (Gleason and Wellington, 1993; Rowan *et al*., 1997; Jones *et al*., 1998). There have been 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, in fact, 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 – that "coral bleaching occurs when the photosynthetic symbionts of corals (zooxanthellae) become increasingly vulnerable to damage by light at higher than normal temperatures." As we shall see, however, the story is considerably more complicated, more so, even, than what almost *everyone* has assumed.

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1.4. Other Phenomena

In a review of the causes of coral bleaching, Brown (1997) listed (1) elevated seawater temperature, (2) decreased seawater temperature, (3) intense solar radiation, (4) the combination of intense solar radiation and elevated temperature, (5) reduced salinity, and (6) bacterial infections. In a similar review, Meehan and Ostrander (1997) additionally listed (7) increased sedimentation and (8) exposure to toxicants. We have already commented on the four most prominent of these phenomena; and we now address the remaining four.

With respect to seawater salinity, Meehan and Ostrander (1997) noted that, 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 events or storm runoff; while high values are much more rare, typically occurring only in the vicinity of desalinization plants.

A number of studies have also clearly delineated the role of bacterial infections in causing coral reef bleaching (Ritchie and Smith, 1998); and 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) concluded that 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 that this high temperature effect may operate by enhancing the ability of the bacterium to adhere to the coral.

In discussing their findings, Kushmaro *et al*. (1998) commented on the “speculation that increased seawater temperature, resulting from global warming or El Niño events, is the direct cause of coral bleaching.” In contradiction of this presumption, they cited several studies of coral bleaching events that were not associated with any major sea surface temperature anomalies; and they explicitly stated that “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) noted that the extensive bleaching that occurred on the Great Barrier Reef during the summer of 1982 was also not associated with any major sea surface temperature increase; and they stated that “several authors have reported on the patchy spatial distribution and spreading nature of coral bleaching,” which they correctly noted is inconsistent with the global-warming-induced coral bleaching hypothesis. Instead, they noted that “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.

With respect to sedimentation, high rates have been conclusively 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,

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drilling, dredging and tourism. Nowlis *et al*. (1997) also discussed “how land development can increase the risk of severe damage to coral reefs by sediment runoff during storms.” But it has been difficult to determine just how much these phenomena have varied over the last few centuries.

Knowledge in this area took a quantum leap forward, however, with the publication of a study (McCulloch *et al*., 2003) that provided 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. According to the authors of that study, 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). Hence, when more sediments are carried to the sea by periodic flooding and more gradual longer-term changes in land use that lead to enhanced soil erosion, the resultant increases in sediment load are recorded in the Ba/Ca ratio of coral skeleton material. Inspired by these facts, 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.

Results of the analysis revealed that prior to 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, however, 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, in fact, the transport of suspended sediment to the reef increased by fully *five to ten-fold* over what had been characteristic of pre-European settlement times.

In a companion article, Cole (2003) reported that 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," a phenomenon that was also evident in the Australian data.

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

Taken together, these findings suggest that the natural course of human population growth and societal and economic development over the period of the Industrial Revolution may have predisposed coral reefs to ever-increasing incidences of bleaching and subsequent mortality via a gradual intensification of near-coastal riverine sediment transport rates.

Lastly, a number of poisonous substances are known to have the capacity to induce coral bleaching. Some of them are of human origin, such as herbicides, pesticides and even excess nutrients that ultimately make their way from farmlands to the sea (Simkiss, 1964; Pittock, 1999). 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.

2. Responding to Stress: The Power of Adaptation

Considering the many threats to the health of coral reefs in today's world of extensive socioeconomic and environmental change – including the global warming of the past century or so, which may or may not be CO_2-induced – is there any way that these incomparable repositories of underwater biodiversity can ever be expected to escape irreversible bleaching and death?

In an illuminating response to this important question, Glynn (1996) answered with an observation that is pertinent to concerns about predictions of future CO_2-induced increases in air and water temperatures. Glynn began by pointing out "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." In fact, Glynn went so far as to state that "an increase in sea warming of less than 2°C would result in a greatly *increased* [our italics] diversity of corals in certain high latitude locations."

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So how does it happen? Why, with so many local and global threats to their continued existence, do reefs persist and sometimes even flourish? To what do they owe their amazing resilience? And how do they meet the physiological challenges presented by the combination of high light intensities and water temperatures that many climate alarmists consider to be the primary cause of mass coral bleaching? In a word, the answer is *adaptation*.

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Living organisms are resilient. Various lifeforms can tolerate temperatures from below freezing to the boiling point of water; while others inhabit niches where light intensity varies from complete darkness to full sunlight. One reason for this great versatility is that, *given time to adapt*, nearly all living organisms can learn to survive in conditions well outside their normal zones of environmental tolerance. As noted by Gates and Edmunds (1999), results of numerous studies indicate that "corals routinely occupy a physically heterogeneous environment," which "suggests they should possess a high degree of biological flexibility." And indeed they do, as evidenced by their successful responses to the different threats that cause coral bleaching, which are examined in the following subsections.

2.1. Response to Solar Radiation Stress

With respect to coral responses to stress imposed by high solar irradiance, one simple example of such adaptation 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). It has also been demonstrated that 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 adaptive mechanism proposed to lessen the stress of solar irradiance is coral tissue retraction, according to Brown *et al*. (1994a), who 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. Results of their analysis showed that extreme tissue retraction was observed approximately 85 minutes after initial sub-aerial coral exposure. Tissue retraction, however, did not involve any reduction in chlorophyll concentration or algae symbiont abundance; and the tissues expanded over the coral skeletons to pre-retraction conditions following the return of the tide. The adaptive benefits of tissue retraction, according to the authors, "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."

Another intriguing idea was proposed by Nakamura and van Woesik (2001), who upon evaluating the bleaching of large and small coral colonies along the western coast of Okinawa, Japan, during the summers of 1998 and 2001, argued that small coral colonies should survive thermal and light stress more readily than large coral colonies based on mass transfer theory, which suggests that rates of passive diffusion are more rapid for small colonies than for large colonies. Still another reason why large coral colonies suffer more than small colonies during environmental conditions conducive to bleaching is the fact that small *Acropora* recruits,

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according to Bena and van Woesik (2004), "contain high concentrations of fluorescent proteins (Papina *et al*., 2002), which have photoprotective properties (Salih *et al*., 2000)," and they note that "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, the earth appears to possess an amazingly effective meteorological "ThermoSolarStat" that jumps into operation to suppress the intensity of solar radiation to which corals are exposed whenever dangerously-high water temperatures are approached, and which thereby tends to suppress further increases in water temperature that may be prompted by increases in the intensity of *any* thermal forcing factor, such as the CO_2-augmented greenhouse effect.

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How does the mechanism, which is composed of at least two major components, work? 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. However, as Sud *et al*. (1999) have demonstrated in elucidating the functioning of the first of the ThermoSolarstat's two primary components (based on data obtained from the Tropical Ocean Global Atmosphere Coupled Ocean-Atmosphere Response Experiment), 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.

Initially, according to this concept, the tropical ocean acts as a net receiver of energy in its warming phase; but as SSTs reach 28-29°C, the cloud-base airmass 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. This particular component of the atmosphere's ThermoSolarstat, i.e., the component that creates towering cumulonimbus clouds at the appropriate critical SST, also greatly reduces the flux of solar radiation received at the surface of the sea, thereby providing a dual approach to relieving the two main stresses (solar and

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thermal) that may be experienced by corals that are teetering on the brink of potentially irreversible bleaching.

Some other intriguing observations also point to the existence of a natural phenomenon of this nature. Satheesh and Ramanathan (2000), for example, determined that 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°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 that this atmospheric heating would decrease cloud-layer relative humidity and reduce boundary-layer mixing, thereby leading to a 25-50% drop in daytime cloud cover relative to that of an aerosol-free atmosphere, which could well negate the surface cooling effect suggested by the findings of Satheesh and Ramanathan. But in a test of this hypothesis based on data obtained from the Extended Edited Cloud Report Archive, Norris (2001) determined that daytime low-level ocean cloud cover (which tends to cool the water surface) not only did *not* decrease from the 1950s to 90s, it actually *increased* ... in both the Northern and Southern Hemispheres and at essentially all hours of the day.

Commenting on this finding, Norris remarked that "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'." Hence, he says, "other processes must be compensating," one of which, we suggest, could well be the one described by Sud *et al*.

Another process – and our proposed second component of earth's ThermoSolarstat – is the "adaptive infrared iris" phenomenon that has been described by Lindzen *et al*. (2001). Working with upper-level cloudiness data obtained from the Japanese Geostationary Meteorological Satellite and SST data obtained from the National Centers for Environmental Prediction, the inquisitive 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% for each 1°C increase in the SST of the cloudy regions.

"Essentially," in the words of the scientists, "the cloudy-moist 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 substantial is this phenomenon, Lindzen *et al*. are confident it could "more than cancel all the positive feedbacks in the more sensitive current climate models," which are routinely used to predict the climatic consequences of projected increases in atmospheric CO_2 concentration.

All this is well and good; the meteorological aspects of the ThermoSolarstat are clearly supported by significant bodies of real-world data. But is there any real-world evidence the ThermoSolarstat has actually been instrumental in preventing coral bleaching that would

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otherwise have occurred during periods of unusually high thermal stress? The answer, of course, is *yes*; and it comes in an important paper published by Mumby *et al*. (2001), wherein they 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."

With respect to the great El Niño of 1998, Mumby and his colleagues determined that 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. However, 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."

As living entities, corals are not only acted upon by the various elements of their environment, they also *react* or *respond* to them.

What provided the relief from extreme sun and heat, without which, Mumby *et al*. have concluded, "mass bleaching would have occurred"? As he and his associates describe it, "exceptionally high cloud cover significantly reduced the number of sun hours during the summer of 1998," much as one would have expected earth's ThermoSolarstat to have done in the face of such anomalously high SSTs. The marine scientists also note that 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."

In conclusion, although the ThermoSolarstat 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 insure that sufficiently large numbers of corals survive to perpetuate their existence, since living reefs have persisted over the eons in spite of the continuing recurrence of these ever-present environmental threats. And perhaps that is how it has always been, although there are currently a host of unprecedented anthropogenic forces of site-specific origin that could well be weakening the abilities of some species to tolerate the types of thermal and solar stresses they have successfully "weathered" in the past.

2.2. Response to Temperature Stress

As living entities, corals are not only acted upon by the various elements of their environment, they also *react* or *respond* to them. And when changes in environmental factors pose a challenge to their continued existence, they sometimes take major defensive or adaptive actions to insure their survival. A simple but pertinent example of one form of this phenomenon is *thermal adaptation*, which feature has been observed by several researchers to operate in corals.

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Fang *et al*. (1997), for example, experimented with samples of the coral *Acropora grandis* that were 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, Fang *et al*. report that "samples taken from the same area did not even start bleaching until six days after exposure to 33°C temperatures."

Similar findings have been reported by Middlebrook *et al*. (2008), who 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 that were maintained at the mean local ambient temperature (27°C) and exposed to natural reef-flat summer daily light levels. Then, two weeks prior to a simulated bleaching event -- where water temperature was raised to a value of 34°C for a period of six days -- they boosted the water temperature in one of the tanks to 31°C for 48 hours, while 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 pre-heating treatment, while in the fourth tank they had no pre-heating nor any simulated bleaching event. And at different points throughout the study, they measured photosystem II efficiency, xanthophyll and chlorophyll *a* concentrations, and *Symbiodinium* densities.

Results of the study indicated that the symbionts of the corals that were exposed to the 48-hour pre-bleaching thermal stress "were found to have more effective photoprotective mechanisms," including "changes in non-photochemical quenching and xanthophyll cycling," and they further determined that "these differences in photoprotection were correlated with decreased loss of symbionts, with those corals that were not pre-stressed performing significantly worse, losing over 40% of their symbionts and having a greater reduction in photosynthetic efficiency," whereas "pre-stressed coral symbiont densities were unchanged at the end of the bleaching." In light of these findings, Middlebrook *et al*. (2008) 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."

Moving out of the laboratory and into the real world of nature, 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, with the goal of documenting 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), while prior to this period, the sites had experienced an additional seven bleaching events and fifteen cyclones, as well as several *Acanthaster planci* outbreaks.

Results of the monitoring program revealed that the impacts of the bleaching events were variable among the different study locations. In their ten-year survey, for example, they

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observed three different 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." In addition, they report that "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)."

Commenting on their and other researchers' observations, 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," such that "coral colonies and/or their endosymbiotic zooxanthellae may be phenotypically (acclimation) and possibly genotypically (adaptation) resistant to bleaching events," citing the work of Rowan *et al*. (1997), Hoegh-Guldberg (1999), Kinzie *et al*. (2001) and Coles and Brown (2003) in support of this conclusion.

Other researchers have also confirmed the phenomenon of thermal adaptation in coral reefs. 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), in particular, they found in a survey of three representative reefs, which they conducted in 1987, that remaining live coral cover was only 3% of what it had been prior to the occurrence of 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 that "the recovery of the reefs' framework would take centuries, and recovery of live coral cover, decades." In 2002, therefore, nearly 20 years after the disastrous coral-killing warming, they returned to see just how prescient they might have been after their initial assessment of the El Niño's horrendous damage, quantifying "the live coral cover and species composition of five reefs, including the three previously assessed in 1987."

So what did they find?

The two researchers report that overall mean live coral cover increased nearly *five-fold*, from 2.99% in 1987 to 14.87% in 2002, at the three sites studied during both periods, while the mean live coral cover of all five sites studied in 2002 was 22.7%. In addition, they found that "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."

With respect to the subject of thermal tolerance, however, the most interesting aspect of the study was the fact that a second major El Niño occurred between the two assessment periods; and Guzman and Cortes state that "the 1997-1998 warming event around Cocos Island was more intense than all previous El Niño events," noting that temperature anomalies "above 2°C lasted 4 months in 1997-1998 compared to 1 month in 1982-83." Nevertheless, they report that

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"the coral communities suffered a *lower* and *more selective* mortality in 1997-1998 [our italics], as was also observed in other areas of the eastern Pacific (Glynn *et al*., 2001; Cortes and Jimenez, 2003; Zapata and Vargas-Angel, 2003)," which is indicative of some type of *thermal adaptation* following the 1982-83 El Niño.

One year later in a paper published in *Marine Biology*, Maynard *et al*. (2008) described how they analyzed the bleaching severity of three genera of corals (*Acropora*, *Pocillopora* and *Porites*) via underwater video surveys of five sites in the central section of Australia's Great Barrier Reef in late February and March of 1998 and 2002, while contemporary sea surface temperatures were acquired from satellite-based Advanced Very High Resolution Radiometer data that were calibrated to local ship- and drift buoy-obtained measurements, and surface irradiance data were obtained "using an approach modified from that of Pinker and Laszlo (1991)."

With respect to temperature, the four researchers report that "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 that "average surface irradiance during the 2002 thermal anomaly was 15.6-18.9% higher than during the 1998 anomaly." Nevertheless, they found that "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, they found that the "coral genera most susceptible to thermal stress (*Pocillopora* and *Acropora*) showed the greatest increase in tolerance."

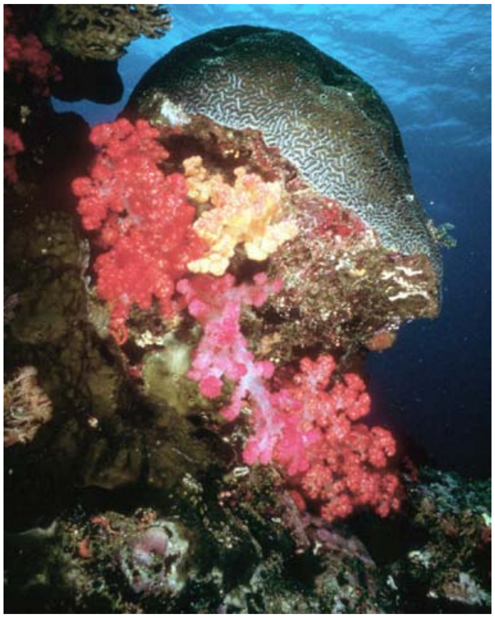
In discussing their findings, Maynard *et al*. write that they are "consistent with previous studies documenting an increase in thermal tolerance between bleaching events (1982-1983 vs. 1997-1998) in the Galapagos Islands (Podesta and Glynn, 2001), the Gulf of Chiriqi, the Gulf of Panama (Glynn *et al*.,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

As for the significance of these and other observations, the Australian scientists say that "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 the work of Coles and Brown (2003) and Riegl (1999, 2002). In addition, they note that "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." Above and beyond that, however, they say their results additionally suggest "a capacity for acclimatization or adaptation."

In concluding their paper, Maynard *et al*. say "there is emerging evidence of high genetic structure within coral species (Ayre and Hughes, 2004)," which suggests, in their words, that "the capacity for adaptation could be greater than is currently recognized." Indeed, as stated by Skelly *et al*. (2007), "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." Consequently, it can be appreciated that if global warming were to start up again (it has been in abeyance for about the last decade), it need not spell *the end* for earth's highly adaptable corals.

But how is it done? How do corals adjust to rising temperatures?

One adaptive mechanism that corals have developed to survive the thermal stress of high water temperature is to replace the zooxanthellae expelled by the coral host during a stress-induced bleaching episode by one or more varieties of zooxanthellae that are more heat tolerant, a phenomenon we describe in greater detail in the next section of our report. Another mechanism is to produce 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 that sub-tidal specimens of *Goniopora djiboutiensis* typically have much lower constitutive levels of a 70-kD heat shock protein than do their intertidal con-specifics; and they have shown that corals transplanted from sub-tidal to intertidal locations (where temperature extremes are greater and more common) typically increase their expression of this heat shock protein.



Similar results have been reported by Roberts *et al*. (1997) in field work with *Mytilus californianus*. In addition, Gates and Edmunds (1999) have 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, which is followed by another heat shock protein increase at the 48-hour point of exposure to elevated water temperature. They state that 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 that the second increase "indicates another shift in protein turnover perhaps associated with an attempt to acclimatize to the more chronic level of temperature stress."

So how resilient are corals in this regard? No one knows for sure; but they've been around a very long time, during which climatic conditions have changed dramatically, from cold to warm and back again, over multiple glacial and interglacial cycles. And in this regard, we see no reason why history cannot be expected to successfully repeat itself, even as the current interglacial experiences its "last hurrah."

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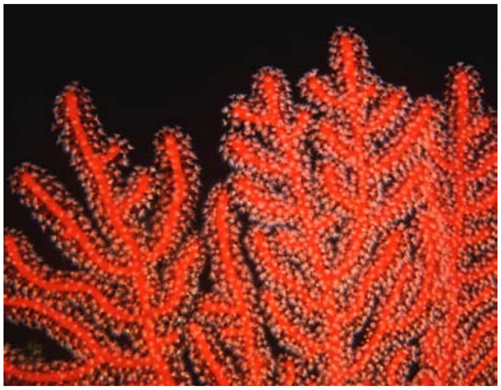
2.3. Symbiont Shuffling

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, of which several are typically found in each species of coral (Trench, 1979; Rowan and Powers, 1991; Rowan *et al*., 1997). Consequently, a particularly ingenious way by which almost any adaptive response to any type of environmental stress may be enhanced in the face of the occurrence of that stress would be to replace the zooxanthellae expelled by the coral host during a stress-induced bleaching episode by one or more varieties of zooxanthellae that are more tolerant of the stress that caused the bleaching.

Coral bleaching is actually an adaptive strategy for "shuffling" symbiont genotypes to create associations better adapted to new environmental conditions that challenge the *status quo* of reef communities.

Rowan *et al*. (1997) have suggested that this phenomenon occurs in many of the most successful Caribbean corals that act as hosts to dynamic multi-species communities of symbionts, and that "coral communities may adjust to climate change by recombining their existing host and symbiont genetic diversities," thereby reducing the amount of damage that might subsequently be expected from another occurrence of anomalously high temperatures. In fact, Buddemeier and Fautin (1993) have suggested that coral bleaching is actually an adaptive strategy for "shuffling" symbiont genotypes to create associations better adapted to new environmental conditions that challenge the *status quo* of reef communities. Saying essentially the same thing in yet another way, Kinzie (1999) has suggested that coral bleaching "might not be simply a breakdown of a stable relationship that serves as a symptom of degenerating environmental conditions," but that it "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."



This process of replacing less-stress-tolerant symbionts by more-stress-tolerant symbionts is also supported by the investigations of Rowan and Knowlton (1995) and Gates and Edmunds (1999); and the strategy seems to be working, for as Glynn (1996) has 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 that coral bleaching events "may be frequent and part of the expected cycle." Gates

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and Edmunds (1999) additionally report that "several of the prerequisites required to support this hypothesis have now been met," and 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." In fact, this phenomenon may provide the explanation for the paradox posed by Pandolfi (1999), i.e., that "a large percentage of living coral reefs have been degraded, yet there are no known extinctions of any modern coral reef species." Surely, this result is exactly what would be expected if periods of stress lead to the acquisition of more-stress-resistant zooxanthellae by coral hosts.

In spite of this early raft of compelling evidence for the phenomenon, Hoegh-Guldberg (1999) challenged the symbiont shuffling hypothesis on the basis that the stress-induced replacement of less-stress-tolerant varieties of zooxanthellae by more-stress-tolerant varieties "has never been observed." Although true at the time it was written, a subsequent series of studies has produced the long-sought proof that transforms the hypothesis into fact.

Baker (2001) conducted an experiment in which he transplanted corals of different combinations of host and algal symbiont from shallow (2-4 m) to deep (20-23 m) depths and vice versa. After 8 weeks nearly half of the corals transplanted from deep to shallow depths had experienced partial or severe bleaching, whereas none of the corals transplanted from shallow to deep depths bleached. After one year, however, and despite even more bleaching at shallow depths, upward transplants showed no mortality, but nearly 20 percent of *downward* transplants had died. Why?

The symbiont shuffling hypothesis explains it this way. The corals that were transplanted upwards were presumed to have adjusted their algal symbiont distributions, via bleaching, to favor more tolerant species, whereas the corals transplanted downward were assumed to not have done so, since they did not bleach. Baker suggested that 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, as he continued, "suboptimal host-symbiont combinations persist, leading eventually to significant host mortality." Consequently, Baker proposed that coral bleaching may "ultimately help reef corals to survive." And it may also explain why reefs, though depicted by climate alarmists as environmentally fragile, have survived the large environmental changes experienced throughout geologic time.

One year later Adjeroud *et al*. (2002) provided additional evidence for the veracity of the symbiont shuffling hypothesis as a result of their assessment 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. However, they report

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that 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)." In fact, they report that between 1991 and 1992 total coral cover dropped from 51.0% to 24.2%, but that "coral cover did not decrease between 1994 and 1995."

In discussing these observations, Adjeroud *et al*. write that 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," noting that "one may assume that these coral colonies and/or their endosymbiotic zooxanthellae were phenotypically and possibly genotypically resistant to bleaching events," which is exactly what the symbiont shuffling hypothesis would predict. Hence, they further state that "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."

In the same year, Brown *et al*. (2002) published the results of an even longer 17-year 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. As they describe it, "many corals bleached during elevated sea temperatures in May 1991 and 1995, but no bleaching was recorded in 1997." In addition, they report that "in May 1998 very limited bleaching occurred although sea temperatures were higher than previous events in 1991 and 1995 (Dunne and Brown, 2001)." What is more, when bleaching did take place, they say "it led only to partial mortality in coral colonies, with most corals recovering their color within 3-5 months of initial paling," once again providing real-world evidence for what is predicted by the symbiont shuffling hypothesis.

The following year, Riegl (2003) reviewed what is known about the responses of real-world coral reefs to high-temperature-induced bleaching, focusing primarily on the Arabian Gulf, which experienced high-frequency recurrences of temperature-related bleaching in 1996, 1998, and 2002. In response to these high-temperature events, Riegl notes that *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 actually *recovered* along the coast of Dubai between Jebel Ali and Ras Hasyan. As a result, Riegl states that "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 that "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."

In a contemporaneous paper, Kumaraguru *et al*. (2003) reported the results of a study wherein they assessed the degree of damage inflicted upon 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

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event that produced monthly mean sea surface temperatures of 29.8 to 32.1°C from April through June of 2002, after which they assessed the degree of recovery of the reefs. They determined that "a minimum of at least 50% and a maximum of 60% bleaching were noticed among the six different sites monitored." However, as they continue, "the corals started to recover quickly in August 2002 and as much as 52% recovery could be noticed." By comparison, they note that "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," i.e., to achieve what was experienced in one *month* in 2002. Consequently, in words descriptive of the concept of symbiont shuffling, the Indian scientists say "the process of natural selection is in operation, with the growth of new coral colonies, and any disturbance in the system is only temporary." Consequently, as they conclude in the final sentence of their paper, "the corals will resurge under the sea."

Although these several 2001-2003 findings were very significant, a quartet of papers published in 2004 - two in *Nature* and two in *Science* - finally "sealed the deal" with respect to establishing the symbiont shuffling hypothesis as a fact of life, and an ubiquitous one at that.

Writing in *Nature*, Rowan (2004) described how he measured the photosynthetic responses of two zooxanthellae genotypes or clades -- *Symbiodinium C* and *Symbiodinium D* -- to increasing water temperature, finding that the photosynthetic prowess of the former decreased at higher temperatures while that of the latter increased. He then noted that "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 that "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*," concluding that these observations "indicate that symbiosis recombination may be one mechanism by which corals adapt, in part, to global warming."

Clinching the concept, was the study of Baker *et al*. (2004), who "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 that "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." Even more importantly, they found that "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*. summarized their results by stating they indicate that "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 predominates. Hence, they concluded their landmark paper by noting that the symbiont

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changes they observed "are a common feature of severe bleaching and mortality events," and by predicting that "these adaptive shifts will increase the resistance of these recovering reefs to future bleaching."

Meanwhile, over at *Science*, 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. Also, in a somewhat analogous study, Little *et al*. (2004) described how they 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 wrote that the results of their study show that "the repopulation of the symbiont community involved residual populations within *Briareum* sp., as well as symbionts from the surrounding water," noting that "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 that "these symbioses also have the flexibility to establish new associations with symbionts from an environmental pool." Similarly, Little *et al*. reported that "initial uptake of zooxanthellae by juvenile corals during natural infection is nonspecific (a potentially adaptive trait)," and that "the association is flexible and characterized by a change in (dominant) zooxanthella strains over time."

Lewis and Coffroth thus concluded that "the ability of octocorals to reestablish symbiont populations from multiple sources provides a mechanism for resilience in the face of environmental change," while Little *et al*. concluded that the "symbiont shuffling" observed by both groups "represents a mechanism for rapid acclimatization of the holobiont to environmental change." Hence, the results of both studies demonstrate the reality of a phenomenon whereby corals may indeed "grasp victory from the jaws of death" in the aftermath of a severe bleaching episode, which is also implied by the *fact* - cited by Lewis and Coffroth - that "corals have survived global changes since the first scleractinian coral-algal symbioses appeared during the Triassic, 225 million years ago."

In the years that have followed since 2004, many more studies have further elevated the symbiont shuffling hypothesis to a full-fledged *theory*.

Writing in the journal *Marine Ecology Progress Series*, Chen *et al*. (2005) studied 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. Results of the analysis revealed two levels of symbiont shuffling in host corals: (1) between *Symbiodinium* phylotypes C and D, and (2) among different variants within each phylotype. Furthermore, the most significant changes in symbiont composition occurred at times of significant increases in seawater temperature

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during late spring/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."

Also in 2005, Van Oppen *et al*. 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 some 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. Results of the analysis revealed that "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." However, they say "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."

With respect to the post-bleaching abundance of clade D zooxanthellae at the high heat-stress site, the Australian researchers say they suspect it was due to "a proliferation in the absolute abundance of clade D within existing colonies that were previously dominated by clade C zooxanthellae," and that in the four to five months before sampling them, "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.

In 2006, working within Australia's Great Barrier Reef system, Berkelmans and van Oppen investigated the thermal acclimatization potential of *Acropora millepora* corals to rising temperatures through transplantation and experimental manipulation, finding that 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 same two researchers reported similar findings following the occurrence of a natural bleaching event.

Prior to the bleaching event, Jones *et al*. report that "*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 further report that "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," while corals harboring a mix of *Symbiodinium* C2 and D were "mostly pale in appearance." Then, 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 of which types had not been detected in any of the corals prior to bleaching; and they report that "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%)." In addition, they report that all of the colonies that

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harbored low levels of D-type symbionts prior to the bleaching event survived and changed from clade C2 to D predominance.

In conclusion, Jones *et al*. say that "as a direct result of the shift in symbiont community, the Miall Island *A. millepora* population is likely to have become more thermo-tolerant," as they note that "a shift from bleaching-sensitive type C2 to clade D increased the thermal tolerance of this species by 1-1.5°C." As a result, 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 bleaching-sensitive symbionts in favor of symbionts that make the new holobiont more thermally tolerant." In fact, they state that 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," a finding that bodes especially well for earth's corals in a warming climate.

In a much larger geographical study, Lien *et al*. (2007) examined the symbiont diversity in a scleractinian coral, *Oulastrea crispata*, throughout its entire latitudinal distribution range in the West Pacific, i.e., from tropical peninsular Thailand (<10°N) to high-latitudinal outlying coral communities in Japan (>35°N), convincingly demonstrating in the words of the six scientists who conducted the study, "that phylotype D is the dominant *Symbiodinium* in scleractinian corals throughout tropical reefs and marginal outlying non-reefal coral communities." In addition, they learned that this particular symbiont clade "favors 'marginal habitats' where other symbionts are poorly suited to the stresses, such as irradiance, temperature fluctuations, sedimentation, etc." Being 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, according to Lien *et al*., "a flexible means for corals to *routinely cope* [our italics] with environmental heterogeneities and survive the consequences (e.g., recover from coral bleaching)."

Also in 2007, Mieog *et al*. 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 eleven different locations on Australia's Great Barrier Reef for evidence of the presence of background *Symbiodinium* clades. Results of the analysis showed that "ninety-three percent of the colonies tested were dominated by clade C and 76% of these had a D background," the latter of which symbionts, in their words, "are amongst the most thermo-tolerant 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." Consequently, Mieog *et al*. concluded that the clade D symbiont backgrounds detected in their study can potentially act as *safety-parachutes*, "allowing corals to become more thermo-tolerant through symbiont shuffling as seawater temperatures rise due to global warming." As a result, they suggest that symbiont shuffling is likely to play a role in the way

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"corals cope with global warming conditions," leading to new competitive hierarchies and, ultimately, "the coral community assemblages of the future."

In spite of the hope symbiont shuffling provides -- that the world's corals will indeed be able to successfully cope with the possibility of future global warming, be it anthropogenic-induced or natural -- some researchers have claimed that few coral symbioses host more than one type of symbiont, which has led alarmists to argue that symbiont shuffling is not an option for most coral species to survive the coming thermal onslaught of global warming. But is this claim correct? Not according to the results of Apprill and Gates (2007).

Working with samples of the widely distributed massive corals *Porites lobata* and *Porites lutea* - which they collected from Kaneohe Bay, Hawaii - Apprill and Gates compared the identity and diversity of *Symbiodinium* symbiont types obtained using cloning and sequencing of *internal transcribed spacer region 2* (ITS2) with that obtained using the more commonly applied downstream analytical techniques of *denaturing gradient gel electrophoresis* (DGGE).

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

In a "perspective" that accompanied Apprill and Gates' important paper, van Oppen (2007) wrote that "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 of corals to acclimatize to environmental perturbations through changes in the composition of their algal endosymbiont community," which assessment, it is almost unnecessary to say, suggests a far greater-than-previously-believed ability to do just that in response to any further global warming that might occur.

In a contemporaneous study, Baird *et al*. (2007) also discount the argument that symbiont shuffling is not an option for most coral species, because, "as they see it," 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, of course, is that most if not all of them likely do; for they note that "biogeographical data suggest that when species need to respond to novel environments, they have the flexibility to do so."

So how and when might such sub-clade changes occur? Although most prior research in this area has been on adult colonies switching symbionts in response to warming-induced bleaching episodes, Baird *et al*. suggest that "change is more likely to occur between generations," for

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initial coral infection typically occurs in larvae or early juveniles, which are much more flexible than adults. In this regard, for example, they note that "juveniles of *Acropora tenuis* regularly harbor mixed assemblages of symbionts, whereas adults of the species almost invariably host a single clade," and they indicate that larvae of *Fungia scutaria* ingest symbionts from multiple hosts, although they generally harbor but one symbiont as adults.

Because of these facts, 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 to new heights 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 the course of an entire year, which they then studied by means of molecular techniques to identify unique *internal transcribed spacer-2* (ITS-2) types of *ribosomal DNA* (rDNA), in a project self-described as "the most targeted and exhaustive sampling effort ever undertaken for any group of *Symbiodinium*-bearing hosts."

Throughout the course of their analysis, 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. In addition, they report that "the majority of mixed genotypes observed during this survey were usually harbored by the smallest hosts." As a result, the authors speculate that "juvenile foraminifera may be better able to switch or shuffle heterogeneous symbiont communities than adults," so that as juveniles grow, "their symbiont communities become 'optimized' for the prevailing environmental conditions," suggesting that this phenomenon "may be a key element in the continued evolutionary success of these protests in coral reef ecosystems worldwide."

In support of the above statement, we additionally cite the work of Mumby (1999), who analyzed the population dynamics of juvenile corals in Belize, both prior to, and after, a massive coral bleaching event in 1998. Although 70 to 90% of adult coral colonies were severely bleached during the event, only 25% of coral *recruits* exhibited signs of bleaching. What is more, one month after the event, it was concluded that "net bleaching-induced mortality of coral recruits ... was insignificant," demonstrating the ability of juvenile corals to successfully weather such bleaching events.

In light of these several observations, earth's corals will likely be able to successfully cope with the possibility of further increases in water temperatures, be they anthropogenic-induced 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 throughout numerous similar periods during a number of prior interglacial periods; and there is no reason to believe they cannot do it again, if the need arises.

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2.4. Bacterial Shuffling

One final adaptive bleaching mechanism is discussed in the literature by Reshef *et al*., (2006), who developed a case for what they call the Coral Probiotic Hypothesis. This concept, in their words, "posits that a dynamic relationship exists between symbiotic microorganisms and environmental conditions which brings about the selection of the most advantageous coral holobiont."

This concept is analogous to the *adaptive bleaching hypothesis* of Buddemeier and Fautin (1993), or what was referred to in the preceding section as *symbiont shuffling*, wherein 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 that are better suited to the stress conditions. In fact, 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 case by the corals rearranging their *bacterial* populations (Bacterial Shuffling).

In seeking evidence for their hypothesis, the team of Israeli researchers concentrated their efforts on looking for examples of corals developing resistance to *emerging diseases*. This approach makes sense, because corals lack an adaptive immune system, i.e., they possess no antibodies (Nair *et al*., 2005), and they 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*. begin by describing 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*. But they then report that (1) "during the last two years *O. patagonica* has developed resistance to the infection by *V. shiloi*," that (2) "*V. shiloi* can no longer be found on the corals," and that (3) "*V. shiloi* that previously infected corals are unable to infect the existing corals." In fact, they say that "by some unknown mechanism, the coral is now able to lyse the intracellular *V. shiloi* and avoid the disease," and 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 the *coral probiotic phenomenon*, as described by Reshef *et al*., must be what produced the welcome results.

With respect to the future of earth's corals within the context of global warming, the Israeli scientists note that "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." However, they report that considerable evidence has been collected in support of the *adaptive bleaching hypothesis*; and they emphasize that the hundreds of different bacterial

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species associated with corals "give the coral holobiont an *enormous* [our italics] genetic potential to adapt *rapidly* [our italics] to changing environmental conditions." In fact, they say "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 that "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 every coral.

2.5. A Role for Elevated CO_2?

It is a general principle – applicable to the vast majority of all plants – that as temperatures rise, photorespiration consumes ever more of the recently-fixed products of photosynthesis, creating a decrease in the rate of net carbon uptake (Hanson and Peterson, 1986) and thereby reducing the plant's ability to withstand any number of environmental stresses. If more CO_2 can be delivered to the site of photosynthesis, however, more CO_2 can be made available to compete with oxygen for active sites on the carboxylating/oxygenating enzyme *rubisco* (Grodzinski *et al*., 1987). Hence, anything that increases the concentration of CO_2 at the site of photosynthesis should enhance the net fixation of carbon more at higher temperatures than it does at lower temperatures, as atmospheric CO_2 enrichment clearly has been shown to do in numerous terrestrial plants (Idso *et al*., 1987; Mortensen, 1987; Idso and Idso, 1994).

One of the major consequences of this phenomenon is that the optimal temperature for plant growth generally rises with CO_2 enrichment. For terrestrial C_3 plants, Long (1991) has calculated that their optimal temperatures should rise by about 5°C for a 300 ppm increase in the air's CO_2 content; while in an analysis of the results of seven studies that experimentally evaluated this response in terrestrial C_3 plants, Idso and Idso (1994) found plant optimal temperature to rise by approximately 6°C for such a rise in atmospheric CO_2 concentration. In addition, Chen *et al*. (1994) demonstrated that there may even be a modest increase in terrestrial C_4 plant optimal temperature in response to atmospheric CO_2 enrichment.

At the highest temperatures experienced by plants, elevated CO_2 concentrations are especially helpful. When photorespiration is so high as to drive net carbon fixation all the way to zero, for example, more CO_2 can sometimes mean the difference between a plant's living or dying (Kriedemann *et al*., 1976; Converse and George, 1987), as it may enable the plant to maintain a positive carbon exchange rate, when plants growing under ambient CO_2 concentrations exhibit negative rates that ultimately lead to their demise. Idso *et al*. (1995) demonstrated this fact explicitly with a terrestrial C_3 plant, while Idso *et al*. (1989) demonstrated it with a floating *aquatic* C_3 plant. Hence, it is not illogical to think that as the air's CO_2 content continues to rise, forcing more CO_2 to dissolve in the surface waters of the world's oceans, this same phenomenon may operate to protect the algal symbionts of the oceans' corals from dying at what would normally have been a lethal water temperature under pre-industrial atmospheric CO_2 concentrations.

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A likely major consequence of this phenomenon is that coral reefs would *expand* their ranges throughout the world in the face of a CO_2-induced global warming, or even in the face of a non-CO_2-induced global warming, if atmospheric CO_2 concentrations rose concurrently for some other reason. With temperatures and CO_2 concentrations both rising everywhere, for example, coral symbionts would be able to extend their ranges poleward in response to the global warming; and with the protective effect of higher aqueous CO_2 concentrations helping them to withstand the stress of increased temperature at the other end of their latitudinal distributions, they would be able to continue to survive in the warmest regions of their ranges.

But what about the coral animals that act as hosts to the zooxanthellae? Would elevated levels of CO_2 help them in some way, so that they too could withstand a temperature increase in the warmest regions of their ranges? Although no experiments have broached this subject, some real-world terrestrial observations suggest that such might well be the case.

A crude terrestrial analogy to the coral/zooxanthellae relationship of the aquatic realm – but where the animal provides little of value to the plant that sustains it – is that of the butterfly and the plant species upon which its larvae feed. It is thus instructive to observe that in a study of shifts in the ranges of more than 50 European butterfly species over the past century, Parmesan *et al*. (1999) found that most of them moved northward in response to a regional warming of approximately 0.8°C. However, in the words of the authors, "nearly all northward shifts involved extensions at the northern boundary with the southern boundary remaining stable" – such as would be expected for the plants on which they feed in the face of concurrent increases in air temperature and atmospheric CO_2 concentration – so that "most species effectively expanded the size of their range when shifting northwards." Furthermore, this northward range expansion did not displace other butterflies from the southern portions of their ranges, so that the numbers of butterfly species inhabiting many areas of the continent, or butterfly species richness, *increased*. And in a similar study of shifts in the ranges of an equally large number of British bird species (which feed on such things as butterfly larvae), Thomas and Lennon (1999) found essentially the same behavior: northern boundaries moved northward in response to regional warming and concurrent increases in atmospheric CO_2, while southern boundaries remained constant, which thus increased the diversity of bird species inhabiting many of the affected areas.

> The rising CO_2 concentration of earth's atmosphere may give corals an enhanced ability to successfully cope with the specific stress of global warming.

Thus we see there are a number of ways in which corals may adapt to high temperature and solar radiation stresses. In addition, the rising CO_2 concentration of earth's atmosphere may give them an enhanced ability to successfully cope with the specific stress of global warming. And certain terrestrial plant-animal associations exhibit responses to CO_2 and global warming that are in harmony with predictions based upon this latter phenomenon, thereby providing a

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solid basis for being optimistic about the fate of earth's coral reef ecosystems in the face of the ongoing rise in the air's CO_2 content.

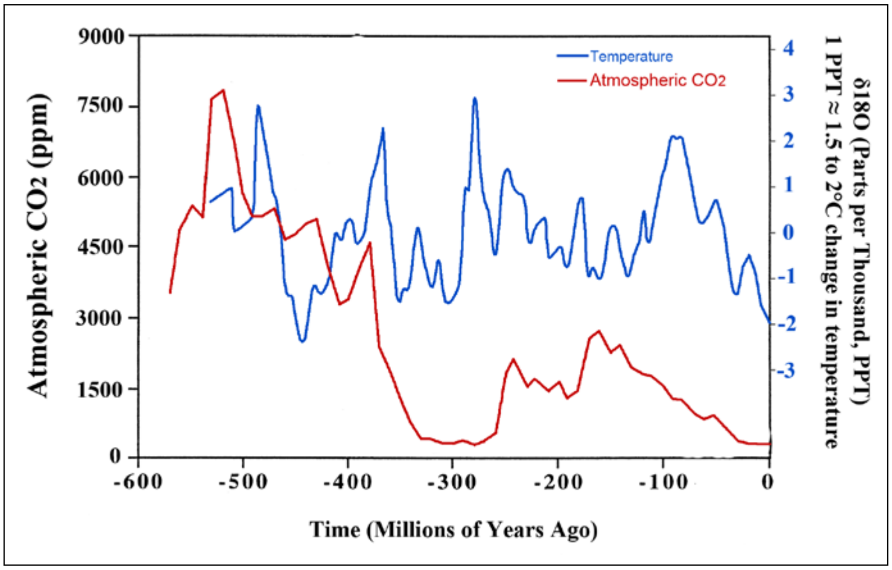
3. Massive, Widespread Coral Bleaching

3.1. Is it Caused by Global Warming?

In an impressive analysis of one of the major environmental questions of our day, Hoegh-Guldberg (1999) concludes that "coral bleaching is due to warmer than normal temperatures" and that "increased sea temperature is the primary reason for why coral bleaching has occurred with increasing intensity and frequency over the past two decades." As outlined in the preceding sections, there is indeed a significant body of evidence that points towards these conclusions; but there is much other evidence that points to alternative possibilities.

Consider, for example, the persistence of coral reefs through geologic time, which provides substantive evidence that these ecological entities can successfully adapt to a dramatically changing global environment (Veron, 1995). What can their history tell us about bleaching and global warming in our day?

The earliest coral reefs date to the Palaeozoic Era, over 450 million years ago (Hill, 1956); while the scleractinian corals, which are 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 the earth was considerably *warmer* than it is currently (Chadwick-Furman, 1996). Although reef-building ceased for a time following the extinctions at the end of the Triassic, the Scleractinia came back with a vengeance during the Jurassic (Newell, 1971; Veron, 1995); and they continued to exhibit great robustness throughout the Cretaceous, even when temperatures were as much as 8-15°C (Chadwick-Furman, 1996; Veizer *et al.*, 1999), and atmospheric CO_2 concentrations 2 to 7 times (Berner and Kothavala, 2001), *higher* than present.



Source: CO_2 data from Berner and Kothavala (2001); temperature data from Veizer *et al*. (1999), updated in 2004 and available at http://www.science.uottawa.ca/~veizer/isotope_data/.

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 possibly have been caused by a large asteroid impact (Alvarez *et al*., 1980, 1984). They developed again, however, throughout the Cenozoic, particularly the Oligocene and Miocene (Chadwick-Furman, 1996). Finally, throughout the past two million years of the Pleistocene, they survived at least seventeen glacial-interglacial cycles of dramatic climate change and sea level fluctuation, successfully adapting, over and over again, to these enormous environmental challenges (Pandolfi, 1999). In the words of Benzie (1999), this evidence suggests that "coral reef communities are relatively resilient, have survived previous global climate change, and appear likely to survive future changes." And this conclusion leads us to wonder why corals should be succumbing to global warming now.

To answer such an inquiry we must first address the question of what is "normal" for coral reefs in our day? Is it what they look like now? Or what they looked like thirty years ago? Or 300 years ago? Or whenever? Kinzie (1999) has emphatically stated that "it is clear that the definition of a healthy reef as 'what it looked like when I started diving' is fraught not only with hubris but strong temporal bias." Indeed, as Greenstein *et al*. (1998a) have observed, "it must be demonstrated that the classic reef coral zonation pattern described in the early days of coral reef ecology, and upon which 'healthy' versus 'unhealthy' reefs are determined, are themselves representative of reefs that existed prior to any human influence." Only when this criterion is met will we have, in the words of Greenstein *et al*. (1998b), a good replacement for "the temporally myopic view afforded by monitoring studies that rarely span a scientific career." Clearly, therefore, there should be no argument over the *key fact* that we need a proper understanding of the *past* to correctly judge the *present* if we ever are to foretell the *future*.

In an attempt to obtain a true picture of pristine coral conditions in the western North Atlantic and Caribbean, Greenstein *et al*. (1998a, 1998b) conducted systematic censuses of "life assemblages" and "death assemblages" of corals on healthy modern patch reefs and compared the results with similar censuses they conducted on "fossil assemblages" preserved in Pleistocene limestones in close proximity to the modern reefs. What they found was most interesting. The data revealed a recent decline in thickets of *Acropora cervicornis*, as evidenced by their abundance in the death assemblage, and a concurrent increase in *Porites porites*, as evidenced by their abundance in the life assemblage. In comparing these results with those obtained from the fossil assemblage, they found that the present Caribbean-wide decline of *A. cervicornis* is "without historical precedent" and that it is a dramatic departure from "the long-term persistence of this taxon during Pleistocene and Holocene Optimum time," when "intensifying cycles in climate and sea level" recurred again and again throughout a roughly one-million-year time period.

These observations, along with the similar findings of Jackson (1992) and Aronson and Precht (1997), suggest that if little change in coral community structure occurred throughout the Pleistocene – when it was often warmer than it is now (Petit *et al.*, 1999) – the recent die-off of *A. cervicornis* cannot be due to global warming alone, or even primarily; for this particular coral

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has clearly weathered several major episodes of global warming and elevated water temperatures in the past with no adverse consequences. Neither can the coral's die-off be due to the CO_2-induced decrease in seawater calcium carbonate saturation state that might possibly be occurring at the present time (see the section following on *Coral Calcification*); for the air's CO_2 content has not risen sufficiently to have caused this parameter to decline enough to significantly impact reef coral calcification rates (Gattuso *et al*., 1998, 1999), as is also demonstrated by the opportunistic replacement of *A. cervicornis* by *P. porites*. In addition, in their detailed reconstruction of the history of calcification rates in massive *Porites* colonies from Australia's Great Barrier Reef, Lough and Barnes (1997) report that the mid-twentieth century had the second highest coral growth rate of the past 237 years. Hence, although *A. cervicornis* has indeed suffered an extreme decrease in abundance throughout the Caribbean in recent years (Hughes, 1994), its precipitous decline cannot be attributed to either global warming or the direct effects of rising CO_2.

In light of these data-driven considerations, Greenstein *et al*. (1998a, 1998b) have attributed the increasing coral bleaching of the past two decades to a host of local anthropogenic impacts; and this conclusion is accepted in a much wider context as well, as Buddemeier and Smith (1999) have noted that "reviews of the problems facing coral reefs have *consistently emphasized* [our italics] that local and regional anthropogenic impacts are a far greater immediate threat to coral reefs than Greenhouse-enhanced climate change." It is possible, however, that yet another natural phenomenon may be playing an important role on the global stage as well.

3.2. An Alternative Hypothesis

The preceding considerations clearly indicate that global warming cannot be the primary cause of the massive coral bleaching the earth has experienced in recent years. However, many climate alarmists tenaciously cling to this hypothesis because of the fact that (1) no significant massive and widespread coral bleaching was reported in the 1970s and (2) the global warming hypothesis can account for this observation. Specifically, Hoegh-Guldberg (1999) has suggested that the reason "why mass bleaching events are not seen prior to 1980" is that "increases in sea temperatures have only become critical since in the 1980s, when El Niño disturbances began to exceed the thermal tolerances of corals and their zooxanthellae" as a result of global warming increasing the background temperature to which El Niño thermal effects are added.

This reasoning assumes that no other theory is capable of accounting for the fact that modern mass bleaching events did not begin to occur until 1980; and on the basis of this *assumption*, Hoegh-Guldberg (1999) concludes that the global warming hypothesis *must* be correct, even in light of the many problems associated with it. This assumption, however, is not true; for there *are* other ways of satisfying this critical criterion that *do* account for the lack of bleaching episodes before 1980, which we describe below.

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The North Atlantic Oscillation (NAO) is a phenomenon that is responsible for multiannual to decadal variability in Northern Hemispheric climate that is numerically represented by the pressure difference between the Azores high and the Icelandic low (Dugam *et al*., 1997). It has been documented over the past 350 years in Greenland ice core reconstructions (Appenzeller *et al*., 1998) and explicitly quantified from 1864 through 1994 via actual pressure records (Hurrell, 1995), which have been updated through 1998 by Uppenbrink (1999).

Plots of these NAO data sets reveal a shift from strong negative index values in the 1950s and 60s to what Hurrell (1995) describes as “unprecedented strongly positive NAO index values since 1980.” This observation is especially important, for during times of high NAO index values, there is a significant reduction in atmospheric moisture transport across southern Europe, the Mediterranean, and north Africa (Hurrell, 1995); and Richardson *et al*. (1999) note that this phenomenon has led to the development of prolonged drought in the Sahel region of Africa since the NAO shift to positive index values in 1980.

One consequence of this drought has been a gradual increase in the dust content of the atmosphere, which in some areas has grown to five-fold what was deemed normal prior to this climatic transition (Richardson *et al*., 1999). Of particular significance to corals is the fact that this airborne dust carries bacteria, viruses and fungi that can kill them; and Pearce (1999) notes that outbreaks of a number of coral diseases “have coincided with years when the dust load in the atmosphere was highest.” In 1983, for example – when the NAO index reached its highest value since 1864 (Hurrell, 1995) and the atmosphere was exceptionally dusty – a soil fungus of the *Aspergillus* genus appeared in the Caribbean, initiating an onslaught of soft coral sea fans that has now destroyed over 90% of them; and Pearce (1999) notes that there are solid scientific reasons for concluding that “the speed and pattern of the fungus’s spread indicates that it could only have arrived on the trade winds from Africa.”

In addition to carrying its deadly biological cargo, the positive-NAO-induced airborne dust is rich in iron, which extra supply, in the words of R.T. Barber as quoted by Pearce (1999), "may have spurred the worldwide growth of a variety of invader organisms harmful to coral ecosystems.” What is more, such iron-rich dust has the capacity to fertilize algae that compete with zooxanthellae for other scarce nutrients and reef living space. Abram *et al*. (2003), for example, reported that a massive coral bleaching event that killed close to 100% of the coral and fish in the reef ecosystem of the Mentawai Islands (located southwest of Sumatra, Indonesia, in the equatorial eastern Indian Ocean) in 1997-1998 was brought about by an anomalous influx of iron provided by atmospheric fallout from the 1997 Indonesian wildfires, which they describe as being “the worst wildfires in the recorded history of southeast Asia.” The enhanced burden of iron, in turn, spawned a large phytoplankton bloom that likely caused the coral and fish death via asphyxiation. In concluding their paper, Abram *et al*. warn that “widespread tropical wildfire is a recent phenomenon, the magnitude and frequency of which are increasing as population rises and terrestrial biomass continues to be disrupted,” and by further stating that “reefs are likely to become increasingly susceptible to large algal blooms triggered by episodic nutrient enrichment from wildfires,” which phenomenon, in their words, “may pose a new threat to coastal marine ecosystems that could escalate into the 21st century.”

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The time-line for the appearance and progression of these several related phenomena matches perfectly with the timeline of the historical buildup of modern coral reef bleaching throughout the 1980s and 90s. This is not to say, however, that these aggregate phenomena comprise *the* answer to the problem to the exclusion of all other possible causes, even including global warming. We only suggest that they too must be seriously considered in attempts to identify the true cause or causes of this most distressing development in coral reef history.

Thus, although one can make a rational case for coral bleaching being caused by global warming, there are too many pieces of evidence that contradict this hypothesis for it to be deemed the sole, or even primary, cause of this modern curse of reefs. Furthermore, there is at least one alternative explanation – and possibly others yet to be described – for the observed historical development of massive coral bleaching episodes that are not contradicted by ancillary considerations.

4. Global Warming-Induced Sea Level Rise: Good or Bad for Corals?

If rising temperatures don't decimate earth's corals, many people believe that rising sea levels will, by gradually reducing the amount of life-sustaining light that reaches their algal symbionts, upon which they depend for food. This assumption, in fact, is a major concern that is often expressed in discussions of reef responses to global climate change (Hopley and Kinsey, 1988); but it is probably not valid, and for a number of different reasons.

First of all, the 18- to 59-cm warming-induced sea level rise that is predicted for the coming century (IPCC, 2007) – which could be greatly exaggerated if predictions of CO_2-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 year during the Holocene and can be more than double that value in certain branching corals (Hopley and Kinsey, 1988; Done, 1999). Second, most coral reefs are known to have successfully responded to the sea level rises that occurred between 14,000 and 6,000 years ago – which were accompanied by large changes in "CO_2 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). Third, earth's oceans have undergone – and their coral reefs have survived (Chadwick-Furman, 1996) – at least seventeen 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). Fourth, most coral reefs handle increases in sea level – even *rapid* increases – much better than decreases (White *et al*., 1998). Yet even if reef vertical growth rates could not keep up with rising sea levels, that fact would still 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. Possessed of this capacity, Kinzie (1999) notes that "no matter how quickly sea level might rise, propagules of the species could

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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." In fact, Done (1999) notes that "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 that "coral communities have historically had a good capacity to track their re-distributed preferred physical niches."

It is not at all surprising, therefore, as Kinzie and Buddemeier (1996) recount, that 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. Hence, it is highly unlikely that anticipated increases in sea level would spell the doom of earth's coral reefs.

"Many coral reefs have already reached their upward limit of growth at present sea level, and may be released from this vertical constraint by a rise in sea level."

Strange as it may seem, however, it is possible that rising sea levels may have a *positive* effect on earth's coral reefs (Roberts, 1993). Over the past 6,000 years, for example, relatively stable sea levels have limited upward reef growth, resulting in the development of extensive reef flats; and as Buddemeier and Smith (1988) and Wilkinson (1996) have noted, the sea level rises predicted to result from CO_2-induced global warming should actually be beneficial, permitting increased growth in these growth-restricted areas. In the words of Chadwick-Furman (1996), "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 that 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." Hence, she too concludes that "coral reefs are likely to survive predicted rates of global change."

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Part 2: Direct Threats

In addition to the CO_2-induced indirect threats postulated to harm the world's coral reefs, as discussed in Part 1 of this document, the global increase in the atmosphere's CO_2 content has been hypothesized to possess the potential to harm coral reefs *directly*. By inducing changes in ocean water chemistry that can lead to reductions in the calcium carbonate saturation state of seawater, it has been predicted that elevated levels of atmospheric CO_2 may reduce rates of coral calcification, possibly leading to *slower-growing* – and, therefore, *weaker* – coral skeletons, and in some cases even death.

We begin this part of our review by discussing the important role biology plays in driving the physical-chemical process of coral calcification, followed by a discussion of several real-world observations that depict *increasing* rates of coral calcification in the face of rising temperatures and atmospheric CO_2 concentrations. Indeed, as ever more pertinent evidence accumulates, the *true* story appears to be just the *opposite* of what the ocean acidification hypothesis promotes.

1. 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 CO_2 content rises in response to ever-increasing anthropogenic CO_2 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 CO_2 concentration; and they predict that the reductions could reach 17 to 35% by 2100, as a result of expected increases in the air's CO_2 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 certainly is not as solid as acidification alarmists 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 CO_2 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 CO_2 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 CO_2 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 CO_2."

The rising CO_2 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.

Furthermore, with more CO_2 in the air, additional weathering of terrestrial carbonates is likely to occur, which would increase delivery of Ca^{2+} to the oceans and partly compensate for the CO_2-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. Considerations of a suite of interrelated biological phenomena, for example, also make it much more difficult to draw such sweeping negative conclusions as are currently being discussed. Indeed, as shown in the next section, they even suggest that the rising CO_2 content of earth’s atmosphere may well be a

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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.

1.1. The Important Role of Biology

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 CO_2 from the atmosphere to the world's oceans, i.e., *hydrospheric* CO_2 enrichment, were to lead to increases in coral symbiont photosynthesis – as *atmospheric* CO_2 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 CO_2-enhanced symbiont photosynthesis. One of the first mechanisms to come to mind 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 CO_2 partial pressure in coral tissues that is driven by the drawdown of aqueous CO_2 caused by the photosynthetic process. With CO_2 being removed from the water *in intimate contact with the coral host* via its fixation by photosynthesis (which CO_2 drawdown is of far greater significance to the coral than the increase in the CO_2 content of the surrounding *bulk* water that is affected by the ongoing rise in the air's CO_2 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* CO_2 enrichment stimulates zooxanthellae photosynthesis to the same degree that *atmospheric* CO_2 enrichment stimulates photosynthesis in terrestrial plants, i.e., by 30 to 50% for a 300 ppm increase in CO_2 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 CO_2 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 CO_2 concentration.

Another reason why coral calcification may proceed at a higher rate in the presence of CO_2-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

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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 CO_2-induced rates of symbiont photosynthesis would enhance this important "environmental protection activity."

Such observations invoke a number of questions. With ever more CO_2 going into the air, driving ever more CO_2 into the oceans, might we not logically expect to see increasingly greater rates of coral symbiont photosynthesis, due to the photosynthesis-stimulating effect of hydrospheric CO_2 enrichment? Would not this phenomenon, in turn, increasingly enhance *all* of the many positive photosynthetic-dependent phenomena we have described and thereby increase coral calcification rates? And might it not increase these rates well beyond the point of overpowering the modest negative effect of the purely chemical consequences of elevated dissolved CO_2 on ocean pH and calcium carbonate saturation state?

The answers to these several questions are probably all "yes," but 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 CO_2 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*., 1993a), 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 (Burris *et al*., 1983; Al-Moghrabi *et al*., 1996; Goiran *et al*., 1996).

Nevertheless, in yet another positive twist to this complex story, Gattuso *et al*. (1999) report 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 CO_2*, together with an increase in the rate of CO_2 generation by bicarbonate dehydration in host cells, may favor a transition to the diffusional mode of carbon supply, which *is* sensitive to hydrospheric CO_2 concentration. Consequently, if such a change in mode of carbon supply were to occur – prompted, perhaps, by hydrospheric CO_2 enrichment itself – this shift in CO_2 fixation strategy would indeed allow the several biological mechanisms we have described to operate to enhance reef calcification rates in response to a rise in the air's CO_2 content.

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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 CO_2 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 ($\delta^{13}C$ and $\delta^{15}N$) 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.

Why is this study an important scientific undertaking? It is *because*, in the words of Muscatine *et al*., 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."

So what did Muscatine *et al*. learn from their experiments? They say their "most striking observation is the significant difference in mean OM $\delta^{15}N$ between symbiotic and nonsymbiotic corals," which makes OM $\delta^{15}N$ an important proxy for photosymbiosis. As an example of its usefulness, they applied the technique to a fossil coral (*Pachythecalis 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)."

Yes, in some respects it is true that life is at the mercy of the elements, but in other respects it is equally true that *life rules*.

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 clear 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

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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 we examine next.

1.2. Coral Calcification

Many are the people who have predicted that rates of coral calcification, as well as the photosynthetic rates of their symbiotic algae, will dramatically decline in response to what they typically refer 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 what these acidification alarmists continue to tell us.

We begin with the recent study of Herfort *et al*. (2008), who 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 who 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*. (1993b), 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* [our italics]," 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%

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increase in oceanic HCO_3^-," and they say that this development "could stimulate photosynthesis and calcification in a wide variety of hermatypic corals," a conclusion that stands in stark contrast to the contention of the world's acidification alarmists.

In another study, Pelejero *et al*. (2005) developed a reconstruction of seawater pH spanning the period 1708-1988, based on the boron isotopic composition ($\delta^{11}B$) 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 $\delta^{11}B$ values" over the 300-year period investigated. Instead, they say that "the dominant feature of the coral $\delta^{11}B$ record is a clear interdecadal oscillation of pH, with $\delta^{11}B$ values ranging between 23 and 25 per mil (7.9 and 8.2 pH units)," which "is synchronous with the Interdecadal Pacific Oscillation." 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* [our italics]."

Thus, contrary to acidification-alarmist 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 what one would expect from climate-alarmist 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.

Moving a little *backward* in time, 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 are quick to 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."

"The 20th century has witnessed the second highest period of above average calcification in the past 237 years..."

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 CO_2 emissions made much of an impact on the air's CO_2 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 climate-alarmist 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 CO_2 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."

So what did Bessat and Buigues learn? First of all, they found 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."

Another major blow 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 0.00)," 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."

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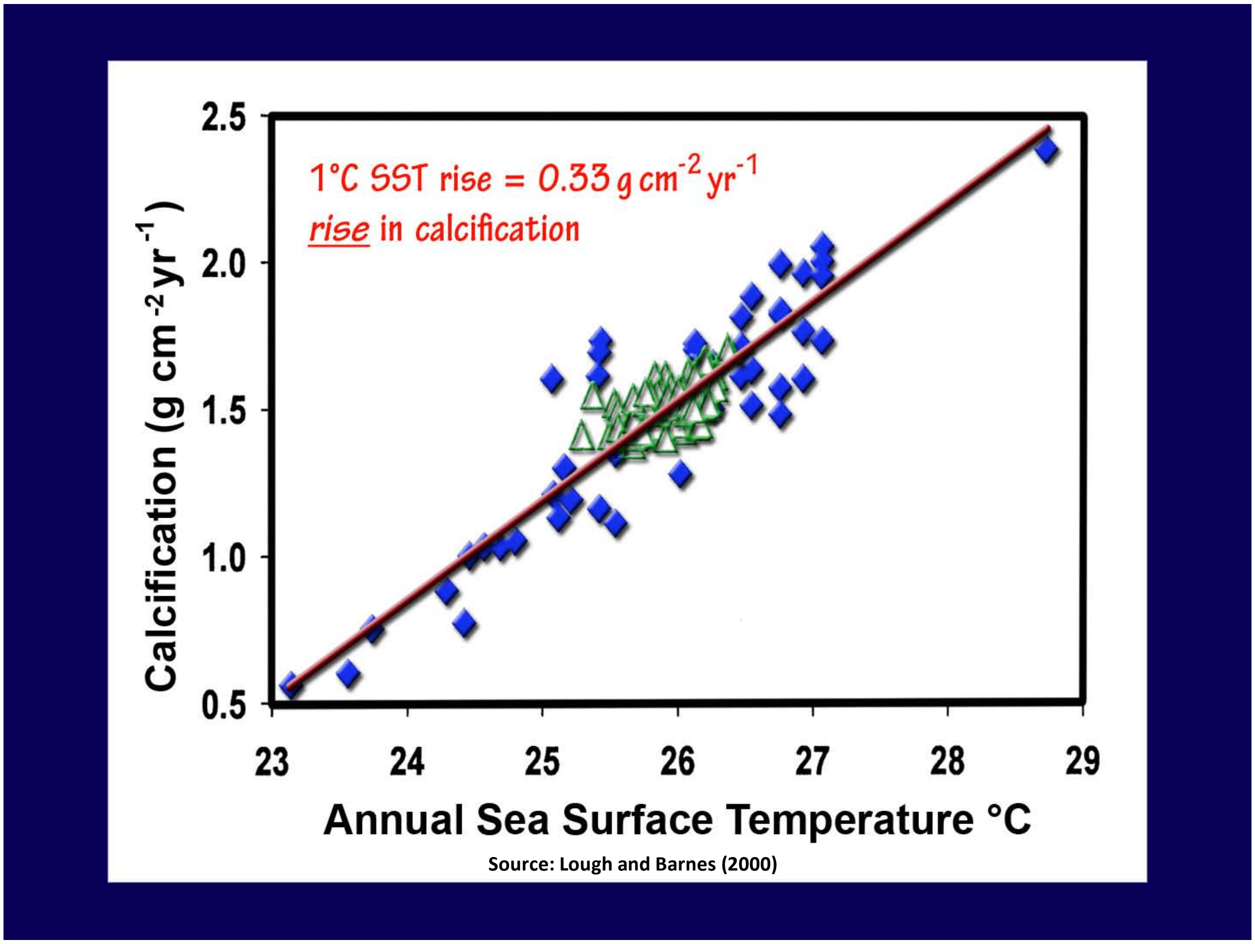
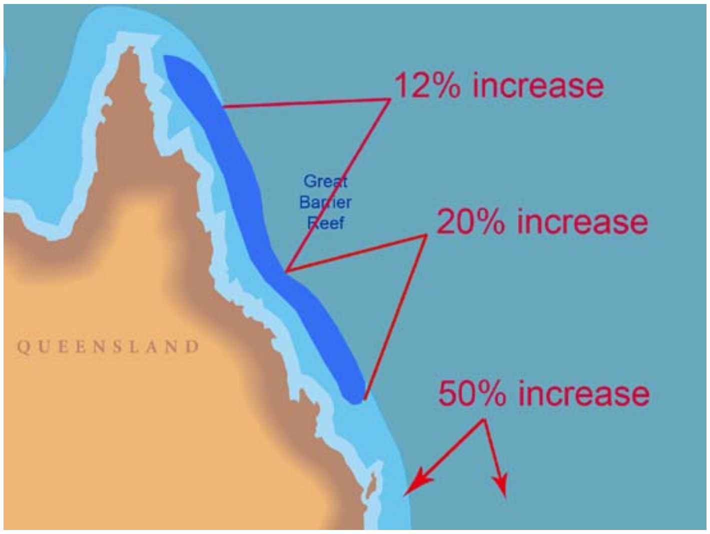


Source: Lough and Barnes (2000)

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." Even more stunning is their observation 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, and in stark contrast to the doom-and-gloom prognostications of the world's climate alarmists, Lough and Barnes concluded that coral calcification rates "may have already significantly increased along the GBR in response to global climate change." But in spite this compelling evidence, as well as the similar findings of others, claims of impending coral doom caused by rising air temperatures and CO_2 concentrations have continued to rear their ugly heads ... on a regular basis ... and in the usual places.

In *Nature*, it was Caldeira and Wickett (2003) who kept the catastrophe ball rolling. Based on a geochemical model, an ocean general-circulation model, an IPCC CO_2 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 CO_2 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 CO_2 concentration could approach 2000 ppm around the year 2300, leading to an ocean-surface pH reduction of 0.7 units, 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, of course, proves deadly for earth's corals in their scenario.

The following year, similar concerns were aroused by 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 CO_2 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) were forced to acknowledge 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 doom derive from the 2009 *Science* 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 that there was a 14% decline in *Porites* calcification rate between 1990 and 2005, which observation the authors claim “is unprecedented in at least the past 400 years.” As one might expect, the media’s regurgitations of the these scientists’ findings included some ominous declarations. The headline of a BBC News report, for example, proclaimed “coral reef growth is slowest ever,” while a Sky News headline read “Barrier Reef coral growth ‘will stop’.” And ABC News actually stated *when* it might stop, concluding their

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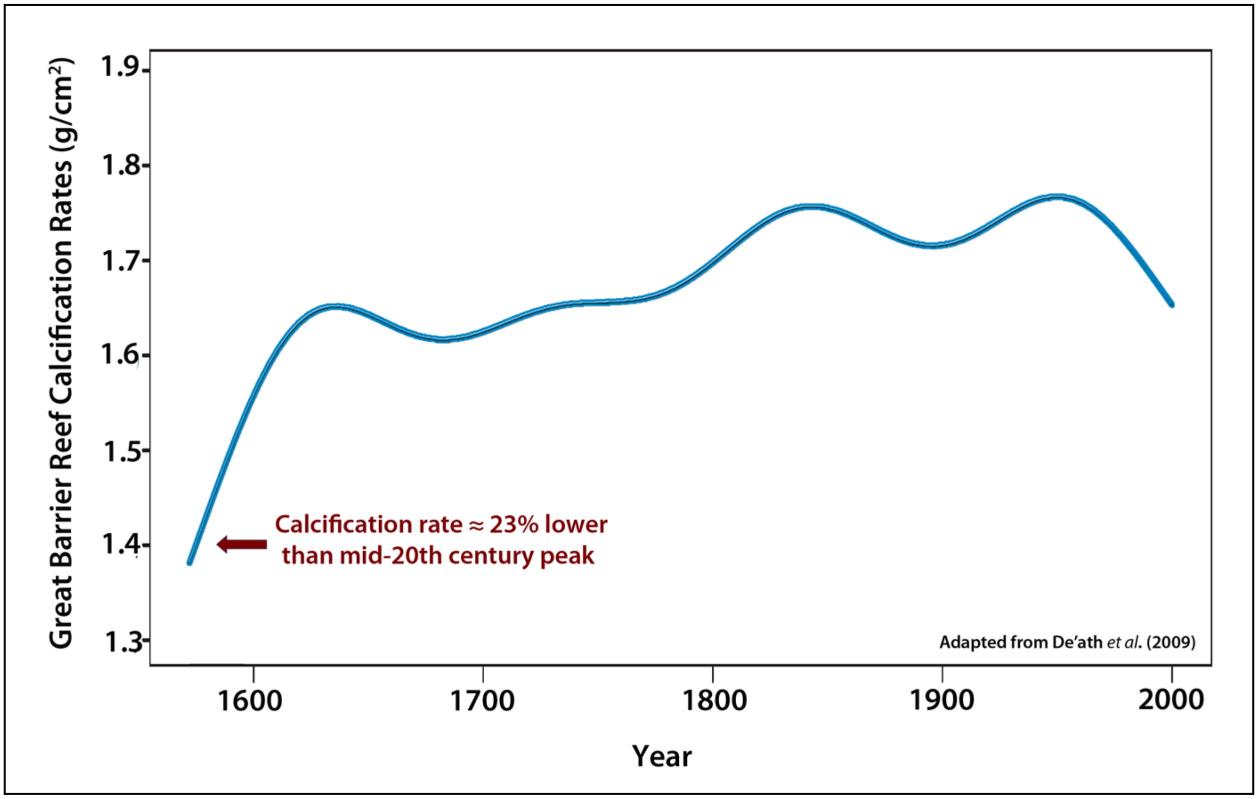
report by quoting the research paper's senior author as saying "coral growth could hit zero by 2050."

But how correct are such claims? Beginning with the first claim that "coral reef growth is slowest ever," *ever*, in this context, is a *very* long time, which suggests that *for as long as there have been corals to grow* the recent decline is unprecedented. So, no, it can't possibly be right. Or at least it can't be *known* to be right. But as we intimated earlier in Part 1 of this document, corals have been around for quite a long time, even longer than all of mankind. In fact, the scleractinian corals, which are the major builders of the reefs of today, have been around some 200 *million* years, during most of which time both the atmosphere's CO_2 concentration and its temperature were *much* greater than they are today, which should immediately raise a red flag about the proffered *cause* of the recent decline in reef growth. And in regard to the recent decline in calcification being unprecedented in the past 400 years, all one needs to do is follow the published De'ath *et al*. calcification history back in time a mere 33 more years, from 1605 to 1572, to see that claim washed away. For the coral calcification rate during that earlier time was approximately *23%* **lower** than what it was at its 20th-century peak, not to mention the fact that the air's CO_2 concentration was more than 100 ppm *less* than what it is today and, therefore, supposedly so much more *healthier* for corals (if you believe climate alarmists!).



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 "twin evils" of the radical environmentalist movement -- atmospheric CO_2 concentration and air

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temperature -- rose concurrently, after which calcification rates declined, but by a smaller 14%, as these same air temperature and CO_2 trends continued, further obfuscating the issue.

But why would anyone believe that the recent calcification decline implies that *Porites* coral growth “will stop,” and that the end will come “by 2050”? They believe it because certain scientists (such as James Hansen) and politicians (such as Al Gore) imply much the same thing, as even De’ath *et al*. do. But when they feel compelled to be as *correct* and as *true to their data* as possible, such as when writing in *Science*, the three researchers from the Australian Institute of Marine Science *clearly state* that “the causes for the Great Barrier Reef-wide decline in coral calcification of massive *Porites* remain unknown.” And when the causes of the recent decline in coral calcification rate are admitted to be *unknown*, it seems foolish indeed to predict, not only that the decline will *continue*, but that it will lead all the way to the *demise of the studied coral*, and especially at a specified future date, which, we might add, De’ath *et al*. appropriately *do not do* in their *Science* paper.

Moving on, a *second* good reason for not believing that the ongoing rise in the air's CO_2 content will 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; Santhanam, 1994; 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 recent 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."

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With each succeeding year, the physical evidence against the CO_2-reduced calcification theory continues to grow ever more compelling, while support for the positive view promoted here continues to accumulate. Working in the laboratory, for example, 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 climate alarmists claim will result from a 300 ppm increase in the air's CO_2 concentration; and this positive temperature effect *far* outweighs the negative effect of rising CO_2 concentrations on coral calcification via ocean acidification.

Working in the field, or, more correctly, 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.

In another important 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 CO_2 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 CO_2 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, it can be appreciated that 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 CO_2-induced decrease in aragonite saturate 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, of course, they found that the *area* of coral reef habitat *expands* in association with the projected ocean warming.

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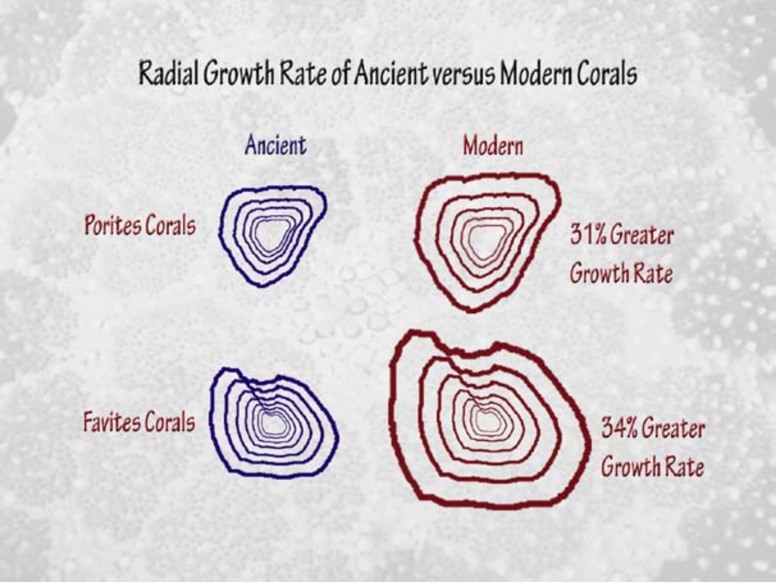
Finally, in a study devoted to corals that involves a much longer period of time than all of the others we have discussed, another research team (Crabbe *et al.*, 2006) determined the original growth rates of long-dead Quaternary corals found in limestone deposits of islands in the Wakatobi Marine National 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, of course, for the air's CO_2 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. Most interestingly, therefore, 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.



To these papers we could add many others (Clausen and Roth, 1975; Coles and Jokiel, 1977; Kajiwara *et al.*, 1995; Nie *et al.*, 1997; Reynaud-Vaganay *et al.*, 1999; Reynaud *et al.*, 2007) that *also* depict increasing rates of coral calcification in the face of rising temperatures and atmospheric CO_2 concentrations. Clearly, the *net impact* of 20th-century increases in atmospheric CO_2 and temperature has not been anywhere near as catastrophically disruptive to earth's corals as climate-alarmist dogma suggests it should have been. Quite to the contrary, the temperature and CO_2 increases appear to not have been hurtful *at all*. In fact, they actually appear to have been *helpful*. Why? Because, as noted above, coral calcification is a *biologically-driven* process that can overcome physical-chemical limitations, which in the *absence of life* would appear to be insurmountable. But what about *other* calcifying and even *non*-calcifying marine organisms? Have they been harmed in any way?

> Clearly, the *net impact* of 20th-century increases in atmospheric CO_2 and temperature has not been anywhere near as catastrophically disruptive to earth's corals as climate-alarmist dogma suggests it should have been.

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1.3. Other Marine Organisms

In a paper recently published in *Limnology and Oceanography*, Richardson and Gibbons (2008) say there has been a drop of 0.1 pH unit in the global ocean since the start of the Industrial Revolution, and 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* [our italics] 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* [our italics] in recent times," which they say has been "linked predominantly to warming (Kirby *et al*., 2007)." Likewise, they further note that even in the most recent IPCC report, "there was no empirical evidence reported for the effect of acidification on marine biological systems (Rosenzweig *et al*., 2007)," in spite of all the concern that has been raised by acidification alarmists claiming that such is, or should be, occurring.

In light of this body of real-world evidence, or *non*-evidence, Richardson and Gibbons conclude (rather generously, we might add) that "the role of pH in structuring zooplankton communities in the North Sea and further afield at present is tenuous."

In another study, Vogt *et al*. (2008) examined the effects of atmospheric CO_2 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 Espegrend, Norway. Three of the mesocosms were maintained at ambient levels of CO_2 (~375 ppm), three were maintained at levels expected to prevail at the end of the current century (760 ppm or 2x CO_2), and three

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were maintained at levels predicted for the middle of the next century (1150 ppm or 3x CO_2), 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 CO_2 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," which is just the *opposite* of what the world's acidification alarmists characteristically predict about CO_2-induced "ocean acidification."

Expanding the subject of CO_2 effects on other marine organisms, 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 CO_2, 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 CO_2 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 CO_2 in the water and the correspondingly reduced pH had no acute effects on the mussels." Thereafter, however, some mortality was observed in the highest CO_2 (lowest pH) treatment from day 23 to day 37, after which deaths could also be

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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 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 (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 CO_2 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 CO_2 concentration might rise* yields a value that approaches 2000 ppm around the year 2300, representing a surface oceanic pH reduction of 0.7 units, 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 *never* be bothered, even in the *least* degree, by the tendency for atmospheric CO_2 enrichment to lower oceanic pH values.

In a study of a very different creature, 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 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 of these observations, in their words, "refute the notion of a linear relationship of calcification with the carbonate ion concentration and carbonate saturation state," which refuted notion is championed by the world's climate alarmists. 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 CO_2 most coccoliths show normal morphology," at both "higher and lower CO_2 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 CO_2 perturbation applied in experimental treatments are *not* [our italics] mirrored in the sedimentary record." This finding indicates, as they suggest, that "in the natural environment *C. leptoporus* has adjusted to the 80-ppm CO_2 and 180-ppm CO_2 difference between present [and] preindustrial and glacial times, respectively."

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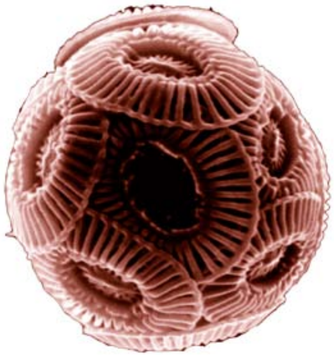
In further discussing these observations, Langer *et al*. say "it is reasonable to assume that *C. leptoporus* has adapted its calcification mechanism to the change in carbonate chemistry having occurred since the last glacial maximum," suggesting as a possible explanation for this phenomenon that "the 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 CO_2 level for calcification of the species *tracks the environmental value* [our italics]." With respect to the future, therefore, Langer *et al*. end on a strongly positive note, stating that "genetic diversity, both between and within species, may allow calcifying organisms to prevail in a high CO_2 ocean."

Focusing on another coccolithophore species , Riebesell (2004) notes that "a moderate increase in CO_2 facilitates photosynthetic carbon fixation of some phytoplankton groups," including "the coccolithophorids *Emiliania huxleyi* and *Gephyrocapsa oceanica*." Hence, in a major challenge to the climate-alarmist claim that atmospheric CO_2 enrichment will definitely harm such marine organisms, Riebesell suggests that "CO_2-sensitive taxa, such as the calcifying coccolithophorids, should therefore *benefit more* [our italics] from the present increase in atmospheric CO_2 compared to the non-calcifying diatoms."



Emiliania huxleyi

In support of this suggestion, Riebesell describes the results of some CO_2 perturbation experiments conducted south of Bergen, Norway, where nine 11-m^3 enclosures moored to a floating raft were aerated in triplicate with CO_2-depleted, normal and CO_2-enriched air to achieve CO_2 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 CO_2 levels during the build-up of the bloom." He further reports that "CO_2-related differences in primary production continued after nutrient exhaustion, leading to higher production of transparent exopolymer particles under high CO_2 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 important finding of this experiment was that the community that developed under the high CO_2 conditions expected for the end of this century was dominated by *Emiliania huxleyi*. Consequently, Riebesell finds even more reason to believe that "coccolithophores may benefit from the present increase in atmospheric CO_2 and related changes in seawater carbonate chemistry," in contrast to the many negative predictions that have been made about rising atmospheric CO_2 concentrations in this regard. Finally, in further commentary on the topic, Riebesell states that "increasing CO_2 availability may improve the overall resource

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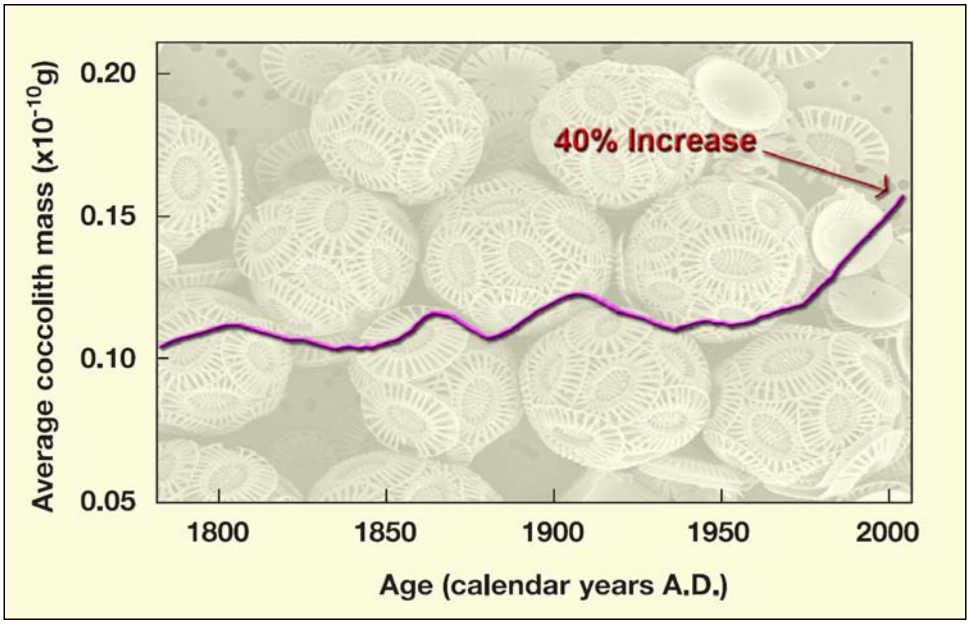
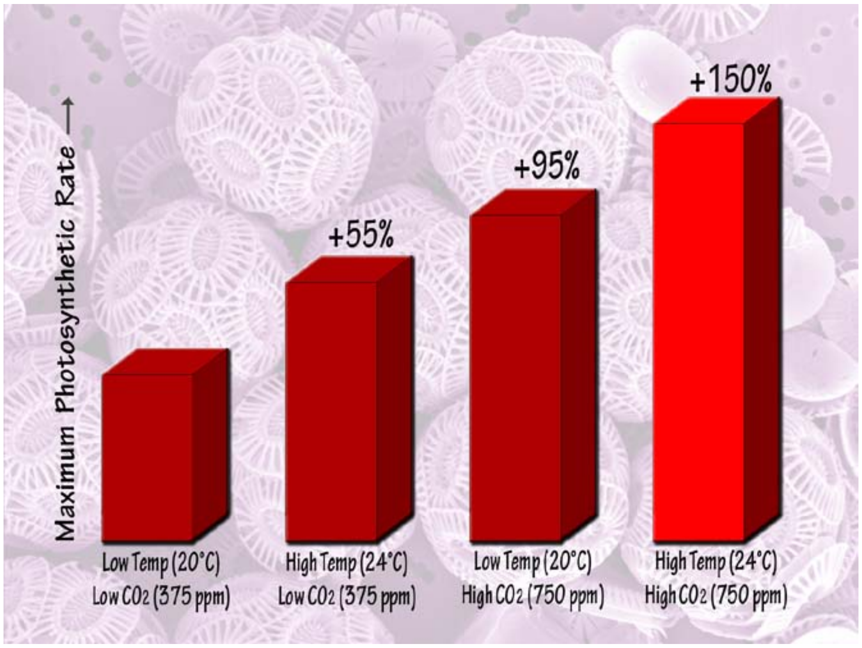
utilization of *E. huxleyi* and possibly of other fast-growing coccolithophore species," concluding that "if this provides an ecological advantage for coccolithophores, rising atmospheric CO_2 could potentially increase the contribution of calcifying phytoplankton to overall primary production." In fact, noting that "a moderate increase in CO_2 facilitates photosynthetic carbon fixation of some phytoplankton groups," including "the coccolithophorids *Emiliania huxleyi* and *Gephyrocapsa oceanica*" - and in a major challenge to the climate-alarmist claim that atmospheric CO_2 enrichment will *harm* such marine organisms - Riebesell suggests that "CO_2-sensitive taxa, such as the calcifying coccolithophorids, should therefore benefit *more* [our italics] from the present increase in atmospheric CO_2 compared to the non-calcifying diatoms."

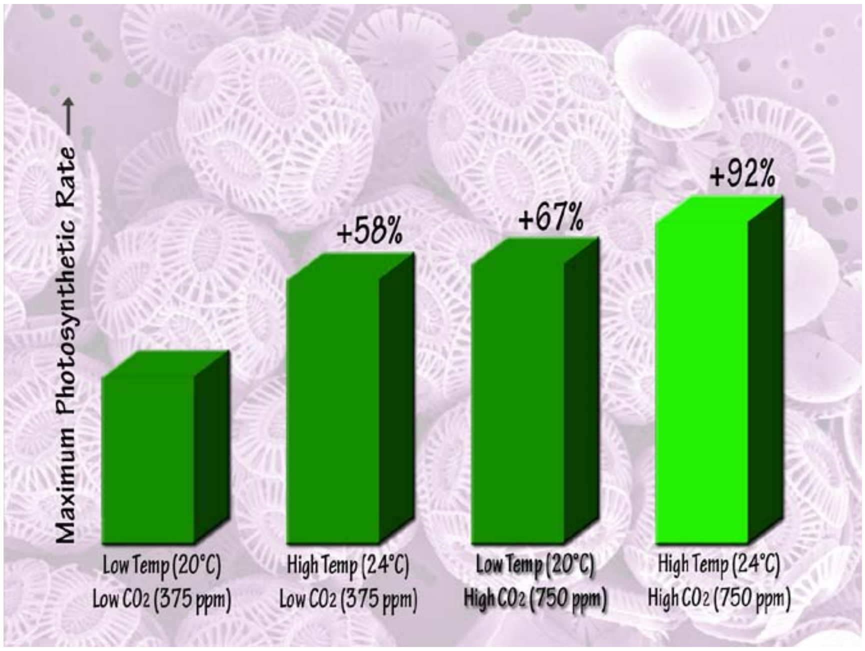
Support of Riebesell's findings was recently provided by an international team of thirteen researchers (Iglesias-Rodriguez *et al.*, 2008), who bubbled air of a number of different atmospheric CO_2 concentrations through culture media containing the phytoplanktonic coccolithophore species *Emiliania hyxleyi*, 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 CO_2 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 CO_2 concentration and the culture media in equilibrium with air of 750 ppm CO_2. 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 CO_2 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-CO_2 or *ambient* treatment, but was increased by 55% by *elevated temperature alone* and by 95% by *elevated CO_2 alone*, while in the high-temperature, high-CO_2 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 CO_2 alone* and *greenhouse* treatments, respectively. Consequently, the researchers concluded, in their words, that "future trends of CO_2 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, of course, that "large influence" will be *positive*, and tremendously so.



Clearly, climate-alarmist claims of impending marine species extinctions due to increases in both temperature and atmospheric CO_2 concentration are not only *not supported* by real-world evidence, they are actually *refuted* by it.

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Concluding Comment

Atmospheric CO_2 enrichment has been postulated to possess the potential to harm coral reefs both directly and indirectly. With respect to marine life -- and especially that of calcifying organisms such as corals and coccolithophores -- neither increases in *temperature*, nor increases in atmospheric *CO_2 concentration*, nor increases in both of them *together*, have had any ill effects on the important processes of calcification and growth. In fact, out in the real world of nature, these processes have actually responded *positively* to the supposedly unprecedented concomitant increases in these “twin evils” of the radical environmentalist movement.

If there is a lesson to be learned from the materials discussed in this review, it is that people should be paying much more attention to real-world observations than to theoretical predictions. Far too many predictions of CO_2-induced catastrophes are treated as sure-to-occur, when real-world observations show them to be highly unlikely or even virtual impossibilities. The cases of CO_2-induced coral bleaching and ocean acidification are no different. We have got to realize that rising atmospheric CO_2 concentrations are *not* the *bane of the biosphere*, but a *boon* to the planet’s many life forms.

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