

Low coral cover in a high-CO₂ world

Ove Hoegh-Guldberg

Centre for Marine Studies, University of Queensland, St. Lucia, Queensland, Australia

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[1] Coral reefs generally exist within a relatively narrow band of temperatures, light, and seawater aragonite saturation states. The growth of coral reefs is minimal or nonexistent outside this envelope. Climate change, through its effect on ocean temperature, has already had an impact on the world's coral reefs, with almost 30% of corals having disappeared since the beginning of the 1980s. Abnormally warm temperatures cause corals to bleach (lose their brown dinoflagellate symbionts) and, if elevated for long enough, to die. Increasing atmospheric CO₂ is also potentially affecting coral reefs by lowering the aragonite saturation state of seawater, making carbonate ions less available for calcification. The synergistic interaction of elevated temperature and CO₂ is likely to produce major changes to coral reefs over the next few decades and centuries. Known tolerances of corals to projected changes to sea temperatures indicate that corals are unlikely to remain abundant on reefs and could be rare by the middle of this century if the atmospheric CO₂ concentration doubles or triples. The combination of changes to sea temperature and carbonate ion availability could trigger large-scale changes in the biodiversity and function of coral reefs. The ramifications of these changes for the hundred of millions of coral reef-dependent people and industries living in a high-CO₂ world have yet to be properly defined. The weight of evidence suggests, however, that projected changes will cause major shifts in the prospects for industries and societies that depend on having healthy coral reefs along their coastlines.

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1. Introduction

[2] Coral reefs cover an estimated 284,300 to 600,000 km² of the world's tropical and subtropical oceans [Spalding *et al.*, 2001; Smith, 1978]. These regions are typically warm, have abundant sunshine and are shallow minimal turbidity. Reef-building or Scleractinian corals are symbiotic with single-celled dinoflagellate algae, and build the scaffolding or framework of this extensive ecosystem. This framework becomes home to hundreds of thousands of other species that dwell in coral reefs [Reaka-Kudla, 1996]. Without the presence and activities of reef-building corals, coral reefs would be vastly different from the diverse and productive ecosystems that typify shallow tropical and subtropical seas today. Coral reefs are a critical resource to people and industries in many countries despite only representing less than 1.2% of the world's continental shelf area [Spalding *et al.*, 2001].

[3] Reef-building corals, as with most other organisms live within an envelope that is defined by the chemical, physical and biological environment around them. The environment surrounding coral reefs has been relative stable over long periods punctuated by abrupt periods of relatively rapid change (e.g., Dansgaard-Oeschger events [Rahmstorf, 2002]) in which the atmospheric carbon dioxide, sea tem-

perature and ocean circulation probably varied significantly. Our knowledge, however, of how coral reefs responded to these changes is minimal due to the difficulty of detecting ecological disturbances in coral reef deposits over appropriate temporal scales.

[4] Current atmospheric concentrations of carbon dioxide (375 ppm) are high relative to atmospheric concentrations that have not risen above 300 ppm over the past 420,000 years [Barnola *et al.*, 1987; Petit *et al.*, 1999]. Atmospheric carbon dioxide and global temperatures are currently increasing at rates that are high relative to anything seen during this period. As this review will outline, these changes to temperature and ocean chemistry have already had major impacts on corals and the reefs they build, both through the effects of carbon dioxide as a greenhouse gas [Glynn, 1991; Hoegh-Guldberg, 1999] and its effect on ocean pH. Key changes are likely through the effect of atmospheric CO₂ on the availability of carbonate ions in oceanic waters for calcification [Gattuso *et al.*, 1998, 1999; Kleypas *et al.*, 1999a]. Both are likely to dramatically reduce the growth and survivorship of corals and hence to have major implications for the integrity of the Earth's most diverse marine ecosystem. This paper reviews recent changes in coral reef abundance and distribution, particularly with respect to changes in global temperature and atmospheric carbon dioxide concentration. It then uses the behavior of coral reefs over the past three decades to project how coral reefs will fare in a high-CO₂ world. Understanding these ram-

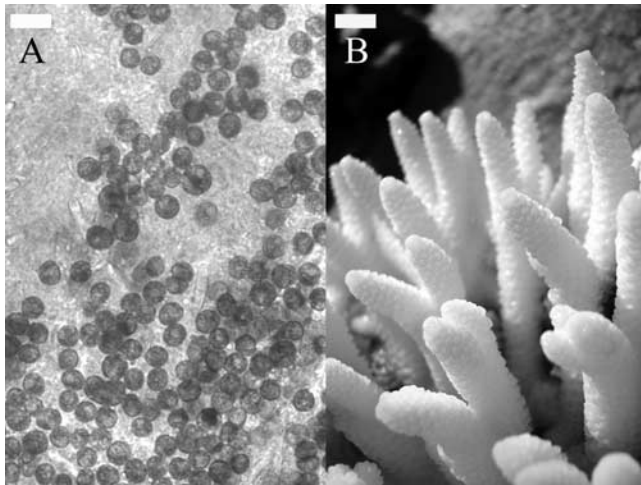


Figure 1. (a) Symbiotic dinoflagellates (*Symbiodinium* sp.) from a reef-building coral. These brown symbionts power the extraordinary calcifying abilities of reef-building corals. Scale bar approximately 30 μm . (b) Bleached but living reef-building coral (*Acropora* sp). Surfaces have lost the brown symbionts and are brilliant white due to exposure of underlying skeleton, which is now seen through the transparent coral tissues. Scale bar approximately 1 cm.

ifications is important if we are to identify the direction and rate of change, and if we are to properly prepare for a future in which ecosystems like coral reefs may be vastly changed.

2. Environmental Envelope Surrounding Reef-Building Corals

[5] Reef-building corals belong to the order Scleractinia within the class Anthozoa and the phylum Cnidaria. They are characterized by the ability to precipitate large amounts of calcium carbonate, a consequence of the abundant photosynthetic energy supplied by symbiotic dinoflagellate algae belonging to the genus *Symbiodinium* (Figure 1a) [Trench, 1979]. The light requirements of these intracellular symbionts restricts the distribution of reef-building corals to locations that receive substantial amounts of sunlight. Corals for this reason generally grow in shallow seas (depths not generally exceeding 100 m) within 30° north or south of the equator. Coastlines that are inundated by sediment laden rivers tend not to have rich coral communities, primarily due to the turbid water column preventing enough light from reaching available substrates for coral growth. Added stress from sediments lying over the top of corals may also contribute to the demise of coral populations at some sites, although the direct effects of sediments may be positive in some instances [Anthony, 1999].

[6] Reef-building corals are also generally restricted to temperatures that decrease no lower than 18°C during the winter months. These temperatures coincide with the higher light levels of the lower latitudes. Corals lay down more calcium carbonate than is eroded away by physical and biological forces on reefs that are closer to the equator. The fast rates of calcification relative to erosion at low latitudes means that calcium carbonate has built up over time, creating reefs made of the skeletons of corals which are

then “cemented” together by the activities of other reef calcifiers such as red coralline algae.

[7] While the surface waters of the ocean are currently supersaturated with respect to the formation of aragonite, the degree of saturation varies primarily with temperature and declines in a poleward direction. As a result, corals at higher latitudes have to cope with the reduced aragonite saturation state of seawater (Ω -arag [Gattuso *et al.*, 1998, 1999; Kleypas *et al.*, 1999b; Langdon *et al.*, 2000]) as well as the direct effects of reduced light and sea temperatures. The aragonite saturation state is a measure of relative ease with which aragonite, the principal crystal form of CaCO₃ in reef-building corals, will form. Atmospheric CO₂ has a major effect on the availability of the carbonate ion and hence on Ω -arag. Upon entering the ocean, most CO₂ interacts with water to form bicarbonate as shown in the following equation:



Carbonate ions are increasingly converted into bicarbonate ions as CO₂ enters the ocean. This in turn results in the reduction of the aragonite saturation state which is defined as

$$[\text{Ca}^{2+}][\text{CO}_3^{2-}]\Omega\text{-arag} = K'_{sp},$$

where K'_{sp} is the solubility product for aragonite and is temperature sensitive. Ω -arag greater than 1 indicates supersaturation with respect to aragonite and higher values indicate greater ease of aragonite precipitation.

[8] Aragonite saturation state is considered to influence the distribution of coral reefs, primarily due to the correlation between with Ω -arag and their distribution, and the linear effects of Ω -arag on coral in the laboratory (see below). Kleypas *et al.* [1999b] investigated the correlation between environmental conditions and coral growth using a database of coral reef locations ReefBase (<http://www.reefbase.org>). Aragonite saturation and light availability were found to be as important as temperature in defining where coral reefs could be found. Kleypas *et al.* [1999b] also identified a series of marginal coral reefs which fell outside the environmental envelope in which the majority of coral reefs were found. The identification of these reef systems indicated evidence of corals and coral reefs that exhibited adaptation to local conditions. The latter will be discussed below with respect to the significant evidence that corals and their symbionts have indeed adapted to changes in the environmental conditions around them.

3. Stepping Outside the Envelope: The Biology of Stress

[9] Relatively gentle seasonal variation can drive changes to the biochemistry and physiology of reef-building corals and their dinoflagellate populations [Jones, 1995; Fagoonee *et al.*, 1999; Fitt *et al.*, 2000]. This situation is contrasted by rapid changes that outpace these slow physiological adjustments, and result in syndromes associated with stress. “Bleaching” is one example that is characterized by the disassociation of the symbiotic dinoflagellates (Figure 1a)

and corals. In doing so, corals are transformed from brown (the color of the symbionts) to a brilliant white (Figure 1b). Bleaching occurs in response to a range of stresses including changes to reduced salinity [Goreau, 1964; Egana and Di Salvo, 1982; Kerswell and Jones, 2003], high or low irradiance [Vaughan, 1914; Yonge and Nichols, 1931; Hoegh-Guldberg and Smith, 1989; Gleason and Wellington, 1993; Lesser et al., 1990], elevated toxin concentrations (e.g., cyanide [Jones and Hoegh-Guldberg, 1999] and copper ions [Jones, 1997]), microbial infection (e.g., *Vibrio* [Kushmaro et al., 1996]) and elevated or reduced temperatures [Jokiel and Coles, 1977, 1990; Coles and Jokiel, 1978; Hoegh-Guldberg and Smith, 1989; Glynn and D'Croz, 1990; Saxby et al., 2003; Hoegh-Guldberg and Fine, 2004].

4. Climate Change and Coral Reefs

4.1. Sea Temperature

[10] The bleaching of coral had been reported for small-scale events (meters to hundreds of meters) up until the late 1970s. In these cases, corals might bleach in response to the inundation of rain onto exposed reefs [Goreau, 1964] or from warm water flowing from the water cooling exhaust of a power plant [Jokiel and Coles, 1977, 1990; Coles and Jokiel, 1978]. Large-scale events (referred to as mass bleaching event) began to be recorded in the early 1980s. In these events, large areas (often involving hundreds or even thousand of kilometers of coral reef) bleached almost simultaneously [Glynn, 1991; Hoegh-Guldberg, 1999]. There have been six major global cycles of mass coral bleaching over the past 20 years, with a pattern of increasing frequency and intensity. Since 1995, most coral reefs world-wide have been affected by mass coral bleaching [Hoegh-Guldberg, 1999; Global Coral Reef Monitoring Network (GCRMN), 2000], irrespective of whether they were close or far from other more direct anthropogenic influences (e.g., increased nutrients, toxins, sediments). Mass mortalities have also occurred as a result of these global events. In 1997–1998, 16% of corals found in surveys immediately prior to the event had disappeared by the following year. In the Western Indian Ocean alone, the losses were higher regionally, with an estimated 46% of corals disappearing by the end of the event. These losses come after major coral mortality over the preceding decades in which as much as 27% of the world's coral may have been removed from coral reefs due to both local and global stressors [GCRMN, 2000].

[11] Mass bleaching events are triggered by warmer than normal sea temperatures [Glynn, 1988; Hoegh-Guldberg and Smith, 1989; Glynn and D'Croz, 1990; Hoegh-Guldberg, 1999]. Thermal stress affects the photosynthetic reactions of the symbiotic dinoflagellates causing dysfunction [Coles and Jokiel, 1977; Hoegh-Guldberg and Smith, 1989; Iglesias-Prieto et al., 1992; Warner et al., 1996; Jones et al., 1998]. Small increases (1°C or more) above the long-term summer average under natural light levels will lead to the advent of bleaching (Figure 2a) [Hoegh-Guldberg, 1999]. Elevating CO₂ on its own (without any temperature increase) has not been observed to cause bleaching [e.g., Marubini et al., 2001, 2003; Leclercq et al., 2002; Langdon et al., 2003]. Elevated temperature slows the processing of

captured light by blocking electron flow at or downstream from the light reactions. The resulting blockage of excitation processing triggers the production of active oxygen and resulting photodamage to the symbiotic cells (photoinhibition [Iglesias-Prieto et al., 1992; Warner et al., 1996; Jones et al., 1998]). Several mechanisms have been suggested for how host and symbiont disassociate, including exocytosis or release of both damaged symbionts and/or host cells [Gates et al., 1992; also see Brown, 1997a] and/or apoptosis (programmed cell death by symbiont and/or host cells [Gates et al., 1992; Dunn et al., 2002]). It is highly likely that the underlying cellular mechanisms include a combination of damage to Photosystem II, oxidative stress, DNA damage, and eventually apoptosis [Lesser et al., 1990; Gates et al., 1992; Lesser, 1996, 1997, 2004; Warner et al., 1996].

[12] The role of elevated sea temperatures in triggering mass coral bleaching has been extensively supported by field and laboratory studies (for recent reviews, see Brown [1997a], Hoegh-Guldberg [1999], and Lesser [2004]). These data highlight the existence of thermal thresholds that vary with geographic location, species, genotype, physical factors (e.g., light, salinity) and history [Coles et al., 1976; Edmunds, 1994; Jones et al., 1998; Hoegh-Guldberg, 1999; Berkelmans and Willis, 1999; Brown et al., 2002]. Despite this secondary source of variability, satellite measurements of sea surface temperature anomalies can still be used to predict bleaching events several weeks in advance with greater than 90% accuracy at large scales [Strong et al., 2000; Hoegh-Guldberg, 1999]. Sea surface temperature measurements also appear to deliver information on the intensity and outcome of bleaching events, especially if the time period of exposure above threshold levels for a coral reef is also considered. Strong et al. [2000] have developed an index (degree heating weeks (DHW) or degree heating months (DHM)) that is the multiple of exposure intensity (degrees above the threshold) and time, and which has been highly successful in predicting mass bleaching events (Hotspot program, coordinated by the National Oceanic and Atmospheric Administration, <http://www.orbit.nesdis.noaa.gov/star/index.html>). In the 1997–1998 global bleaching event, for example, coral reefs that experienced degree heating month (DHM) (a variant on DHW) values of less than 1.5° month largely recovered while those that experienced DHM values of 3 or more experienced large-scale mortalities [Hoegh-Guldberg, 2001].

[13] The correlation of DHM values to the impact and outcome of mass bleaching events also allows one to examine how rising sea temperatures in a high-CO₂ world might potentially affect coral reefs. These studies [Hoegh-Guldberg, 1999, 2001, 2004a] and others [e.g., Done et al., 2003] conclude that even small increases in sea temperature are likely to have large-scale impacts on the distribution and abundance of reef-building corals, largely due the fact that corals live very close to their upper thermal threshold. Models built using the IS92A IPCC reference scenario project that oceanic waters will warm at rates in which the thermal threshold of extant corals in most areas of the tropics and subtropics will be exceeded by as soon as 2030–2050 (Figures 2a and 2b) [Hoegh-Guldberg, 1999]. Taking this further, one can use the DHM values to project the types of changes that may occur. For example, calcu-

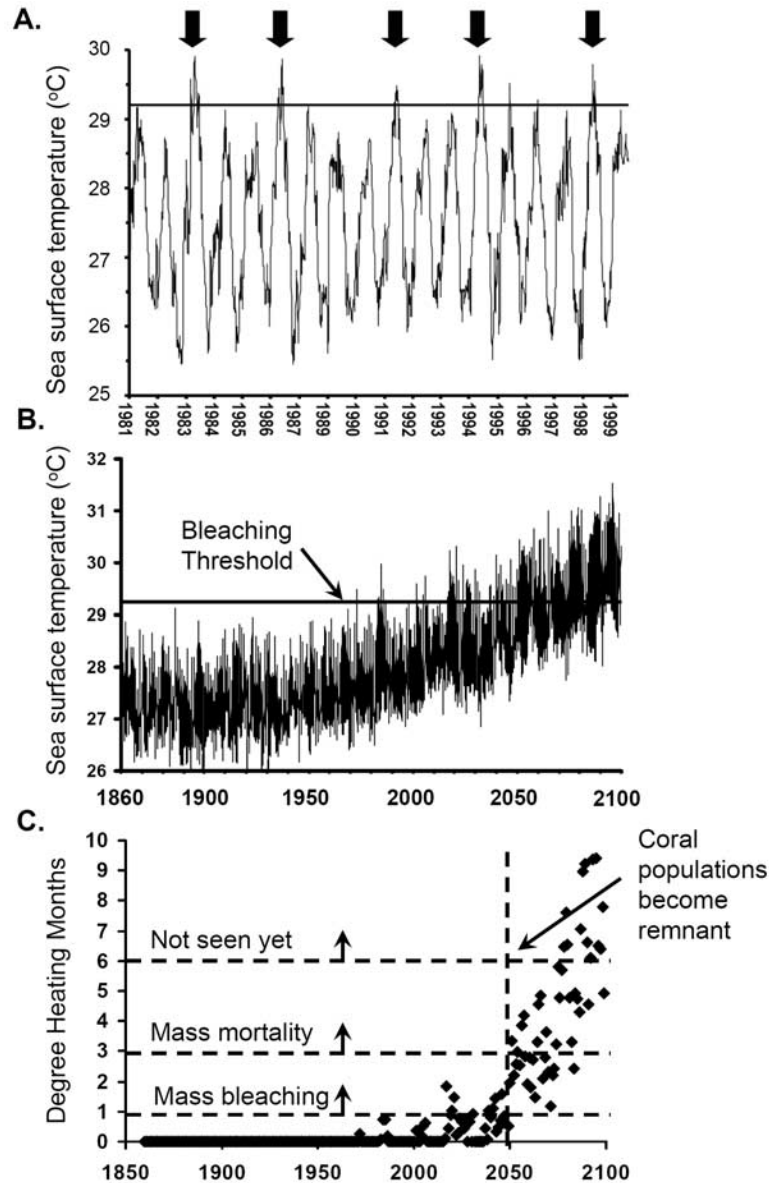


Figure 2. Thermal stress, bleaching, and projections of change for coral reefs in Moorea, French Polynesia (17.5°S, 149.5°W). (a) Weekly sea surface temperature data. Arrows indicate bleaching events reported in the literature [Hoegh-Guldberg, 1999] (permission of Journal of Marine and Freshwater Research). Horizontal line indicates the temperature above which large-scale bleaching events occur (threshold temperature). Temperature data are IGOSN-nmc blended data courtesy of the Lamont-Doherty Climate Center at Columbia University. (b) Sea surface temperature data generated by the global coupled atmosphere-ocean-ice model (ECHAM4/OPYC3 [Roekner *et al.*, 1996]) and provided by A. Timmermann of KNMI, Netherlands (for full description, see Hoegh-Guldberg [1999]). Temperatures were generated for each month from 1860 to 2100 and were forced by greenhouse gas concentrations that conform to the IPCC scenario IS92A (CO₂ doubling). Horizontal lines indicate the thermal threshold of corals in Moorea, French Polynesia, as indicated in Figure 2a. (c) Projected changes to the yearly accumulated heat stress (degree heating months, °C month) for corals in French Polynesia. Data calculated using model data shown in Figure 2b using the approach of Hoegh-Guldberg [2001]; degree heating months are simple multiples of the extent to which temperatures exceed thresholds and the length of time that corals were exposed to these anomalies. Data only considered when temperatures exceeded long-term summer maxima by 0.5°C or more. The date at which corals are likely to be remnant on these reefs is indicated by line (2050), which is the time at which mass mortality events (DHM > 3) occur more than once every 3 years.

lating DHM values for corals using data from corals in French Polynesia shown in Figure 2b reveals DHM values that climb to almost 10 by the later part of this century (Figure 2c) [Hoegh-Guldberg, 2004a]. Given that DHM values of 3 or more are correlated with major mortality events, and that reefs take 10–30 years to recover from events of this severity [GCRMN, 2000], regular excursions to thermal stresses that entail DHM values of 3 or more leads to the conclusion that reefs under these scenarios will have low abundances of coral by the end of this century.

4.2. Aragonite Saturation State

[14] Kleypas, Gattuso, Langdon and others argued that changing levels of carbon dioxide will also have a direct effect on the calcification rates of corals and other calcifying organisms [Gattuso *et al.*, 1999; Kleypas *et al.*, 1999a; Feely *et al.*, 2004]. These authors calculated that calcification rates of corals would decrease by 10–30% under a doubling of atmospheric CO₂ concentrations due to the reduced availability of carbonate ions. They considered evidence indicating that coral calcification was directly proportional to the aragonite saturation (Ω -arag). The evidence of a strong relationship between Ω -arag and calcification is now well supported [Gattuso *et al.*, 1999; Marubini and Atkinson, 1999; Langdon *et al.*, 2000; Leclercq *et al.*, 2000; Marubini *et al.*, 2001, 2003; Leclercq *et al.*, 2002; Langdon *et al.*, 2003]. These studies, done in laboratory or mesocosm settings reveal that doubling atmospheric CO₂ causes a 3–54% decrease in carbonate production.

[15] Aragonite saturation state measurements made during ocean monitoring show a decrease during the 1990s (e.g., Hawaii Ocean Time Series, slope = $-0.022 \pm 0.08 \text{ yr}^{-1}$, 95% CI (C. Langdon, Lamont-Doherty Earth Observatory, Columbia University, personal communication, 2004)) which is enough (if it continues) to reduce the overall aragonite saturation state of the ocean by 40–50% by the end of the century. This decrease in Ω -arag is likely to have started up to 100 years ago as carbon dioxide began to increase in the atmosphere. According to the experiments of Kleypas and colleagues, this decrease in Ω -arag should be matched by decreasing calcification over the past century. Measurements of coral calcification measured from coral cores that stretch back hundreds of years have in cases, however, reveal a different story. Lough and Barnes [2000], for example, did not detect long-term decrease in calcification in cores of the long-lived coral *Porites* collected on the Great Barrier Reef. These authors found increasing rates of skeletal extension and hence calcification in the period 1979–1998 when compared to 1903–1922. They also found that calcification was highly correlated with average annual sea surface temperature (SST), with the annual extension increasing by 3 mm yr^{-1} and annual calcification by $0.3 \text{ g cm}^{-2} \text{ yr}^{-1}$ for each degree of increase in temperature. Lough and Barnes [2000] concluded that the observed trend through time was dominated by the increase of 0.25°C of Great Barrier Reef water temperatures between these two periods.

[16] The data of Lough and Barnes [2000] are not surprising given the fact that calcification increases with temperature (up to current sea temperatures) and there has been a 0.7°C increase in sea temperatures on the Great Barrier Reef over the past century [Lough, 1999]. Calcifi-

cation does, however, not increase indefinitely with temperature. Strong synergistic effects are also apparent, as shown experimentally by Reynaud *et al.* [2003] and discussed by Kleypas [2005]. Reynaud *et al.*'s [2003] study demonstrates experimentally that calcification decreases by 50% when both temperature and pCO₂ are elevated and that explanations based purely on geochemical grounds will inadvertently leave out the important interactions between different biological processes. Gross photosynthesis, which ultimately provides the energy for calcification, has a temperature optimum that lies between $26^\circ\text{--}30^\circ\text{C}$ for the symbiotic algae of most reef-building corals, after which photosynthesis rapidly decreases with further increases in temperature [Coles and Jokiel, 1977, 1978; Hoegh-Guldberg and Smith, 1989; Jones *et al.*, 1998; Nakamura *et al.*, 2004; Coles *et al.*, 1976]. As already discussed, corals that are exposed to sea temperatures that are more than 1°C above their long-term summer maxima will also start to bleach. At this point, the photosynthetic activity of the dinoflagellates rapidly decreases, being further diminished by the loss of symbiotic dinoflagellates out of the coral tissues. The coincidence of the two challenges (reduced photosynthetic performance and decreased Ω -arag) suggests that coral reefs will face increasing difficulty keeping up with the ecological competition and erosional forces around them. Some authors have contested this. A recent study by McNeil *et al.* [2004] claims that the decrease in calcification due declining aragonite saturation will be compensated by the stimulation of calcification by increasing sea temperatures. This study builds its conclusions on several assumptions that are not supported by the literature. McNeil *et al.* [2004], for example, assume that calcification increases monotonically with temperature and latitudinal changes in calcification are an accurate measure of the thermal acclimation potential of corals. The calcification for corals growing at a single latitude (dependent on locally adapted genotypes), however, reaches a maximal value at or just below the current maximum sea temperature for these sites. For this and other reasons, a large number of authors [Kleypas *et al.*, 2005] have recently soundly refuted the assumptions and conclusions of McNeil *et al.* [2004].

4.3. Other Potential Influences of Climate Change

[17] Climate change also has other implications for the abundance and distribution of corals. Some of these changes (e.g., direct effects of pH and CO₂ on physiological performance at various temperatures [see Pörtner *et al.*, 2005]) have been explored only minimally for corals. Globally, sea level is projected to increase by between 0.2 and 0.8 cm yr^{-1} , due mostly to thermal expansion of the ocean as well as the melting of glaciers and the polar ice caps. Sea level rise has been seen as rather benign relative to the effects of temperature rise and the changes in aragonite saturation [Pittock, 1999; Brown, 1997a]. Palaeological studies show that coral reefs have kept pace with past changes in sea level [Partain and Hopley, 1989]. Corals are also highly mobile larvae and hence settlement of coral recruits into new flooded habitats would be expected to occur rapidly as sea levels rise. The critical element here, however, is the physiological condition of corals in these scenarios. Coral reefs could be left behind by rising sea levels if corals are not growing or reproducing at healthy rates. The latter is

more than likely given the large and demonstrated impacts of both elevated temperature and reduced aragonite saturation state on coral growth and reproduction (discussed above).

[18] There is also growing evidence that storms may become more intense under rapid climate change [Intergovernmental Panel on Climate Change, 2001]. If this were so, coral reefs may experience greater erosional forces on occasions. These may, in turn, affect the balance of reef formation and erosion, with implications for such aspects as coastal protection. Climate change projections also indicate that patterns of rainfall may vary such that some places (e.g., coastlines along the Eastern Australia) will become more significantly drier and more drought ridden [Impacts and Adaptation Working Group, 2001], while others (e.g., west coast of the Americas) may experience either higher or more episodic rainfall. These aspects of the changing climate are likely to affect coastal erosion and hence the sediment loads running down rivers onto coral reefs. These changes may also link to the simultaneous increases in coral disease-like syndromes, which may be associated with a combination of climate change related and unrelated factors [Harvell et al., 1999, 2002].

[19] While these other climate related factors are undoubtedly important, there is little understanding of how these factors affect corals and the reefs that they build either singularly or synergistically. Understanding these other influences should be a priority of projects that aim to build credible scenarios of the future. This may be especially important as we seek strategies to promote greater ecological resilience (i.e., resistance to, and recovery from, impacts) by developing better management of these subsidiary factors. The importance of implementing these approaches is highlighted by the fact that reefs that are relatively less impacted appear more likely to resist or to bounce back from events associated with our rapidly changing climate [Hoegh-Guldberg, 1999; Hughes et al., 2003].

5. Acclimation, Adaptation, and Range Migration

[20] There are two possible escape clauses within the stark scenarios that have been constructed for a high-CO₂ world. The first is that extant individuals within coral populations may vary their physiological tolerance and thereby acclimate to the new conditions. Corals acclimate to changes in the environment around them including seasonal temperature changes [Brown, 1997b; Gates and Edmunds, 1999; Coles and Brown, 2003]. Berkelmans and Willis [1999] revealed that the winter maximum upper thermal limit for the ubiquitous coral *Pocillopora damicornis* was 1°C lower than the threshold for the same species of coral in summer. Similar observations have been made recently by Nakamura et al. [2004]. These shifts are evidence of acclimation by corals to temperature. Like any physiological trait, however, there are limits to the extent to which organisms can acclimate to environmental change. Berkelmans and Willis [1999] made the critical observation that acclimation could occur in winter (when thresholds were lowered) but did not occur in the summer, with the implication that the ability to acclimation in summer had been exceeded. The observation of increasing

(as opposed to decreasing) mortality rates among coral communities over the past 25 years also suggest that acclimation by corals to higher temperatures in the summer may have already been largely exhausted [GCRMN, 2000; Hoegh-Guldberg, 1999].

[21] Acclimation can also occur through the reshuffling of resident dinoflagellate symbionts, such that more thermally tolerant genotypes of symbionts dominate and impart greater thermal tolerance on the host [Buddemeier and Fautin, 1996; Baker, 2001; Toller et al., 2001]. There are a range of genotypes of *Symbiodinium* dinoflagellates that inhabit corals [Trench, 1979, 1997; Baker and Rowan, 1997; Loh et al., 1997; Rowan, 1998; LaJeunesse et al., 2003] with some genetic varieties being correlated with warmer and putatively more stressful habitats (e.g., the coral *Acropora millepora* had dinoflagellates of a genotype referred to as clade D in inshore and more stressful habitats while it had clade C elsewhere [Ulstrup and Van Oppen, 2003]). Rowan [2004] has compared the heat tolerance (as measured using pulsed amplitude modulated fluorometry) of coral *Pocillopora damicornis* with either clade C or clade D dinoflagellates. In this study, clade D was able to maintain higher photosynthetic efficiencies as temperatures were increased. This is an important step to showing that changes in the genetic composition of symbiotic dinoflagellates translate into changes in physiology and ultimately greater survival. Future studies need to focus on how the mortality and reproduction of corals with different strains of symbiotic dinoflagellates varies.

[22] It also remains to be conclusively shown if new types of dinoflagellates can invade de novo to create new symbioses with higher thermal tolerances as has been claimed by some authors but not shown [Baker, 2001; Buddemeier and Fautin, 1996; see also Hoegh-Guldberg et al., 2002]. This mechanism appears to be the only one that might lead to rapid changes in thermal tolerance and might continuously supply new attributes to cope with steadily rising sea temperatures. Important steps in demonstrating this mechanism include showing whether completely new varieties of symbiotic dinoflagellates can invade bleached corals and establish new symbioses. Several research teams are investigating how symbioses are established. Recent work by Little et al. [2004] has shown that different clades of symbiotic dinoflagellate may be dominant in juveniles as opposed to adult colonies of the two staghorn corals, *Acropora tenuis* and *A. millepora*. Owing to the limitations of the techniques used to detect the strains, Little et al. [2004] were unable to distinguish between changing ratios of dinoflagellate clades or de novo invasion of the adult clades. Lewis and Coffroth [2004] have resolved this issue using rare genetic markers for a strain of symbiotic dinoflagellate and showed that symbiotic dinoflagellates which are native to a host will reinvade bleached corals from the external environment. This type of study is important to the resolution of how flexible coral-dinoflagellate symbioses are in a rapidly changing environment. The final step in this area waits to be demonstrated, specifically the invasion of a new variety of symbiotic dinoflagellate that imparts greater thermal tolerance and survivorship.

[23] The second way that the thermal tolerance of corals might change over time is via natural selection. As pointed out by several authors [e.g., Coles et al., 1976; Hoegh-

Guldberg, 1999; Coles and Brown, 2003], corals in warmer seas have thermal optima that match local sea temperatures. How long it took for these geographically based genetic differences to occur is not clear, but it is likely that these changes involve long periods of time (hundreds if not thousands of years) relative to current rates of change (e.g., decadal increases in sea temperature). The speed at which these changes occur depends on genetic diversity, generation times and population connectivity, among other things. Generation times for corals are long (>3 years for many corals) and diversity may be low due to the large component of asexual reproduction within coral populations [Ayre and Hughes, 2000, 2004]. Ayre and Hughes [2004] found relatively little evidence of genetic diversity among corals (with some exceptions, e.g., *Seriatopora hystrix*) along 1700 km of the Great Barrier Reef despite the observation of latitudinal changes in thermal tolerance by several authors [Hoegh-Guldberg, 1999; Berkelmans, 2002]. To some extent, this difference is likely to be a consequence of the precision of the technique used to describe genetic differences. In this respect allozyme electrophoresis (used by Ayre and Hughes [2004]), has a relatively low resolution when compared to other techniques (e.g., microsatellites) and may have missed the genetic structure underlying the apparent differences in physiology.

[24] In discussing rates of gene flow, it is also important to understand that genetic connectivity can be maintained by a relative small number of migrants traveling between populations during each generation. This point is highlighted by Ayre and Hughes [2004] who observed that some corals, for example *S. hystrix*, have very low rates of gene flow yet have enormous geographical ranges, in this case across most of the Indo-Pacific. For these reasons, genetic connectivity does not necessarily mean that a reef which loses coral populations is likely to be rapidly recolonized by another that is genetically connected to it. Ayre and Hughes [2004, p. 177] put this succinctly for the Great Barrier Reef as follows: “Consequently, while long-distance gene flow over multiple generations is sufficient to limit genetic differentiation along the length of the GBR, most recruitment by corals on ecological time frames is decidedly local.”

[25] These features of coral populations (as discussed elsewhere [Hoegh-Guldberg, 1999; Ayre and Hughes, 2004]) dictate that corals are unlikely to show greater rates of evolution and range migration than other comparable organisms. Ayre and Hughes [2004] indicate that the “limited allelic variation within isolated populations means that they are likely to have a limited capacity to respond to environmental change.” With relative low rates of migration across the hundreds of kilometres required to bring more thermally tolerant corals from low to high latitudes, coral populations are likely to experience selection that will lead to fewer but more thermally tolerant species (reduced diversity) with a given location. This may lead to changes in community composition, with more tolerant genera such as *Porites* eventually dominating reefs as opposed to the more sensitive branching forms such as those from the genera *Acropora* and *Pocillopora* [Hoegh-Guldberg and Salvat, 1995; Done, 1999; Loya et al., 2001]. Eventually, however, the most tolerant individuals within even the toughest species will succumb to rising sea temperatures if they reach high enough levels.

[26] This perspective is further emphasized in the light of sublethal changes in coral growth, which may alter the competitive balance between corals and other benthic organisms such as macroalgae away from corals. The observation of DHM values that rise to values that are three or four times those seen during events that removed up to 95% of reef-building corals (as discussed above) suggest that sea temperatures even under low (doubling of CO₂) will exceed the capabilities for most extant coral communities to keep pace genetically with the rapid changes in the environment surrounding them. Only by stabilizing the Earth’s climate will genotypes with higher thermal tolerance have the time required to migrate to different areas and establish sizable coral populations at higher latitudes.

6. Low Coral Cover in a High-CO₂ World

[27] Given the challenges that corals and their symbionts are facing under a changing climate, abundant communities of reef-building corals are likely to become increasingly rare. Current trends [GCRMN, 2000; Bellwood et al., 2004] support this projection. As coral reefs are among the most diverse and productive assemblages along any shoreline, and are fundamental to many societies and industries, it is important to consider the consequences of having tropical and subtropical reef systems that may be almost devoid of the reef-building coral communities that built them.

6.1. Implications for Biodiversity

[28] About 100,000 species have been described from the world’s 284,300 km² of coral reef, which is a small proportion of the estimated 0.5–2.0 million species that are suspected to live there [Reaka-Kudla, 1996]. The implications for the associated biodiversity of coral reefs as coral communities become rare are largely unknown. It is clear, however, that many organisms are highly dependent on corals for their existence. Corals provide food and shelter for many species which are likely to disappear if corals are removed. The large-scale El Niño-related disturbances of 1997–1998 provide some insight into how dependent fauna of coral reefs might be affected if corals are largely lost. Corallivores (those organisms that eat coral) have disappeared from coral reefs after the 1997–1998 event [Sano, 2004]. The orange-spotted filefish (*Oxymonacanthus longirostris*), for example, which eats, lives and reproduces within *Acropora* spp. beds, rapidly disappeared from reefs of Okinawa after the 1998 bleaching event [Kokita and Nakazono, 2001]. Other organisms like the obligate crustacean fauna living in corals such as *Pocillopora* spp. also disappeared from corals that bleached and/or died [Phillips, 2002]. Specific problems may also be faced by organisms that not only require a coral host to live in but also need close contact with conspecifics in other coral colonies in order to undergo sexual reproduction. As corals become rare, the distance between colonies may increase to a point where these species are unable to reproduce [Hoegh-Guldberg, 2004a]. While this has not yet been demonstrated, it may be a significant issue for many coral-obligate species.

[29] The response of some organisms to the loss of coral cover is not always immediate or negative. Spalding and Jarvis [2002], for example, found that the overall structure of fish communities in the Seychelles changed very little

despite a 3- to 20-fold decrease in coral cover after the 1997–1998 bleaching event. Abundances of some fish also appeared to increase following the loss of reef-building corals from reef communities. *Lindahl et al.* [2001], for example, showed an overall increase in fish abundance after the 1998 mass bleaching event on Tanzanian reef systems. This was largely linked to an increase in herbivores. Similar conclusions have been reached in studies at other sites by *Chabanet* [2002]. Clearly, we lack a complete understanding of the changes that will accompany the changes in coral cover as climate change unfolds. Understanding these changes should be a major focus of future studies given the potential implications for how one of the major storehouses of biodiversity might change.

6.2. Extinction Versus Range Extension

[30] There is ample evidence that the Earth's flora and fauna are on the move [*Walther et al.*, 2002; *Parmesan and Yohe*, 2003; *Hoegh-Guldberg*, 2004b]. Birds and butterflies are now between 50–150 km north of where they were 50 years ago [*Parmesan et al.*, 2000], and alpine forests and being replaced by lowland and more temperate flora [*Walther et al.*, 2002]. Similar transitions are occurring in coastal and oceanic environments, with fish and invertebrate populations moving in a poleward direction [*Hoegh-Guldberg*, 2004b]. Evidence that organisms associated with coral reefs are also moving is sparse however. Studies that have tried to reconstruct the historic movements of species are plagued by the shortage and poor quality of records, which is typical of marine environments where access has, until recently, been comparably more difficult and infrequent.

[31] One can speculate, however, as to how or if coral reefs might extend in a polar direction. As discussed above, the distribution of extant coral reefs correlates with temperature, light and aragonite saturation state [*Kleypas et al.*, 1999b] and hence models that rely only on sea temperatures are too simplistic [*Kleypas et al.*, 2001]. Light may be a critical limiting factor at higher latitudes and hence warming may only result in small increases in the latitudinal extent of coral reefs. *Guinotte et al.* [2003] comprehensively analyze this question and highlight the added importance of decreasing seawater alkalinities as CO₂ levels build up in the atmosphere. They conclude that the poleward expansion of corals reefs due to increased temperature is largely countered by falling carbonate ion concentrations. The combination of these factors changing leads to the conclusion by these authors that [*Guinotte et al.*, 2003, p. 557] “rising atmospheric CO₂ concentrations will reduce the saturation state of carbonate minerals in the surface ocean over the next 70 years until nearly all locations are in the category identified as marginal by *Kleypas et al.* [1999a].” The point that needs to be emphasized is that coral species, by virtue of the large global distributions and of their ability to reproduce asexually, are unlikely to become extinct. Most evidence, however, points to their abundance and reef-building capabilities largely diminishing over this century.

6.3. Calcification Versus Erosion

[32] Calcification by corals and other organisms is balanced by biological and as well as physical erosion. The net equilibrium between these two forces determines

the net rate of reef growth. Rates of erosion are high, given that rates of coral growth (1–10 cm yr⁻¹ [*Gladfelter et al.*, 1978; *Gladfelter*, 1984; *Pittock*, 1999]) greatly exceed the rate of reef growth (0.5–1.0 m per 1000 years [*Odum and Odum*, 1955; *Smith and Kinsey*, 1976; *Davies and Hopley*, 1983]). These rates may vary according to biological factors such as the abundance of grazing sea urchins and fish [*Bellwood et al.*, 2003]. Given that the rates of erosion are likely to remain unchanged or possibly even increase due to changes in factors such as the energy of storms, the net rate of reef growth could (under many global climate change scenarios) become negative. This has been reported already for some reefs that largely lost living coral populations during mass bleaching events in the late 1980s and which have not recovered their coral populations due to poor coral recruitment. In one particular case (Faa in French Polynesia [*Pari et al.*, 1998]), thermal stress led to a large-scale mortality of corals, the skeletons of which eroded away. The striking feature of this study was that large sections of the reef framework were also lost. The implications of the loss of the framework of coral reefs is potentially serious given the important role that coral reefs play in protecting coastlines, associated ecosystems and human infrastructure.

6.4. People and Industry

[33] Despite the fact that coral reefs occupy less than 1.2% of the world's continental shelf area, they are enormously important to people globally. An estimated 100 million people depend directly on coral reefs for daily subsistence, and industries such as tourism and fishing generate tens of billions of dollars each year. Our understanding of how changes to coral reefs will affect people and industries is still being undeveloped although it is critically important if these dependent societies are to respond effectively to climate change. In understanding these changes, managing reefs for “ecosystem resilience” in response to these large-scale changes has been suggested as one set of responses [*Hughes et al.*, 2003; *Bellwood et al.*, 2004]. Potential impacts include loss of subsistence livelihoods, income from tourism, biodiscovery and fishing, ecosystem value and services, and coastal protection [*Hoegh-Guldberg*, 1999]. The latter, though at a longer time horizon than the other two, has major implications for human infrastructure and adjacent ecosystems (mangroves and sea grasses) currently protected from wave stress by coral reefs.

[34] Investigation of the potential impacts on people and industries associated with the world's largest coral reef, the Great Barrier Reef, reveals a complex story. Two industries, tourism and fishing, dominate the productivity associated with the Great Barrier Reef. The largest industry in this region is tourism (US\$1.8 versus US\$0.1 billion). It is highly dependent on the still largely pristine values of the Great Barrier Reef, which allows the Australian tourism sector to compete successfully for coral reef-interested tourists in a highly competitive global marketplace. Climate change, however, by potentially reducing the quality of the Australian coral reef experience, threatens to reduce international tourist income by as much as \$8 billion over a 19 year period [*Hoegh-Guldberg and Hoegh-Guldberg*, 2004] (available at <http://www.wwf.org.au>). While coral reefs all

over the world are expected to face similar problems, the Australian industry faces the fact that potential tourists have to travel 2–3 times as far for the same experience. These losses are potentially catastrophic for the coastal communities that fringe the Great Barrier Reef, particularly as some regions are 80% dependent on this source of income. While these studies are just beginning, they highlight the fact that the decline of coral reefs potentially has ramifications that go beyond the loss of biodiversity and an integral coastal ecosystem. Understanding these ramifications will also play a large role in preparing people, industries and governments for these impacts and in designing ways by which to adapt to them.

7. Concluding Remarks

[35] Coral reefs appear to be highly vulnerable to changes in global climate due their sensitivity to changes in sea temperature and aragonite saturation. In the preceding discussion, changes under relatively mild to midrange scenarios of atmospheric CO₂ (doubling) were examined. It is important to point out, however, that greater rates of change or indeed the nonlinear behavior of the climate system could potentially have even greater impacts on coral reefs. Vague hopes that the biology of coral reefs will keep up with the pace of change are not matched by current observations or our understanding of past changes. Evolution is a slow process that is unlikely to keep up with the rapid changes currently being exerted upon the environmental envelope surrounding corals and coral reefs. Significant improvements in coral reef abundance and distribution due to local adaptation and geographic rearrangement of genotypes will only occur once the climate has stabilized again, and only to the extent possible as far as their light and carbonate ion requirements are concerned. For this reason, the possibility that tropical reef systems will be largely devoid of significant coral populations and that they will have vastly lower numbers of associated species appears likely. How this will affect dependent people and industries is still being examined. It is clear, however, that these changes are almost certainly going to affect a large number of people in both developed and developing countries. Getting a better understanding of these changes has to be a priority if we are to better prepare for life within a high-CO₂ atmosphere.

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O. Hoegh-Guldberg, Centre for Marine Studies, University of Queensland, St. Lucia, QLD 4072, Australia. (oveh@mailbox.uq.edu.au)