Reg Environ Change (2011) 11 (Suppl 1):S215–S227
DOI 10.1007/s10113-010-0189-2

ORIGINAL ARTICLE

Coral reef ecosystems and anthropogenic climate change

Ove Hoegh-Guldberg

Accepted: 12 November 2010 / Published online: 8 December 2010

Abstract Coral reef ecosystems are among the most biologically diverse ecosystems on the planet. In addition to their value in terms of biodiversity, coral reefs provide food and resources for over 500 million people. Despite their importance, coral reefs are declining at a rapid rate (1–2% per year) as a result of a range of local (e.g., overexploitation of fisheries, declining water quality) and global (e.g., global warming and ocean acidification) drivers. Extensive experimental and field evidence suggests that atmospheric carbon dioxide concentrations of 450 ppm will lead to the loss of coral-dominated reef systems, with the prospect that dangerous levels of atmospheric carbon dioxide for coral reefs were exceeded in 1979 when mass coral bleaching was reported for the first time. The exact response of coral reefs remains uncertain although it is highly unlikely that coral-dominated reef systems will be present in future oceans at the current rate of warming and acidification of the world's tropical oceans. The loss of these important coastal ecosystems will diminish the resources available to hundreds of millions of people along tropical coastlines. Understanding the impacts on people and industry is an imperative if we are to devise effective systems by which tropical coastal communities are to adapt to rapidly changing tropical coastal environments. Our current understanding of these important issues, however, is in a relatively undeveloped state and must be a priority of future research.

Keywords Coral reef · Climate change · Ocean acidification · Calcification · Marine biodiversity · Coastal communities · Declining resources · Mass coral bleaching

O. Hoegh-Guldberg (✉)
Global Change Institute, The University of Queensland,
St. Lucia 4072, QLD, Australia
e-mail: oveh@uq.edu.au

Introduction

One of the most persistent features of most small island states and other tropical/subtropical countries is the presence of extensive coral reef ecosystems along their coastlines. Here, coral reefs provide number of ecosystem services including food from small-scale fisheries, income from commercial fishing and tourism, and coastal protection against the power of oceanic waves. Coral reefs also play central roles in the history and culture of island populations. Taken together, the social, economic, and cultural benefits of coral reefs are crucially important to island societies and nations (Spalding et al. 2001).

Even though coral reefs are critically important to many island economies, they are among the most threatened ecosystems on the planet. The abundance of coral reefs has declined by as much as 50% on and Western Pacific coral reefs and is continuing to decline at the rate of 1–2% per year (Bruno and Selig 2007). Bruno and Selig's meta-analysis of over 6,000 published studies indicated that both local and global factors were responsible for this decline. At the local level, coral reefs are being affected by declining water quality (increasing nutrient and sediments from disturbed coastlines), over-exploitation of key marine species, destructive fishing, and pollution from expanding urban areas (Hughes et al. 2003). This human-driven signal was particularly evident in regions like South-East Asia. One of the important insights provided by Bruno and Selig (2007) was that global factors (i.e., global warming and acidification) figured strongly in the decline of reef health, with rapid decline occurring equally rapidly in remote areas where local impacts were minimal or non-existent.

This paper explores the threats and implications of climate change and ocean acidification for coral reef ecosystems with reference to how the projected changes will affect small island states as well as many other coastal societies worldwide. In undertaking this analysis, it becomes clear that approaching and exceeding 450 ppm has dire consequences for coastal ecosystems and the people of many small island nations. These effects arise primarily because of unusual and rapid changes to coastal waters and the impacts on millions of coastal dependents who depend on coral reefs and related tropical coastal ecosystems for food, income and coastal protection.

Environmental limits to coral reefs

Coral reefs grow in shallow, sunlit waters of tropical oceans where they often build extensive carbonate reef systems as a result of the activities of calcifying organisms that live in and around coral reefs. Some of the most prominent organisms in this regard are the reef-building corals, which belong to the order *Scleractinia* within the Class *Anthozoa* and the Phylum *Cnidaria*. Reef-building corals form a mutualistic symbiosis with single-celled plant-like organisms known as dinoflagellates. These tiny single-cell organisms live inside the gastrodermal cells of corals where they photosynthesize and pass large amounts of photosynthetic energy to the coral host. In return for the energy that they give to the coral host, the symbiotic dinoflagellates receive access to inorganic nutrients stemming from animal metabolism that are otherwise in low qualities in the normally clear waters of tropical and subtropical oceans (Muscatine et al. 2005). The photosynthetic energy derived from the symbiotic dinoflagellates powers the metabolically expensive process of calcification, allowing corals (and a range of other symbiotic invertebrates such as giant clams) to deposit huge amounts of calcium carbonate (Hoegh-Guldberg 1999). The close relationship between corals and symbiotic dinoflagellates has been in existence for at least 220 million years (Muscatine et al. 2005) and is largely responsible for the huge reserves of limestone found in the upper layers of the earth's crust. Living carbonate structures on a living coral reef provide the habitat for over a million species of plant, animal, fungi, and bacteria, perhaps as much as 90% of which are currently unknown to science (Reaka-Kudla 1996).

The current global distribution of coral reefs provides important insight into the environmental conditions necessary for maintaining corals and the reefs that they build (Kleypas et al. 1999a). Due to the need for abundant light for their photosynthetic symbionts, corals grow in shallow seas (depths not exceeding 100 m) in regions within 30° north or south of the equator. They also do not grow in regions inundated by sediment laden rivers because the turbidity prevents light from penetrating far enough for significant coral growth. Coral reefs are also dependent on warm and thermally stable oceans, where temperature does not decrease below 18°C in the winter (Kleypas et al. 1999a). The third major factor coinciding with the global distribution of corals is the concentration of carbonate ions, which is ultimately determined by ocean acidity and atmospheric carbon dioxide. While the surface waters of the ocean are currently supersaturated with respect to the formation of aragonite (a form of crystalline calcium carbonate), the degree of saturation varies primarily with temperature and declines toward the poles. As a result of these three factors, coral reefs currently thrive in shallow equatorial coastal regions that are typically warm, sunlit, and supersaturated with carbonate ions. At higher latitudes, the development of carbonate reef systems dwindles until the rate of reef calcification is overwhelmed by the forces of physical and biological erosion, and carbonate structures fail to accumulate. At this point, reefs are still important as unique temperate habitats and communities but, have much lower levels of biodiversity and prominence as coastal features.

Rapid climate change and coral-dominated ecosystems

Rapidly expanding human populations along tropical and subtropical coastlines has put increasing pressure on coral reefs. As a result, they are among the most threatened ecosystems, with many coral reefs having approximately 40–50% less coral cover than they had 30 years ago (e.g., Bruno and Selig 2007). Some regions, such as many parts of the Caribbean, have largely lost dominant coral populations from their reefs (Hughes 1994). This pattern is repeated throughout the world (Wilkinson 2008), reinforcing the fact coral reefs are declining rapidly across the planet. At a local level, many of these changes are coming about due to a range of human activities that result in poor water quality, overexploitation of key species, marine pollution, and destructive fishing practices (Hughes et al. 2003). Unfortunately, these changes are rapidly being exacerbated by the added influence of climate change, which is dramatically changing the circumstances under which corals have prospered for many millions of years.

Warming seas and mass coral bleaching

The rise of greenhouse gases in the earth's atmosphere is driven fundamental changes to its oceans. As a result of these changes, the average temperature of the tropical oceans has increased by approximately 0.7°C (IPCC 2007). These changes in sea temperature combine with the natural variability of ocean temperatures to bring warmer than normal years (e.g., due to ENSO and other sources of inter

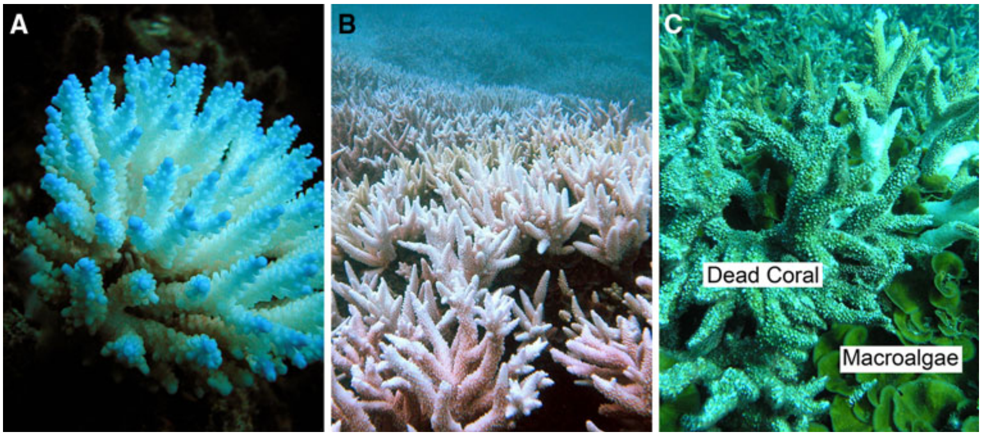

Fig. 1 Bleached corals on the southern Great Barrier Reef in January 2006 after water temperatures reached the summer maximum 2 months before the peak of summer. Close to 100% of the corals bleached and by May, 40% of the corals were dead (Dr. R. Berkelmans, Australian Institute of Marine Science, pers comm.). In late October 2006, a flood reduced salinities in coastal waters killing the remaining corals in shallow regions and highlighting the important interactions that can occur between global warming and other climate-related factors. **a** Close-up of bleached coral; **b** General view of bleached reef in January (Photographs: author); **c** Same reef in May 2006 showing subsequent overgrowth of dead corals by macroalgae (Photograph: Dr. Guillermo Pulido Diaz, Centre for Marine Studies, The University of Queensland)

annual climate variability) to even higher levels, such as those seen in tropical regions during 1997–1998 (Lough 2000) and following years. These higher temperatures (which were once part of natural variability) now exceed the tolerance of reef-building corals undergo a process referred to as ‘coral bleaching’ (Fig. 1a–c). Mass coral bleaching events, affecting thousands of square kilometers of coral reefs worldwide, have emphasized the major toll that even mild rates of climate change can have on the earth’s ecosystems (Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2007).

Coral bleaching is a general response to stress. Corals will bleach in response to a range of conditions including sudden changes to light, temperature, and salinity, the presence of toxins and microbial infections. Bleaching at small scales (1–500 m^2) stresses has been reported for at least 75 years (Yonge and Nichols 1931). Bleaching across entire communities and reefs (referred to as ‘mass coral bleaching’), however, has only been reported in the scientific literature for the past 25 years (since 1979). In this case, coral bleaching may affect up to 100% of the reef-building corals across entire reefs, regions, and countries. The first examples of mass coral bleaching occur in the scientific literature in the early 1980s (Glynn 1979; Glynn et al. 1985) with no reports of events entering the scientific literature prior to that time (Hoegh-Guldberg 1999). Since the early 1980s, mass coral bleaching has rapidly increased in frequency, intensity, and geographical extent (Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2007), driven by increasing sea temperatures. The causal relationship between sea temperature and mass coral bleaching has been established by experimental (Hoegh-Guldberg and Smith 1989; Glynn and Dcroz 1990) and field studies in which mass coral bleaching coincides with warmer than normal conditions (reviews: Brown 1997; Hoegh-Guldberg 1999). The first realization that this might be connected to global climate change started to appear in the literature in the mid 1980s (Glynn 1988, 1991).

The definitive test of this causal relationship is the fact that mass bleaching events can be predicted from satellites measurements of sea surface temperature anomalies relative to summer maxima (Goreau and Hayes 1994; Toscano et al. 2000) with greater than 95% accuracy. The algorithm currently used with satellite data predicts bleaching when temperatures get to 1°C above a regions summer maxima for 4 weeks. Further increases in the thermal anomaly or the length of time that coral remain exposed lead to more severe bleaching and a greater risk of coral death. Other factors, such as light intensity and the flow rate of water around corals, can play a role in modifying the intensity of the response of corals to thermal stress (Jones et al. 1998; Nakamura and van Woesik 2001). Corals also differ in their susceptibility to stress, with some corals such as Staghorn corals (*Acropora* spp.) being very sensitive as opposed to corals such as the long-lived massive corals (*Porites* spp.) that are less sensitive to thermal stress (Hoegh-Guldberg and Salvat 1995; Baird and Marshall 1998, 2002). Even so, events such as the 1997–1998 global mass bleaching event can still eliminate the most tolerant corals such as *Porites* (Wilkinson 1999; Hoegh-Guldberg et al. 2007).

Coral bleaching is not always fatal, and many corals will recover their dinoflagellate symbiotic populations following a bleaching event if the stress conditions are mild and short lived. Symbiotic dinoflagellates may take several months to repopulate the tissues of corals with subchronic impacts on coral growth and reproduction that may last for several years (Ward et al. 2002). Corals will, however, die if conditions are warmer and/or last for long periods of time. Under these conditions, bleaching may be followed by spectacular mortalities in which almost all corals on a reef may die in the space of several months after a thermal stress event. Some of the most spectacular examples of mortalities following mass coral bleaching were documented within the 1997–1998 global mass bleaching event. Starting in late 1997 in the eastern Pacific, mass coral bleaching spreads across most coral reefs of the world by the end of 1998. While some reefs experienced only mild effects of bleaching and recovered their color within a few months of the return of cool temperatures, other reefs did not. In these cases (e.g., the Seychelles, Maldives, Okinawa and Palau), severe coral bleaching was followed by mass mortalities that ranged up to and beyond 80% of all of the corals on these reef systems (Wilkinson and Hodgson 1999). One of the most concerning statistics from the 1997–1998 event is that as estimated 16% of the world's reef-building coral populations died in a single 12-month period, with some regions (e.g., Western Indian Ocean coral reefs) losing nearly 50% of their coral populations (Wilkinson and Hodgson 1999). While some of these sites have recovered to some extent, most of these regions still have much less coral than they had 8 years ago before the 1998 bleaching event (Wilkinson 2004).

Because of the clear relationship between elevated temperature and mass coral bleaching and mortality, it has been possible to project how the incidence of coral bleaching and mortality is likely to change. The first projections (Hoegh-Guldberg 1999) foresaw a steady increase in the frequency and intensity of coral bleaching until it was an annual event by 2050 (Fig. 2a; Hoegh-Guldberg 1999). The conclusions of the study were confirmed by analysis (for the Great Barrier Reef) that investigated regional differences in the thermal tolerance of corals and calculated the probability of different events returning as oceans warmed (Done et al. 2003). Taking into account the growing information on how anomaly size and exposure time were related to bleaching and mortality led to improved models of how large-scale mortality as well as bleaching events might vary within coral populations (Fig. 2b, c; Hoegh-Guldberg 2004). Based on modeling the changes, an index composed on anomaly size multiplied by the exposure time (Degree Heating Weeks or Degree Heating Months, DHM, Strong et al. 2000), the models reveal that stresses that surpass the DHM associated with the mass mortality events of 1997–1998 become annual events later this century. Based on the fact that coral reefs take at least 15–25 years to recover from mass mortality events, the annual return time of these events essentially means that corals are projected to become remnant on tropical reef systems toward the end of this century. These initial models have recently been augmented by increasingly sophisticated models such as that produced by

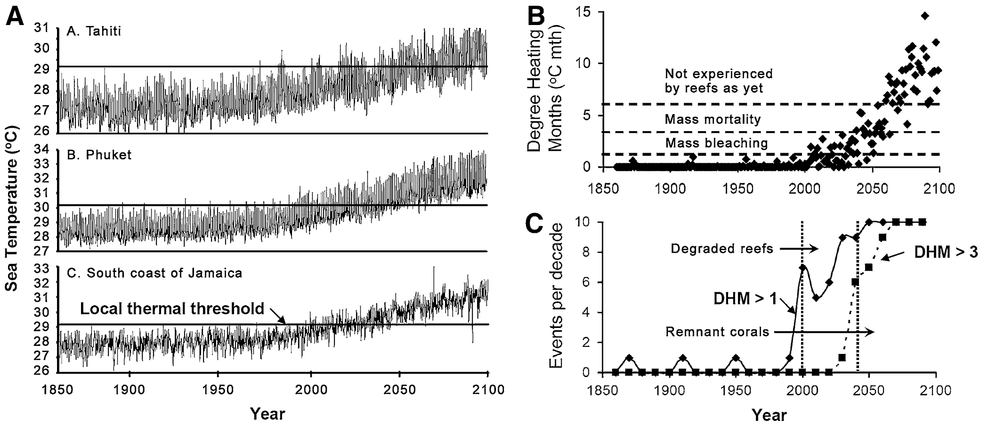

Fig. 2 Projections of change on coral reefs due to the warming of seas associated with a doubling of carbon dioxide over pre-industrial levels (560 ppm by 2100). **a** Sea surface temperature data for Tahiti, Thailand, and Jamaica generated by the global coupled atmosphere–ocean-ice model (ECHAM4/OPYC3, Roeckner et al. 1996). Temperatures were generated for each month from 1860 to 2100 and were forced by greenhouse gas concentrations that conform to the IPCC scenario IS92a (Leggett et al. 1992; IPCC 2007). Further details available in Hoegh-Guldberg (1999). Horizontal line in each panel indicates the local thermal tolerance threshold over and above which bleaching begins. **b** Degree Heating Months (DHM = Anomaly above thermal tolerance threshold exposure × exposure time in months) calculated for the climate modeling data shown in A. *Lines* indicate DHM values that are known to cause bleaching (DHM = 1–3) and mass mortality (DHM = 3–5). Values higher than 6 have not been seen on reefs yet. **c** Frequency of bleaching events (*solid line*; DHM > 1) and mass mortality event (*dashed line*, DHM > 3). Assumption is that reefs will degrade significantly when bleaching events occur 5 times per decade and will no longer have corals on then when mortality events (DHM > 3) occur more than 5 times a decade. *Panel A* was adapted from Fig. 8 in Hoegh-Guldberg (1999), while *Panels B* and *C* were adapted from Fig. 5, Hoegh-Guldberg (2004)

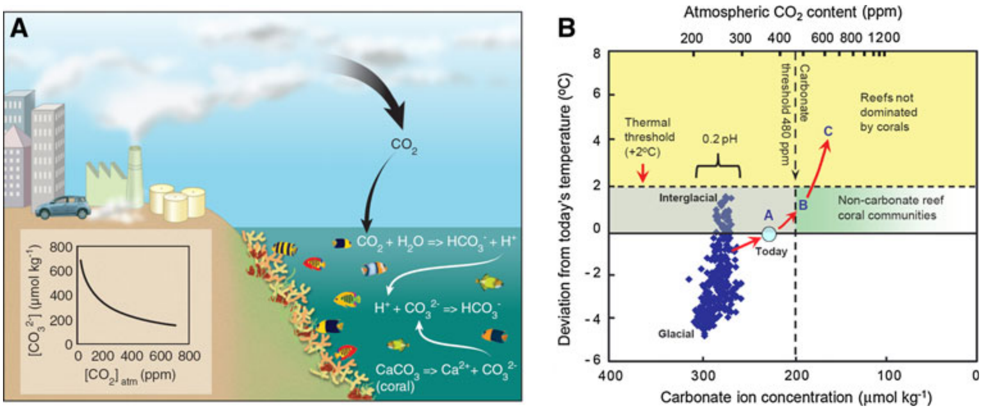

Fig. 3 **a** Ocean acidification is a consequence of higher atmospheric carbon dioxide concentrations. Approximately 30% of the carbon dioxide emitted by human activities is currently taken up by the World's oceans, where it reacts with water to create dilute acid, carbonic acid. The dissociation of carbonic acid leads to a proton that reacts with carbonate ions, converting them to bicarbonate. This leads to a decrease in the availability of carbonate ions (see insert figure showing decrease in carbonate ion concentration is the functional atmospheric carbon dioxide) which impacts marine calcifiers such as corals and calcareous algae. Changing CO_2 and pH may have additional impacts. **b** Temperature, [CO_2 atm] and carbonate concentrations reconstructed for a typical coral reef (mean temperature = 25°C) over the past 420,000 years. Carbonate ion concentrations were calculated from CO_2 atm and temperature deviations from today's conditions using Vostok Ice Core data (Petit et al. 1999). *Red arrows* indicate pathway to the future for A1B stabilization at about 750 ppm CO_2 atm. Further details of the calculations are presented in Hoegh-Guldberg et al. (2007). Figure reprinted courtesy of permission of Science Magazine)

(Donner et al. 2005). Unfortunately, these studies have one unifying conclusion; when carbon dioxide doubles, coral reefs are thrust into conditions in which mass coral bleaching and mortality events become the norm. This magnitude of stress, however mild in the range of possible greenhouse futures, leads to the seemingly inescapable conclusion that future tropical reef systems will have residual coral cover in a high CO_2 world (Hoegh-Guldberg 2005; Hoegh-Guldberg et al. 2007).

Ocean acidification and declining of marine calcification

Several researchers at the end of the 1990s began to argue that increasing atmospheric carbon dioxide levels should have a direct effect on the calcification rates of corals and other calcifying organisms by lowering the availability of carbonate ions in the world's oceans (Gattuso et al. 1999; Kleypas et al. 1999b). More than one-third of the carbon dioxide that has entered the atmosphere has entered the ocean where it combines with water to form the dilute acid, carbonic acid (Raven et al. 2005). Soon after it forms, carbonic acid dissociates to form a bicarbonate ion and a proton (Fig. 3a). The proton then combines with carbonate to produce a second bicarbonate ion and in doing so decreases the overall oceanic concentration of carbonate. Given that sea water is supersaturated relative to the precipitation of calcium carbonate, it might be expected that marine calcifiers might be able to adjust to the decrease in carbonate ions in the ocean as atmospheric carbon dioxide concentrations continue to increase. Extensive experimental studies, however, have shown that the calcifying abilities of marine organisms as diverse as *coccolithophore* (phytoplankton), *pteropods* (molluscs), and corals (Raven et al. 2005; Kleypas and Langdon 2006) are highly dependent on the concentration of carbonate ions in the water column. Importantly, the net accretion of coral reefs approaches zero at carbonate ion concentrations of 200 μmol per kilogram (water) or less. This is also evident from the current worldwide distribution of carbonate coral reefs, which always occur in areas where the concentration of carbonate is higher than this value. Critically, this concentration of carbonate occurs when CO_2 atm reaches 450 ppm or more.

Measurements of the carbonate equilibrium in tropical oceans reveal that the pH and the concentration of carbonate ions have decreased (Sabine et al. 2004) which is enough (if it continues) to reduce the overall carbonate saturation state of the ocean by 40–50% by the end of the century. These changes in concert with rising sea temperatures are already be having an impact on coral reefs, probably also a consequence of increasing temperature stress, with the observation that the calcification of corals on the Great Barrier Reef (De'ath et al. 2009) and in Thailand (Tanzil et al. 2009) has decreased by around 15% since 1990. These changes are significant for two important reasons. The first is that they are unprecedented in the 400 years of coral record inspected by both of these teams, and the second is that small decreases in calcification can cause entire reef systems to fall below the balance between calcification and erosion. In the latter case, it is important to note that the calcification of corals and other organisms is almost entirely balanced by biological as well as physical erosion and that the net equilibrium between these two forces determines whether reefs are maintained by calcifiers. Rates of erosion on reefs are high, with as much as 90% of the calcium carbonate that is deposited by corals and other calcifiers being removed by erosion (Odum and Odum 1955; Smith and Kinsey 1976; Davies and Hopley 1983). Recent work by Silverman et al. (2009) has revealed field evidence that many coral reefs will begin to dissolve if at atmospheric carbon dioxide levels double over this century. Rates may also be influenced by ocean acidification although there is little information on how aspects such as biological erosion will vary with ocean pH and carbonate ion concentration. It is clear, however, that there is the potential for these processes to increase as concentrations of carbonate ions decrease, and hence that current assumptions that biological erosion will stay constant may be optimistic. This said the implications of the changing carbonate balance of coral reefs are highly significant, especially when it comes to the role that coral reefs play in providing coastal protection and other services such as habitat for the multitude of organisms on coral reefs today.

Rising sea levels

The factors associated with rapid climate change that will affect coral reefs are not restricted to rising sea temperatures and falling carbonate ion concentrations. Other factors such as sea level rise, storm intensity, the incidence of drought, and impacts on sediment flux may play important though regional roles in their impact on coral reefs.

Global sea level is currently increasing at the rate of 3.3 mm yr^{-1} (Church and White 2006; IPCC 2007), although it is important to note that the amount varies geographically and that the overall rate is accelerating. The fourth assessment report of the IPCC projected that sea level would increase by between 18 and 59 cm by 2100, above 1990 levels, excluding future rapid dynamical changes in ice flow from the ice sheets of Greenland and Antarctica, for the full range of SRES emission scenarios (IPCC 2007). There are considerable uncertainties around this estimate, particularly given the sudden and precipitous loss of summer Arctic ice over the past 5 years (which exceeds even the worst case scenario of the IPCC, Cressey 2007; Meier et al. 2007; Zhang et al. 2008). Recent evidence that this is being accompanied by rapid melting and breakdown of the Greenland (Witze 2008) and Antarctic (Steig et al. 1998; Steig et al. 2009) ice sheets suggests that scenarios of how sea level will change will need revision, especially given the observation that ice sheet melting now dominates the factors contributing to global sea level rise (Meier et al. 2007). The potential for several meters of sea level rise over this century is growing, and our ability to estimate this change is improving, as glaciologists understand more about ice dynamics and conclude that abrupt climate change can happen in a relatively short period of time (Steffensen et al. 2008).

Current rates of coral growth and reef accretion appear to be able to keep up with the present rate of sea level rise. If sea level rise continues to accelerate, this situation may change, especially if coral growth and calcification has been compromised by the impacts of thermal stress and ocean acidification. For example, if the increase in sea level accelerates to several meters per century, even healthy coral communities and reefs will have difficulty in keeping up. Add to this, the expectation that coral growth may be minimal if atmospheric carbon dioxide increases above 450 ppm, and the specter of drowned coral reefs as sea levels rise becomes an even greater possibility. Crucially, there is growing evidence of coral reefs being left behind by rapid sea level rise in the recent past (Grigg and Epp 1989; Blanchon and Shaw 1995). In the latter case, timing of a sudden shift in the positioning of coral reefs along shorelines (‘back-stepping’) such as that which happened 121,000 years ago suggested that corals had trouble keeping pace with sea level changes that exceeded 30 mm per year (Blanchon et al. 2009).

Changing weather patterns and storm intensity

Changing weather patterns can play a major influence on coastal ecosystems such as coral reefs. In this respect, changes to rainfall and storm intensity can have significant influences on coastal water quality. For example, long periods of drought driven by changing rainfall patterns may lead to the loss of coastal vegetation and the destabilization of soils within river catchments that flow out into coastal environments. These problems might also be aggravated by increasing storm intensities that would lead to huge amounts of water suddenly becoming available within these catchments, leading to the extensive efflux of nutrients and sediments into coastal waters. Warmer seas are likely to drive more intense storms (Emanuel 2005; IPCC 2007) with the prospect that the extent to which coral reefs experience physical damage may increase, both in intensity and frequency. These types of changes along coastlines may lead to a number of insidious effects on the health of coastal ecosystems.

Ramifications of the loss of corals for ecosystem goods and services

The coral-dominated communities a critically important to the biodiversity and productivity of tropical reef systems (Hoegh-Guldberg et al. 2007), especially given the central role that reef-building corals have in providing the three-dimensional topology that forms the habitat for hundreds of thousands of species. Our understanding of these changes is growing but remains restricted to a handful of organisms such as fish. In the latter case, the decline of coral-dominated reef structures is associated with the loss of approximately 25–50% of fish species. Species that depend on corals for recruitment, food, and shelter represent the most sensitive to the loss of coral communities, while others such as herbivores may actually increase in number over time (Graham et al. 2007; Pratchett et al. 2008; Wilson et al. 2008a, b). Our understanding of how other organisms such as invertebrates and marine algae will change as coral communities continue to decline is limited (Poloczanska et al. 2007; Przeslawski et al. 2008). However, given the tight ecological relationships between corals and many other species, it is highly likely that the loss of corals will be accompanied by disappearance of many other species.

It is important to realize that the reefs that are currently coral dominated will not disappear as reef systems per se. Ultimately, however, they will be replaced by other organisms that may have different physiological and ecological characteristics, leading to rapid changes in the quantity and quality of species suitable for harvesting by coastal people. There is also the prospect that issues such as poisoning from toxins such as ciguatera could increase significantly as benthic communities change from coral-dominated systems to ecosystems dominated by cyanobacteria and other types of organisms. In this regard, Hales and coworkers have reported a steady increase in the number of cases of ciguatera in the Pacific over the past several decades, a trend that appears to be associated with the loss of coral-dominated reef systems (Hales et al. 1999). Given that our understanding of these types of interactions is limited, the potential for surprises like that illustrated by the rise in ciguatera in tropical island communities is considerable.

Interaction and synergies between factors

Many of the key uncertainties within our understanding of how local and global factors will affect coral reef ecosystems lie in the synergies and interactions between factors. At the global level, considerable evidence is accumulating which suggests that global warming and ocean acidification are likely to interact in a number of ways. Anthony et al. (2008) recently demonstrated that increasing seawater acidity lowers a coral's thermal bleaching threshold, with bleaching occurring at lower temperatures in acidified circumstances. This influence of acidification is so strong that corals will bleach when the pH drops to 7.6, without being exposed to elevated sea temperatures. This further emphasizes the idea that projections of the impacts of rising temperatures on corals are likely to be optimistic (Hoegh-Guldberg 1999; Done et al. 2003; Donner et al. 2005; Hoegh-Guldberg et al. 2007). Similar interactions are likely to occur with respect to sea level rise, which may not be a problem as long as corals are healthy and growing vigorously. The combination of rapidly increasing sea temperatures plus slower coral growth, however, introduces the possibility that reefs will be unable to keep pace with the surface of the ocean and run the risk of becoming drowned (Blanchon and Shaw 1995; Blanchon et al. 2009).

Similar interactions have been noted between local and global factors. For example, Hughes et al. (2007) found that reducing the number of herbivorous fish on the coral reef reduced the recovery rate of coral communities from mass coral bleaching by a factor of approximately three. These interactions between global and local factors also indicate a number of adaptive strategies, which arise from the fact that increasing the resilience of coral reefs to global disturbances may be most effectively done by reducing local stresses such as poor water quality and the overexploitation of key functional groups such as herbivores (Hughes et al. 2003; Hoegh-Guldberg et al. 2007). This opportunity is likely to become a major theme within strategies aiming to reduce the impacts of climate change and ocean acidification.

Exceeding the limits to adaptation: is 450-ppm carbon dioxide too much for coral reefs?

The preceding discussion outlines the evidence that coral reefs are extremely sensitive to rising ocean temperatures and acidities, and that major changes can be expected as we approach atmospheric concentrations of carbon dioxide of 450 ppm. This atmospheric carbon dioxide concentration, which will conservatively increase sea temperatures by 2°C and decrease the carbonate ion concentrations of the ocean to below the critical level of 200 μmol kg^{-1}, is likely to drive coral reefs to a non coral-dominated state. As discussed below, this has enormous implications for many thousands of coral-dependent species and ultimately tens if not hundreds of millions of people that are dependent directly on coral reefs for their well-being. Hence, the major conclusion of this chapter is that approaching and exceeding 450-ppm carbon dioxide by the end of this century will largely eliminate carbonate coral reefs. This said it is important to realize that the current decline reported by Bruno and Selig (2007) plus those of De'ath et al. (2009) and Tanzil et al. (2009) suggests quite strongly that even today's concentrations are presenting a huge challenge to coral reef ecosystems.

Arguments underpinning the response of many organisms or populations to climate change are generally built on the assumption that genetic change within the organism does not occur rapidly enough such that populations in a set locations can remain and prosper under the rapid climate change (Walther et al. 2002; Parmesan and Yohe 2003; Hoegh-Guldberg et al. 2007). Several authors have challenged this notion for coral reefs, suggesting that corals and their symbionts may have unique abilities as far as the evolution of their thermal tolerance (Buddemeier and Fautin 1993), even suggesting that "reef corals bleach to survive (climate) change" (Baker 2001). These characteristics, if they did exist, could potentially modify the threshold through which corals and their dinoflagellates respond to changes in the conditions that surround them. An upward shifting threshold, for example, that could keep pace with the rate of climate change would ultimately *remove* the problem of changing sea temperatures for corals and their (Hoegh-Guldberg 2000; Hoegh-Guldberg et al. 2002; Done et al. 2003; Donner et al. 2005).

The evidence to support the notion of rapid changes in the tolerance of corals (by changing symbionts) or through a seemingly *mysteriously* evolutionary process whereby a slow-growing, largely asexual organism such as coral can evolve rapidly is very weak and is largely non-existent (see discussions of this issue by Hoegh-Guldberg et al. 2002; Goulet and Coffroth 2003; Hughes et al. 2003; Goulet 2006). As with most other organisms facing one of the most rapid shifts in climate in recent history, the evolutionary capacity of corals is being outstripped by projected rates of climate change (Walther et al. 2002; Parmesan and Yohe 2003). Populations of organisms such as birds and butterflies are experiencing extinction at lower latitudes, and are establishing habitats closer to the poles where habitat is available, populations closer to the poles are being established (Parmesan and Yohe 2003). Similar trends, though less well documented, are occurring in the ocean (Hoegh-Guldberg 2004). Fish that are normally being found at lower more tropical latitudes are appearing on reefs at higher latitudes (Holbrook et al. 1997). While the establishment of more poleward populations may compensate for local extinction at lower latitudes, the distribution of many species can be highly dependent on other physical and biological factors. Corals, for example, are limited in the extent to which their distributions can shift in poleward direction, given that the distribution of carbonate coral reefs is determined by light and carbonate ion concentrations as well as water temperature (Kleypas et al. 1999b). These factors decrease naturally at higher latitudes and are probably more limiting with respect to the formation of carbonate reef systems than is temperature alone. Consequently, limits set by declining light levels and ocean pH as one goes toward the poles dictate that latitudinal expansions of coral reefs is likely to be modest if they occur at all (Guinotte et al. 2003).

In leaving this discussion of the potential for rapid adaptation, it is important to note that greenhouse gas stabilization is a central requirement to any adaptive response by life on our planet. Climate change under mid- to high-range emission scenarios is characterized by continuously changing climate for many hundreds if not thousands of years (IPCC 2007). This has important implications for the expectation of how populations of corals and other coral reef organisms may change. For example, if we were to stabilize global temperatures at 2°C above present-day conditions (i.e., low emission scenarios), coral populations would see an initial decrease in population size as unfit genotypes are eliminated followed by the proliferation of fit genotypes at the new temperature. We might also expect the migration of thermally tolerant lower-latitude genotypes to migrate to more poleward higher latitude reefs over time (probably over decades) and for these genotypes to flourish at these higher latitude sites as conditions stabilized (the influence of ocean acidity set aside). Without stabilization of greenhouse gas concentrations, however, conditions and therefore the associated intense selective pressure would continue to operate on new migrants, preventing their proliferation of across the more high-latitude locations. Corals and their many dependents would necessarily remain at low abundances under these higher emission scenarios.

Implications of the loss of coral-dominated reef systems for human-dependent societies

The projected changes for coral reefs under a rapidly changing climate are likely to have important consequences for coral reef–related industries such as tourism and fisheries, as well as the estimated 500 million people that current depend on coral reefs for their daily existence. It also has serious implications for the somewhat delicate and often narrow nature of the economies of many small island states (Hoegh-Guldberg 2000). The benefits of coral reefs to the human societies range from those related to (a) *provisioning*, which includes food, construction materials (e.g., limestone) and medicines derived from coral reefs; (b) *regulating*, which includes protection of shorelines, the maintenance of water quality and clean sands; (c) *cultural*, which includes traditional spiritual relationships and tourism, and (d) *supporting*, which includes important yet indirect benefits such as the supply of oxygen and other basic life support systems (Millennium Ecosystem Assessment 2005).

Attempts to define the value of reefs in economic terms are complicated by a number of issues. The direct (conservative) benefits have been estimated as lying between US$ 100,000 and US$ 600,000 per km^2 (Costanza et al. 1998; Cesar et al. 2003). Industries such as tourism often form the main driver of coral reef nations, with up to 80%

of total income dependent on visitors from overseas (Hoegh-Guldberg and Hoegh-Guldberg 2004). These industries can also represent millions of dollars of revenue. National estimates vary widely and depend often on the size of reef resources and the state of development of the particular country's economy. For example, approximately US$ 90 billion flows into Caribbean economies from tourism and fishing on their coral reefs (Jameson et al. 1995), while approximately US$ 1.6 billion (Birkeland 1997) has been estimated to flow into US economies each year. In Australia, net income to the national economy from the Great Barrier Reef exceeds $US 4 billion per annum from international tourism alone (Hoegh-Guldberg and Hoegh-Guldberg 2004; Access Economics 2005). In Indonesia, where coastal areas such as beaches are a major draw card for tourism, reefs are estimated to be worth US$ 1 million km^{-1}, based on the cost of maintaining sandy beaches when reefs have become degraded. The economies of countries like the Maldives and the Seychelles are largely dependent on coral reefs through diving and other coastal tourism (Wilkinson et al. 1999; Westmacott et al. 2000). Coral reefs in Sri Lanka have been valued have been valued at between US$ 0.14 and US$ 7.5 million km^{-2} over a period of 20 years (Troëng and Lindén 1998), while those in American Samoa reefs have an estimated value of estimated at US$ 0.14 km^{-2} (Spurgeon and Roxburgh 2005). The direct valuation of reefs is an absolute minimal value, given that these values do not include many ecosystem services such as gas exchange (CO_2 uptake and O_2 production) or the cultural value of coral reefs. Values are also restricted to here and now and do not take into account the fact that these benefits are received each year and will go on for as long as reefs are in existence.

Our understanding of how reef-dependent economies would be affected by a decline in reef resources is still in its infancy. Uncertainties lie in understanding the relationship between tourism and reef resources and in understanding how resilient economies that are dependent on coral reefs may change as a result of changes in the state of these resources. Coastal communities in North Queensland, for example, are highly dependent on income flowing from international tourists that travel to Australia to visit the Great Barrier Reef. In this regard, over 80% of income flowing into the coastal economies of these regions depends on the perception that the Great Barrier Reef is pristine and is one of the best preserved coral reefs in the world (Hoegh-Guldberg and Hoegh-Guldberg 2004). This is seen as a major motivator for tourists to travel from distant destinations such as Europe and North America as opposed to traveling to the closer coral reef destinations such as the Caribbean, where coral reefs are in a relatively poorer state (Pandolfi 2005). Using scenario modeling, Hoegh-Guldberg and Hoegh-Guldberg (2004) projected losses of up to US$ 6 billion over a 19-year period if the Great Barrier Reef lost its pristine reputation to the international tourist market. While these types of studies are rare presently, they are critical to understanding the relationship and value of coral reefs to regional economies.

How small island states might fare if their coral reefs resources dwindle has also been examined for 13 Pacific Island nations (Hoegh-Guldberg et al. 2000). In this study, a range of physical, demographic, social, economic, export, and tourism indicators were explored for each of the 13 nations in order to understand the relative vulnerability of Pacific nations to the projected changes associated with climate change impacts on their coral reef resources. The 13 nations that were involved in this study separated into two groups, of which four Melanesian nations on high mountainous islands were relatively resilient to change (though still facing major problems), while remaining mainly Polynesian nations on low lying atoll systems were generally less resilient and more vulnerable to rapid climate change. In this case, resilience to the effects of rapid climate came down to whether the island economies had alternative livelihoods to those based on healthy coral reef resources (Hoegh-Guldberg 2000). Not surprisingly, this analysis showed that the most vulnerable island nations were Tuvalu and Kiribati, low lying nations islands with few options under rapid sea level rise and warming and acidifying seas that might eliminate the coral reef resources that they almost solely depend.

Clearly, we are in an early stage of our understanding of how the projected changes to coral reefs will affect the industries and people that depend on them. It is apparent, however, that coral reefs are critical to many millions the people across the planet and that degradation of these resources will present serious issues for regional economies and, in some places, food security.

Has article 2 of the United Nations Framework Convention on Climate Change been violated?

The ultimate goal, Article 2 of the United Nations Framework Convention on Climate Change (UNFCCC), is to prevent dangerous interference in the climate system by "greenhouse gas concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system. Such a level should be achieved within a time frame sufficient to allow ecosystems to adapt naturally to climate change, to ensure that food production is not threatened and to enable economic development to proceed in a sustainable manner." (UNFCCC 1992) While the impacts of climate change on biological, social, and economic systems are mounting across a broad front, coral reefs provide a clear example of how the UNFCCC has been violated. Firstly, the evidence is overwhelming that the ability of corals and the reefs they build to keep pace with the current rate of climate change has been exceeded. The fact that a massive disturbance such as mass coral bleaching and mortality events are escalating in frequency and intensity in response to warming seas underscores this fact. Little evidence exists that corals or their dinoflagellate symbionts are adapting at a rate sufficient to counter their extinction as ecosystems. In this regard, the overwhelming evidence points to a massive decline in coral-dominated reefs communities across the planet as their current adapted states are exceeded (Hoegh-Guldberg et al. 2007). Secondly, the linkages between coral reefs, food security, and economic stability for millions of people worldwide are unassailable realities. Because the current patterns and rates of ocean warming are driving the rapid degradation of coral reef resources, food production and the economic security of these nations (many of these being small island states) are currently being severely threatened. It is clear from these two facts that the time frame is not “sufficient to allow ecosystems to adapt naturally to climate change, to ensure that food production is not threatened and to enable economic development to proceed in a sustainable manner”. Lastly, taken with the other factors such as ocean acidification, sea level rise, and changing storm intensities, the current rates of changes are likely to increase significantly leading to further compromise of the intentions and value of Article 2 of the United Nations Framework Convention on Climate Change.

Conclusion: what is a safe level of atmospheric CO_2 for coral reefs?

Twenty-five years since the first large-scale impacts of global warming on coral reefs were reported, we face the stark and inescapable reality that coral reef ecosystems are highly vulnerable to rapid anthropogenic climate change and, like polar ecosystems, likely to be lost within the next few decades and century. Clearly, from the preceding discussion, 450 ppm exceeds the atmospheric carbon dioxide concentration required for the ongoing sustainability of carbonate reef systems. This leads to consideration of what would be a safe level of atmospheric carbon dioxide for coral reefs. The de novo occurrence of mass coral bleaching and its extensive destructive impacts in 1979 (Hoegh-Guldberg 1999) indicates that conditions conducive to the long-term survival of coral reefs were exceeded at that point. The concentration of atmospheric carbon dioxide was approximately 336 ppm in 1979 (Veron et al. 2009). Given an optimistic lag between atmospheric carbon dioxide and sea temperature of 10 years, this would suggest that the safe levels of carbon dioxide for coral reefs must be at or below 324 ppm (Royal Society 2009). While this conclusion is clearly challenging from the point of our ability to return the earth’s atmosphere and climate to safe levels, it emphasizes the extreme risks of adding further greenhouse gases to the atmosphere. The inescapable conclusion from this analysis is that steep and immediate cuts in greenhouse gas emissions are critically important if we are to avoid seriously escalating risks to the millions of people, industries, and entire nations which depend on these critically important coastal ecosystems.

Acknowledgments The author is grateful for the support of Dr. Roberto Iglesias-Prieto and staff at the Unidad Academica Puerto Morelos, Instituto de Ciencias del Mar y Limnologıa, Universidad Nacional Auto′noma de Mexico and the Coral Reef Targeted Research Project (http://www.gefcoral.org). He is also grateful to Dr. Clive Wilkinson for comments and suggestions on an earlier draft.

References

Access Economics (2005) Measuring the economic & financial value of the Great Barrier Reef Marine Park. Report by Access Economics Pty Limited for Great Barrier Reef Marine Park Authority, Townsville

Anthony KR, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. Proc Natl Acad Sci USA 105: 17442–17446

Baird AH, Marshall PA (1998) Mass bleaching of corals on the Great Barrier Reef. Coral Reefs 17:376

Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 237:133–141

Baker AC (2001) Ecosystems—reef corals bleach to survive change. Nature 411(6839):765–766

Birkeland C (ed) (1997) Life and death of coral reefs. Chapman and Hall, New York

Blanchon P, Shaw J (1995) Reef drowning during the last deglaciation; evidence for catastrophic sea-level rise and ice-sheet collapse. Geology 23:4–8

Blanchon P, Eisenhauer A, Fietzke J, Liebetrau V (2009) Rapid sea-level rise and reef back-stepping at the close of the last interglacial highstand. Nature 458:881–884

Brown BE (1997) Coral bleaching: causes and consequences. Coral Reefs 16:S129–S138

Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. PLoS ONE 2(8):e711

Buddemeier RW, Fautin DG (1993) Coral bleaching as an adaptive mechanism—a testable hypothesis. Bioscience 43(5):320–326

Cesar H, Burke L, Pet-Soede L (2003) The economics of worldwide coral reef degradation. Cesar Environmental Economic Consulting, Arnhem

Church JA, White NJ (2006) A 20th century acceleration in global sea-level rise. Geophys Res Lett 33:L01602

Costanza B, d’Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O’Neill RV, Paruelo J (1998) The value of the worlds ecosystem services and natural capital. Ecol Econ 25:3–15

Cressey D (2007) Arctic melt opens Northwest Passage. Nature 449:267

Davies PJ, Hopley D (1983) Growth fabrics and growth-rates of Holocene reefs in the Great Barrier-Reef. J Aust Geol Geophys 8(3):237–251

De'ath G, Lough JM, Fabricius KE (2009) Declining coral calcification on the Great Barrier Reef. Science 323:116–119

Done TJ, Whetton P, Jones R, Berkelmans R, Lough J, Skirving W, Wooldridge S (2003) Global climate change and coral bleaching on the Great Barrier Reef. In: Department of Natural Resources, Mining (ed) Final report to the State of Queensland Greenhouse Taskforce. Department of Natural Resources and Mining, Townsville

Donner SD, Skirving WJ, Little CM, Oppenheimer M, Hoegh-Guldberg O (2005) Global assessment of coral bleaching and required rates of adaptation under climate change. Global Change Biol 11(12):2251–2265

Emanuel K (2005) Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436(7051):686–688

Gattuso JP, Allemand D, Frankignoulle M (1999) Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: a review on interactions and control by carbonate chemistry. Am Zool 39(1):160–183

Glynn PW (1979) Climatic cycles may affect reef growth. Smithson Res Notes 4(4)

Glynn PW (1988) El-Niño Southern Oscillation 1982–1983—Nearshore population, community, and ecosystem responses. Annu Rev Ecol Syst 19:U309

Glynn PW (1991) Coral-Reef Bleaching in the 1980s and possible connections with global warming. Trends Ecol Evol 6(6):175–179

Glynn PW, Dcroz L (1990) Experimental-evidence for high-temperature stress as the cause of El-Niño-coincident coral mortality. Coral Reefs 8(4):181–191

Glynn PW, Peters EC, Muscatine L (1985) Coral tissue microstructure and necrosis: relation to catastrophic coral mortality in Panama. Dis Aquatic Org 1:29–37

Goreau TJ, Hayes RL (1994) Coral bleaching and ocean hot-spots. Ambio 23(3):176–180

Goulet TL (2006) Most corals may not change their symbionts. Mar Ecol Prog Ser 321:1–7

Goulet TL, Coffroth MA (2003) Stability of an octocoral-algal symbiosis over time and space. Mar Ecol Prog Ser 250:117–124

Graham NA, Wilson SK, Jennings S, Polunin NV, Robinson J, Bijoux JP, Daw TM (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries and ecosystems. Conserv Biol 21(5):1291–1300

Grigg R, Epp D (1989) Critical depth for the survival of coral islands: effects on the Hawaiian archipelago. Science 243:638–641

Guinotte JM, Buddemeier RW, Kleypas JA (2003) Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. Coral Reefs 22(4):551–558

Hales S, Weinstein P, Woodward A (1999) Ciguatera (fish poisoning), El Niño, and Pacific sea surface temperatures. Ecosyst Health 5:20–25

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50(8):839–866

Hoegh-Guldberg O (2000) Global Climate Change and the thermal tolerance of corals. Galaxea JCRS 2:1–11

Hoegh-Guldberg O (2004) Coral reefs in a century of rapid environmental change. Symbiosis 37(1–3):1–31

Hoegh-Guldberg O (2005) Low coral cover in a high-CO_2 world. J Geophys Res 110:C09S06

Hoegh-Guldberg H, Hoegh-Guldberg O (2004) Biological, economic and social impacts of climate change on the Great Barrier Reef. World Wide Fund for Nature

Hoegh-Guldberg O, Salvat B (1995) Periodic mass bleaching of reef corals along the outer reef slope in Moorea, French Polynesia. Mar Ecol Prog Ser 121:181–190

Hoegh-Guldberg O, Smith GJ (1989) The effect of sudden changes in temperature, irradiance and salinity on the population density and export of zooxanthellae from the reef corals Stylophora pistillata (Esper 1797) and Seriatopora hystrix (Dana 1846). Exp Mar Biol Ecol 129:279–303

Hoegh-Guldberg H, Hoegh-Guldberg O, Stout DK, Cesar H, Timmerman A (2000) Peril in pacific: biological. Economic and social impacts of climate change on Pacific Coral Reefs. Study for Greenpeace International, Amsterdam

Hoegh-Guldberg O, Jones RJ, Ward S, Loh WK (2002) Ecology—is coral bleaching really adaptive? Nature 415(6872):601–602

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318(5857): 1737–1742. doi:10.1126/science.1152509

Holbrook SJ, Schmitt RJ, Stephens JS (1997) Changes in an assemblage of temperate reef fishes associated with a climate shift. Ecol Appl 7(4):1299–1310

Hughes TP (1994) Catastrophes, phase shifts, and a large-scale degradation of Caribbean coral reef. Science 265:1547–1551

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301(5635):929–933

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr Biol 17:360–365

IPCC, 2007: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, H.L. Miller, Eds., Cambridge University Press, Cambridge, UK and New York, NY, USA

Jameson SC, McManus JW, Spalding MD (1995) State of the reefs: regional and global perspectives. International Coral Reef Initiative, Washington DC, USA

Jones R, Hoegh-Guldberg O, Larkum AWL, Schreiber U (1998) Temperature induced bleaching of corals begins with impairment of dark metabolism in zooxanthellae. Plant Cell Environ 21:1219–1230

Kleypas JA, Langdon C (2006) Coral reefs and changing seawater chemistry. In: Phinney J, Hoegh-Guldberg O, Kleypas J, Skirving W, Strong AE (eds) Coral reefs and climate change: science and management. AGU Monograph Series, Coastal and Estuarine Studies. American Geophysical Union, Washington DC, USA, pp 73–110

Kleypas JA, Buddemeier RW, Archer D, Gattuso JP, Langdon C, Opdyke BN (1999a) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. Science 284(5411): 118–120

Kleypas JA, McManus JW, Menez LAB (1999b) Environmental limits to coral reef development: where do we draw the line? Am Zool 39(1):146–159

Leggett J, Pepper WJ, Swart RJ (1992) Emissions scenarios for IPCC: an update. In: Houghton JT, Callander BA, Varney SK (eds) Climate change 1992: the supplementary report to the IPCC scientific assessment. Cambridge University Press, Cambridge, pp 71–95

Lough JM (2000) 1997–98: unprecedented thermal stress to coral reefs? Geophys Res Lett 27(23):3901–3904

Meier MF, Dyurgerov MB, Rick UK, O'Neel S, Pfeffer WT, Anderson RS, Anderson SP, Glazovsky AF (2007) Glaciers dominate eustatic sea-level rise in the 21st century. Science 317:1064–1067

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: synthesis. Island Press, Washington, DC

Muscatine L, Goiran C, Land L, Jaubert J, Cuif JP, Allemand D (2005) Stable isotopes (delta C-13 and delta N-15) of organic matrix from coral skeleton. Proc Natl Acad Sci USA 102(5):1525–1530

Nakamura T, van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar Ecol-Prog Ser 212:301–304

Odum HT, Odum EP (1955) Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol Monogr 25(3):291–320

Pandolfi JM (2005) Are US coral reefs on the slippery slope to slime? (vol 307, pp 1725, 2005). Science 308(5729):1742–1743

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421(6918):37–42

Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola J-M, Basile I, Bender M, Chappellaz J, Davisk M, Delaygue G, Delmotte M, Kotlyakov VM, Legrand M, Lipenkov VY, Lorius C, Pepin L, Ritz C, Saltzman E, Stievenard M (1999) Climate and atmospheric history of the past 420, 000 years from the Vostok ice core, Antarctica. Nature 399:429–436

Poloczanska E, Babcock R, Butler A, Hobday AJ, Hoegh-Guldberg O, Kunz TJ, Matear RJ, Milton D, Okey TA, Richardson AJ (2007) Climate change and Australian marine life. Oceanogr Mar Biol Annu Rev 45:407–478

Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR, Jones GP, Polunin NVC, Mcclanahan TR (2008) Effects of climate-induced coral bleaching on coral-reef fishes—ecological and economic consequences. Oceanogr Mar Biol 46:251–296

Przeslawski R, Ahyong S, Byrne M, Worheide G, Hutchings P (2008) Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. Global Change Biol 14:2773–2795

Raven J, Caldeira K, Elderfield H, Hoegh-Guldberg O, Liss P, Riebesell U, Shepherd J, Turley C, Watson A (2005) Ocean acidification due to increasing atmospheric carbon dioxide. Royal Society Report. Royal Society, London, UK

Reaka-Kudla ML (1996) The global biodiversity of coral reefs: a comparison with rain forests. In: Reaka-Kudla ML, Wilson DE, Wilson EO (eds) Biodiversity II: understanding and protecting our biological resources. National Academy Press, Washington, DC, pp 83–108

Roeckner E, Arpe K, Bengtsson L, Christoph M, Claussen M, Dumenil L, Esch M, Giorgetta M, Schlese U, Schulzweida U (1996) The atmospheric general circulation model ECHAM4: model description and simulation of present-day climate. MPI Report 218. Hamburg. http://www-pcmdi.llnl.gov/projects/modeldoc/amip1/26mpi_ToC_b.html

Royal Society (2009) The Coral Reef Crisis: Addressing the Threats of Global Warming and Ocean Acidification. Statement prepared by J. E. N. Veron, David Attenborough, Ken Caldeira, Ann Clarke, James Crabbe, Andreas Fischlin, Wendy Foden, Rachel Garthwaite, Ove Hoegh-Guldberg, Simon Harding, Rachel Jones, Tim Lenton, David Obura, Paul Pearce-Kelly, Dirk Peterson, Peter Read, Chris Reid, Callum Roberts, Alex Rogers, Charles Sheppard Mark Spalding, Mary Stafford-Smith, Kristan Teleki, John Turner and Philip Willamson (in press)

Sabine CL, Feely RA, Gruber N, Key RM, Lee K, Bullister J, Wanninkhof R, Wong C, Wallace D, Tilbrook B (2004) The oceanic sink of anthropogenic CO_2. Science 305:367–371

Silverman J, Lazar B, Cao L, Caldeira K, Erez J (2009) Coral reefs may start dissolving when atmospheric CO_2 doubles. Geophys Res Lett 36:L05606

Smith SV, Kinsey DW (1976) Calcium-carbonate production, coral-reef growth, and sea-level change. Science 194(4268):937–939

Spalding MD, Ravilious C, Green EP (2001) World atlas of coral reefs. Prepared at the UNEP world conservation monitoring centre. University of California Press, Berkeley, CA, USA

Spurgeon J, Roxburgh T (2005) A Blueprint for maximising sustainable coastal benefits: the American Samoa case study. In: 10th international coral reef symposium, Okinawa, Japan, 2005

Steffensen JP, Andersen KK, Bigler M, Clausen HB, Dahl-Jensen D, Fischer H, Goto-Azuma K, Hansson M, Johnsen SJ, Jouzel J, Masson-Delmotte V, Popp T, Rasmussen SO, Rothlisberger R, Ruth U, Stauffer B, Siggaard-Andersen ML, Sveinbjornsdottir AE, Svensson A, White JWC (2008) High-resolution Greenland ice core data show abrupt climate change happens in few years. Science 321:680–684

Steig EJ, Brook EJ, White JWC, Sucher CM, Bender ML, Lehman SJ, Morse DL, Waddington ED, Clow GD (1998) Synchronous climate changes in Antarctica and the North Atlantic. Science 282:92–95

Steig EJ, Schneider DP, Rutherford SD, Mann ME, Comiso JC, Shindell DT (2009) Warming of the Antarctic ice-sheet surface since the 1957 International Geophysical Year. Nature 457:459–462

Strong AE, Kearns EJ, Gjovig KK (2000) Sea surface temperature signals from satellites—an update. Geophys Res Lett 27(11):1667–1670

Tanzil J, Brown B, Tudhope A, Dunne R (2009) Decline in skeletal growth of the coral Porites lutea from the Andaman Sea, South Thailand, between 1984, 2005. Coral Reefs 28(2):519–528

Toscano MA, Liu G, Guch IC, Casey KS, Strong AE (2000) Improved prediction of coral bleaching using high-resolution HotSpot anomaly mapping. In: 9th international coral reef symposium, Bali, Indonesia, pp 1143–1147

Troëng S, Lindén O (1998) Environmental economics of coral reef destruction in Sri Lanka. Ambio 27:627–634

UNFCCC (1992) The United Nations Framework Convention on Climate Change. http://unfccc.int/essential_background/convention/items/2627.php (accessed August 13, 2009)

Veron JEN, Hoegh-Guldberg O, Lenton TM et al (2009) The coral reef crisis: the critical importance of <350 ppm CO_2. Mar Pollut Bull 58:1428–1436

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416(6879):389–395

Ward S, Harrison PJ, Hoegh-Guldberg O (2002) Coral bleaching reduces reproduction of scleractinian corals and increases susceptibility to future stress. In: 9th international symposium for reef studies, Bali, Indonesia, pp 1123–1128

Westmacott S, Teleki K, Wells S, West JM (2000) Management of bleached and severely damaged reefs. IUCN, Cambridge, UK

Wilkinson CR (1999) Global and local threats to coral reef functioning and existence: review and predictions. Mar Freshw Res 50(8):867–878

Wilkinson C (2004) Status of coral reefs of the world: 2004. Global coral reef monitoring network. Australian Institute of Marine Science, Townsville

Wilkinson C (2008) Status of coral reefs of the world: 2008. Global coral reef monitoring network. Australian Institute of Marine Science, Townsville

Wilkinson CR, Hodgson G (1999) Coral reefs and the 1997–1998 mass bleaching and mortality. Nat Res 35:16–25

Wilkinson C, Linden O, Cesar H, Hodgson G, Rubens J, Strong AE (1999) Ecological and socioeconomic impacts of 1998 coral mortality in the Indian Ocean: an ENSO impact and a warning of future change? Ambio 28(2):188–196

Wilson SK, Burgess SC, Cheal AJ, Emslie M, Fisher R, Miller I, Polunin NVC, Sweatman HPA (2008a) Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. J Anim Ecol 77:220–228

Wilson SK, Fisher R, Pratchett MS, Graham NAJ, Dulvy NK, Turner RA, Cakacaka A, Polunin NVC, Rushton SP (2008b) Exploitation and habitat degradation as agents of change within coral reef fish communities. Global Change Biol 14:2796–2809

Witze A (2008) Losing Greenland. Nature 452:798–802

Yonge CM, Nichols AG (1931) Studies on the physiology of corals: V. The effect of starvation in light and in darkness on the relationship between corals and zooxanthellae. Scientific Report of the Great Barrier Reef Expedition

Zhang J, Lindsay R, Steele M, Schweiger A (2008) What drove the dramatic retreat of Arctic sea ice during summer 2007. Geophys Res Lett 35:L11505