2. Coral Reefs and Climate Change: Susceptibility and Consequences

Joan Kleypas and Ove Hoegh-Guldberg

Summary

- Coral reefs, both tropical and deep cold water, are global centers of biodiversity that are being damaged by a combination of direct human impacts and global climate change.
- The major threats associated with climate change are increasing sea temperatures and increasing ocean acidity as a result of rising atmospheric carbon dioxide (CO_2), as well as a predicted increase in storms.
- Higher than normal sea surface temperatures cause increased stress to corals and result in coral bleaching, and frequently in mortality. We have a better understanding of why the apparently stable symbiosis between corals and their symbiotic dinoflagellate (zooxanthellae) algae breaks down. Bleaching results in the loss of the algae and a reduction in the coral's energy producing systems; severe stress often results in coral mortality.
- Increasing concentrations of CO_2 lower the pH of seawater, which reduces the capacity of corals and many other marine organisms to make calcium carbonate skeletons because of a coincident decrease in the concentration of carbonate ions.
- These threats acting in combination with local factors, such as declining water quality and over-fishing, will reduce the resilience of coral reefs, and change reef structure and community composition. The result will reduce biodiversity through large-scale loss of functional reef ecosystems and the many other organisms that depend on them.
- Action to conserve these reefs is now urgent and must include global and local strategies via the implementation of strong policies for reductions in greenhouse gas emissions and effective management of local stresses that are also damaging coral reefs.

Introduction

Tropical coral reefs are probably the most sensitive marine ecosystem in the world to global climate change. Reefs are already being devastated by the consequences of climate change, and will probably suffer particularly serious damage in the next 10 to 20 years. This chapter seeks to answer the questions: 'Why are coral reefs particularly susceptible to global climate change?' and 'What consequences will flow from this sensitivity to changing environmental conditions?'

The following possible impacts on coral reefs will be examined in this Chapter:

1. Rising sea surface temperatures;
2. Increasing concentrations of CO_2 in seawater;
3. Sea level rise;
4. Possible shifting of ocean currents;
5. Associated rises in UV concentrations; and
6. Hurricanes and cyclonic storms.

This chapter focuses on the tropical shallow water corals that live in symbiosis with dinoflagellate algae. However, there are vast areas of deep-sea corals that live at great depths in dark, cold waters. These vast and complex ecosystems were largely unknown until very recently, but there are serious concerns that global climate change will result in major damage, especially through increasing concentrations of CO_2 in seawater (see the Box below).

Coral reefs are particularly long-lived and highly evolved ecosystems. Tropical reefs are technically shallow water calcium carbonate deposits that arise from the activities of marine organisms. They have existed in one form or another for more than 650 million years. The major organisms that constructed reefs in the past have included algae, corals, calcified sponges (such as the now extinct 'archaeocyathids' and 'stromatoporoids'), bryozoans, bivalves and crinoids. The ancestors of modern-day stony (scleractinian) corals first appeared about 250 million years ago, during the Triassic, and flourished as the prominent reef builders for many periods during the more recent Jurassic (190–150 million years before present) and Cretaceous (150-65 mybp). Like other ecosystems, they were disrupted by the mass extinction events caused by meteors and volcanic eruptions that also resulted in major climate changes. The Cretaceous-Tertiary extinction event 65 million years ago resulted in the extinction of many coral species, but corals eventually re-established their position as the dominant reef-builders about 36 million years ago (Oligocene). There is strong evidence that the beneficial symbiosis that these reef-building corals developed with dinoflagellates (the zooxanthellae) arose about that time and may be a major reason for their success. The last major disruption to reefs, or at least a shrinking of their habitat, was the ice age between the Pleistocene (last period) and the Holocene (current period) when sea levels fell between 110 and 120 m, exposing the shallow living reefs to the air, thereby 'forcing' reefs to grow downwards on near vertical continental slopes. When that ice age ended at the start of the Holocene, sea level rose rapidly and by about 8000 years ago had flooded the continental shelves, thus greatly expanding the area for modern coral reef growth.

Coral reefs have a number of special features that have allowed them to develop over these long periods. Corals, calcareous algae and other reef-dwellers that secrete calcium carbonate develop the reef base that supports the entire ecosystem. It is the reef structure itself that provides the complex habitat that supports high biodiversity. The features of tropical coral reefs outlined below, are those pertinent to global climate change:

- Corals contain photosynthetic symbiotic dinoflagellate algae, ‘zooxanthellae’, that provide them with abundant energy and assist in nutrient recycling, allowing them to survive in generally low nutrient tropical and sub-tropical oceans;
- The large amounts of energy made available to the corals by zooxanthellae enables rapid growth and skeletal development, thereby assisting them to compete effectively with other organisms such as sponges and macroalgae (seaweeds);
- Many corals currently live near their maximum temperature tolerance. This aids more rapid biochemical reactions, but it leaves them vulnerable to small perturbations in temperature;
- Coral reefs occur in the shallow parts of the photic zone, although they often occur as deep as 60 m in clear waters. Their distribution into more temperate zones may be limited to progressively shallower habitats at higher latitudes, primarily because of light limitations in winter;
- The habitat complexity that provides niches for many reef animals and plants depends on the morphological structure of many corals; e.g. branching coral species provide a structurally complex habitat, whereas massive corals provide a solid, stable base. Thus, selective elimination of certain types of species will have repercussions across the community;
- Many animals (e.g. fish, crustaceans, worms) depend on corals for both habitat and food. Many of these have co-evolved complex symbioses; e.g. gall crabs and some fish (damselfish, butterflyfish, and some gobies) only live on a few coral species.

While coral reefs are long-lived and relatively resilient structures, they are still sensitive to disturbance such as excessive wave action, changes to the clarity of the water through excess sediment input resulting from damaging human activities, pollution and the effects of over-fishing. Now global warming and ocean acidification are developing as additional major threats to their future viability, with some of the first impacts already being felt.

The predominant threats associated with climate change are increasing sea surface temperatures and ocean acidity, sea level rise, and the potential for weather changes, including more frequent and intense cyclonic storms. In addition, climate change will involve other stressors such as the increased incidence of disease in coral colonies weakened by bleaching, possible shifting of ocean currents and rises in the incident UV radiation associated with some greenhouse gases that also deplete atmospheric ozone.

1. Rising Sea Surface Temperatures

Sea surface temperatures have been steadily rising in tropical/subtropical waters; e.g. they rose by an average of 0.3°C between the 1950s and 1990. It is likely that reef-building corals are now 1–1.5°C closer to their upper thermal limits than they were 100 years ago, with the result that warmer than average years, arising as a result of natural variability, now push corals beyond their upper thermal thresholds. Sustained temperatures as little as about 1–2°C above the normal summer maximum are sufficient to stress corals, and cause them to bleach. Bleaching is a generalized response to stress that could arise because of changes to the physical and chemical environment. When sea temperatures exceed the summer maximum by approximately 2–3°C for about 4 weeks under clear tropical skies, corals bleach; that is, they usually expel their brown symbiotic algae and reveal either the pale pastel colors of the host pigments, or bleach brilliant white.

We understand some of the mechanisms behind the temperature stress responses of corals. Thermal stress damage starts in the photosynthetic system of the symbiotic zooxanthellae, causing a collapse of the light processing mechanisms, such that the excess light is diverted from normal photosynthesis to producing excess free oxygen radicals. These are toxic to the coral and the symbiosis falls apart, resulting in the corals ejecting the algae, their major source of energy. While the first damage is to the photosynthetic mechanisms of the algae, other aspects of the coral-zooxanthellae symbiosis are also damaged. Thus, many corals are highly sensitive to changes in sea temperature.

Bleached corals may recover their symbiotic zooxanthellae if the temperature stress is mild or short-lived; but if it is more intense or long-lived, corals begin to die or they may be affected in other ways. For example, reproduction and growth may be affected for up to two years after a bleaching event, thus frequent bleaching events will have major impacts on the corals and the reefs they build. Evidence from the field also indicates that stressed corals are more vulnerable to pathogens that may occur on the outer cell surface layer, resulting in more disease in such colonies.

Corals around the world have developed upper thermal thresholds that are close to local maximum temperatures; corals that live in cooler waters at higher latitudes will bleach at much lower temperatures than corals in warmer, more tropical waters. These differences are the result of past adaptation (evolution) to the local temperatures by corals over thousands of years. The rates of sea temperature changes predicted by models of global climate change indicate that coral bleaching will be more frequent and severe in the future. Bleaching was virtually unheard of 30 years ago; now bleaching occurs in some places as frequently as every 3–4 years and could become an annual event in the near future.

Why most potential adaptation mechanisms will not work: A core assumption in the predictions of rapid reef decline is that there will be insufficient genetic change in the corals to keep pace with climate change. The thermal stress thresholds of corals have been relatively stable over several decades and have shown no tendency to shift upwards. However, bleaching and mortality are increasing, which indicates that stress thresholds are not changing rapidly enough to prevent bleaching in rapidly warming seas.

One alternative hypothesis is that corals, via their symbiont zooxanthellae, may evolve rapidly through the acquisition of more thermally tolerant symbionts. If new symbiotic relationships can be rapidly formed within a few decades, corals will become more thermally tolerant, allowing them to keep pace with rapid climate change. Unfortunately there is no evidence that corals can form new symbiotic relationships easily, or that thermal tolerances will rise sufficiently to protect coral reefs from bleaching. No lasting changes have been observed in coral-zooxanthellae partnerships before and after major bleaching events.

The 2007 Intergovernmental Panel on Climate Change Report (IPCC 4th Assessment Report) predicts that climate change will continue for hundreds of years, with increases in greenhouse gases such as CO_2. Current predictions of future coral reef bleaching events indicate that corals will not adapt to warmer water without either a stabilization of greenhouse gas emissions or even a decrease. If low emission technologies result in global temperatures stabilizing at 2°C above the present, coral populations will initially decrease with the loss of temperature sensitive species, until they are replaced by more temperature resistant species. That will take decades if not centuries. However, if greenhouse gases do not stabilize, the most likely scenario is that coral populations will decrease, with growing rates of extinction of corals and the thousands of other species that depend on coral reefs. This will mean an end to the all-important ecological services provided by coral reef ecosystems.

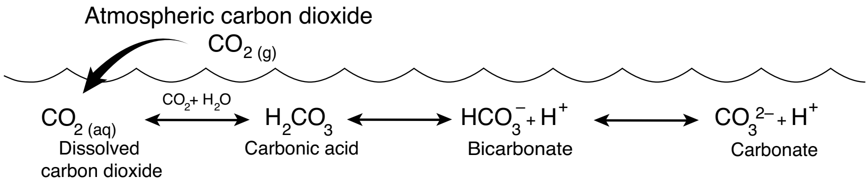
2. Increasing Concentrations of CO_2 in Seawater

The cascading effects on ocean chemistry of rising atmospheric CO_2 levels are referred to as 'ocean acidification'. This does not generally invoke the same sense of urgency as coral bleaching, probably because:

- it is a creeping environmental problem;
- ocean acidification has only recently been accepted as a reality (partly because seawater carbonate chemistry is not intuitive); and
- the process is relatively invisible and does not appear to physiologically harm adult corals.

How ocean acidification will affect all life stages of organisms, reef communities, and reef structures, however, is largely unstudied. While the nature and rate of ocean acidification is well-known and predictable, the potential ecosystem effects of ocean acidification constitute a problem of high uncertainty, but high risk.

The uptake of atmospheric CO_2 by the oceans is a double-edged sword. So far, the oceans have absorbed about a third of the excess CO_2 released into the atmosphere from burning fossil fuels and other human activities. Another third has been taken up by activities on the land, and the remaining third has remained in the atmosphere such that the concentration of CO_2 has gone from 280 parts per million by volume (ppmv) before the industrial revolution to about 380 ppmv today. Ocean uptake of CO_2 from the atmosphere reduces the severity of the greenhouse effect and climate change (and indeed the conditions that cause coral bleaching). Unfortunately, it also alters the chemistry of seawater resulting in lower pH ('ocean acidification') and decreased carbonate ion concentrations. Low pH values represent high hydrogen ion concentrations and more acid conditions, and high pH values represent low hydrogen ion concentration and alkaline conditions. pH is reported on a logarithmic scale; such that a 1.0 change in pH represents a 10-fold change in hydrogen ion concentration. The pH of tropical seawater has remained around 8.2–8.3 for about a half million years, but will decrease to around 7.9–8.0 when atmospheric CO_2 concentrations are double the pre-industrial levels; that represents about a 30% increase in hydrogen ion concentration. This change in ocean acidity will also cause a shift in the relative proportions of the inorganic forms of carbon: dissolved CO_2; bicarbonate; and carbonate. A lowering of seawater pH also means that the carbonate ion concentration will decrease by more than 30%. This represents a substantial change in the chemical conditions supporting calcification, because the carbonate ion is a major skeletal building block for the calcium carbonate ($CaCO_3$) skeletons of corals and other reef-building organisms.



Preindustrial versus doubled preindustrial CO2 concentrations

$CO_{2\,(g)}$ ppmv	$CO_{2\,(aq)} + H_2CO_3$ µmol kg^{-1}	HCO_3^- µmol kg^{-1}	CO_3^{2-} µmol KG^{-1}	pH
280	8	1635	272	8.11
560	16	1867	177	7.93

This diagram illustrates what will happen to ocean chemistry as more CO_2 dissolves in seawater. When CO_2 concentrations in the atmosphere effectively double from the pre-industrial levels, there will be an increase in dissolved bicarbonate and a decrease in the available carbonate in seawater. Thus it will become more difficult and energy consuming for coral reef animals and plants to make skeletons.

DEEP-SEA CORALS AND OCEAN ACIDIFICATION

Most people are familiar with tropical coral reefs, but many are unaware of the wide distribution of deep-sea corals that live in cold waters below the photic zone, in depths of 50-1000 m. The scientific world was unaware of the vast expanses of 'deep-sea coral bioherms' that occur along the edges of continental shelves until a few decades ago, when underwater mapping by remote cameras came into common use. These coral ecosystems are known to support many fisheries, particularly in the North Atlantic Ocean and off the coast of Alaska. A major threat to these communities has been bottom trawling, which physically destroys these slow-growing reefs. Now the global problem of ocean acidification is threatening their existence.

Deep-sea corals are considered to be particularly sensitive to ocean acidification because they often grow just above depths where waters become under-saturated with calcium carbonate. As CO_2 concentrations rise and ocean acidification proceeds, that depth is 'migrating' upwards, and many deep-sea coral ecosystems will soon be immersed in under-saturated waters. Since the distribution of cold water corals today appears to be limited to depths above the saturation depth, it is likely that the deeper coral ecosystems will disappear.

Guinotte JM, Orr J, Cairns S, Freiwald A, Morgan L, George R (2006). Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? Frontiers in Ecology and the Environment 4:141-146.

The significance of these changes: Experiments with corals and coral communities cultured in predicted future seawater chemistry conditions show that calcification rates will decrease by 20–50% of pre-industrial levels by 2050 (the predicted date for a doubling of atmospheric CO_2 concentrations). However, there will be variations in calcification rates between species, and particularly between major organism groups. This will depend on where calcification occurs (e.g. intracellular versus extracellular), and the biological mechanisms of calcification. A puzzling aspect of biological calcification is that corals and other calcifying organisms have the ability to isolate calcifying fluids and strongly control the chemistry of those fluids. Why will the chemistry of the external seawater strongly affect the calcification rates? There are several hypotheses on the coupled nature of calcification and photosynthesis, but no hypothesis has been fully accepted by the science community.

Coral calcification is not only determined by seawater carbonate chemistry, but also by other factors such as temperature, light and nutrients. Evidence that coral calcification rates are declining is now appearing in the scientific literature although some studies up until the early 1980s recorded a rise in calcification over the majority of the 20th century. The increase is probably a result of global warming, because many coral species calcify faster in warmer waters. Coral calcification rates increase with rising temperatures to some optimal temperature, which is near the summer maximum. Calcification then declines when temperatures exceed this maximum. This appears to have been happening over the past 15 years, during which time calcification rates have started to decline, most probably because of the combined impacts of increasing thermal stress and the reduced availability of carbonate ions.

Our understanding of how rises in atmospheric CO_2 will affect seawater chemistry has greatly improved over the last decade. There is little doubt that the carbonate system in seawater is changing according to predictions, and evidence is mounting that calcification rates will decrease, and carbonate dissolution rates will increase. The main area of uncertainty relates to how changes in calcification and dissolution will affect an organism's fitness and survival. Several functions of $CaCO_3$ precipitation have been proposed, but there have been few studies to test how they affect the organism or the community. Some coral species grown under extremely high CO_2 levels completely lost their ability to secrete skeletons; but regained their skeleton-building ability when conditions returned to normal. This is hopeful news that some coral species can survive without their skeletons, but even if 'naked' corals survive they will not retain their original ecological functions and roles within coral reef communities.

Coral reef ecosystems are unique because the excess production of calcium carbonate results in building the reef; the very basis of a coral reef habitat. As calcification rates decline and dissolution rates rise, the balance between reef growth and reef destruction will also change. Reefs that already have a low surplus of carbonate production, e.g. those at high latitudes, may shift from net reef building to net reef loss, and lowered calcification rates will reduce the ability to keep up with rising sea levels.

3. Sea Level Rise

The 2007 4th IPCC Report suggests that there will be a rather modest sea level rise of 20–60 cm by 2100, principally caused by thermal expansion of the oceans but including some melting of glaciers and ice caps. However, the authors of this report acknowledge that the models did not include processes related to increased ice flow. It is also important to realize that the inherently conservative consensus opinion of the fourth assessment report of the IPCC does not include some of the perspectives of the expert committee on sea level. When these opinions are included, the prospect of much higher sea level rise over the 21st century becomes a greater reality. For example, continued melting of the Greenland ice sheet could cause an additional

The list below details some of the functions of Calcium Carbonate skeletons in reef-building organisms.

Function	**Description**
Protection	Skeleton protects organism from predators, strong hydrodynamic conditions, sedimentation, etc.
Enhances photosynthesis	In photosynthetic calcifiers, calcification releases protons that converts bicarbonate to CO_2
Light modification	$CaCO_3$ skeleton enhances light field for photosynthesis by focusing and reflecting light
Reproduction	Colony size sometimes determines fecundity or age of reproductive maturity; rates of fragmentation may be affected by skeletal density
Anchoring to substrate	Secures the organism to the substrate, may also affect initial settlement of recruits
Extension above the bottom	Upward growth limits time that an organism is subjected to bottom sedimentation or scour
Competition for space, light and other resources	Many reef-builders compete for space and light by growing faster than their competitors

rise of a meter or more this century, and with complete melting, an additional 6–7 m rise in sea level over the next few centuries. Such rises would not normally pose problems for most coral reefs; indeed sea level rise provides more space for corals to grow upwards without being exposed to the air.

There will, however, be major problems for islands and low lying coastlines. Coral cays develop via a combination of winds and waves concentrating carbonate sediments; seeds and vegetation carried in by winds and birds help to consolidate these sediments. The combination of sea level rise and possibly more tropical storms will counteract any accretion. A reduction in carbonate production because of ocean acidification will add another negative factor. Many of these coral islands and atolls in the Pacific and Indian Oceans, and in the wider Caribbean will become uninhabitable as seawater washes over the islands during storm surges, penetrates into the fresh groundwater and disrupts food crops. There are no predicted mechanisms for the sand on these islands to build up sufficiently rapidly to keep up with expected sea level rise; therefore human populations will be displaced and parts of some countries including the Bahamas and Colombia, and whole Indo-Pacific states such as Tuvalu, Kiribati, the Marshall Islands and the Maldives may cease to exist.

4. Possible Shifting of Ocean Currents

We have a good understanding of how coral reef ecosystems will be affected by ocean warming, acidification, and sea level rise; however, we know less about other factors associated with climate change. Changing climate conditions may cause oceanic currents to slow or even change direction; and large scale events such as the El Niño Southern Oscillation may change in frequency and/or intensity. Given that currents connect coral reefs to other coral reefs and related marine ecosystems, these changes could have profound effects on the sustainability and management of coral reef ecosystems.

5. Associated Changes in UV Radiation Intensity

The incidence of UV radiation in the tropics is usually very high, particularly in passing through the clear waters bathing coral reefs. Most coral reef animals have evolved structural, chemical and behavioral mechanisms to cope with UV radiation. Thus, no major problems are anticipated with predicted thinning of the ozone layer and a likely increase in UV radiation. Shifting ocean currents and sediment input may cause changes in the clarity of the water column, which will change visible and UV radiation penetration.

6. Weather, Hurricanes and Storms

Global climate change predictions all emphasize greater variations in weather, such as more intense periods of rainfall followed by longer periods of drought. Such climate changes over land will affect runoff and sedimentation (which are also affected by land-based human activities), and affect water quality on many reefs. More extreme rainfall events, for example, will intensify flooding and river-plume damage to reefs, while a decrease in rainfall should lead to improvements in water quality. Tropical cyclonic storms have become more frequent and intense in some regions such as the Caribbean since about 1970, with some evidence that this is fuelled by warmer oceans. Climate models predict that cyclones are likely to be more intense, with more category 4 and 5 storms; but the number of storms may not necessarily increase (see Page 14). Strong storms can cause massive damage to coral reefs; for example Hurricane Andrew in 1992 severely damaged the coral reefs in Florida and other parts of the Caribbean through violent wave impacts. A rise in storm intensity or frequency may put reefs into a permanent state of recovery, because it takes about 10–15 years for a reef to recover from a major storm. How stronger storms are likely to affect reefs is reviewed in the next chapter.

Synergies, Consequences and Opportunities for Management Intervention

Corals build the framework of coral reefs and therefore support thousands of other species. Many of these are totally dependent on corals for food, shelter and reproduction, and will disappear with a loss of coral. Other reef organisms rely only partly on the corals, perhaps needing only the complex structure for survival. The loss of coral will result in some local extinctions and reduced diversity of fish species. For example, some fish species are more sensitive than others, with corallivorous (coral eating) species being the most sensitive; herbivores may actually multiply because there will be more algae to eat. It is probable that many of the large food fish and visiting pelagic fish will not be markedly affected, but our knowledge of these systems is not sufficient to predict which species will or will not show changes with climate change. Several recent estimates suggest that as much as 50% of the fish diversity currently on coral reefs will disappear if coral communities are severely damaged.

An understanding of how coral dependent organisms on reefs will change with the loss of corals is still being developed. However, given the extremely tight relationships between organisms and corals, the loss of corals will almost certainly be accompanied by the loss of many thousands of species. It is also important to realize that corals may not have to completely disappear to cause big effects on the organisms that use them as habitat. For example, some coral dwelling species may require dense coral populations to enable them to live close enough to the opposite sex for reproductive success.

Some climate change impacts, particularly in combination with other influences, will likely reduce the overall resilience of coral reefs. Changes in a coral community (such as reduced biodiversity) may severely undermine system resilience, resulting in a phase shift to a non-coral reef community. For example, the loss of some fish and invertebrates may leave a coral reef more susceptible to episodic outbreaks of pests or invading species. Effects like this tend to be unpredictable, but such unpredicted changes are likely to increase.

Climate change also affects coral reefs in another, fundamental way that is unique to this ecosystem; that is the effects on the geological reef structure itself. Reduced coral cover (e.g. from coral bleaching) coupled with lowered calcification rates and increased dissolution rates (ocean acidification) will reduce the net calcium carbonate production rates on reefs. By the end of this century, the overall balance of carbonate production on many reefs is expected to decline to the point where reef-building may cease or reverse. In addition, any ecosystems that are influenced by the reef structure and reef sediment production will also be affected. These could include mangroves, seagrass beds, and low-lying coral cays. It might also have significant implications for human infrastructure on coastlines protected by coral reefs.

Against the background of these dire predictions facing coral reefs, implementing management of local damage may seem irrelevant unless the current growth in greenhouse gas emissions is constrained. Even with drastic reductions in CO_2 concentrations, there will be changes and challenges for coral reefs. However, after the massive coral bleaching in 1998, coral reefs recovered better and more rapidly where stresses related to poor water quality and over-fishing were well managed. For example, where grazing fish are retained on a reef, corals will repopulate damaged areas 2–3 times faster than on over-fished reefs; similarly, growth rates of corals are faster in non-polluted waters. Managing local stresses on reefs may not prevent damage from climate change, however it will enhance recovery.

Recent evidence indicates it is imperative that there is strong action on reducing greenhouse emissions to ensure that we don't exceed much more than 450-500 ppm CO_2 in the atmosphere. Any response, however, must include local strategies to increase the effective management of local stresses, such as declining water quality and overfishing, damaging coral reefs. Reefs will persist longer under the stresses of the next 50–100 years if they are given the best chance of recovering from the inevitable ecological shocks; this will 'buy time'. These two approaches, decreasing emissions and increasing protective management, are an integral part of effectively addressing the current coral reef crisis and are discussed in Chapter 10, p. 115.

Author Contacts

Joan Kleypas, National Center for Atmospheric Research Boulder, Colorado, USA, kleypas@ucar.edu; Ove Hoegh-Guldberg, Centre for Marine Studies, University of Queensland, Australia. oveh@uq.edu.au

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