

The background of the page is an underwater photograph. The top half shows a view looking up towards the surface, with sunlight filtering through the water, creating a shimmering, dappled light effect. The bottom half shows a close-up of a coral reef. The coral is mostly white, indicating it is bleached, with some brownish-orange patches. Several small fish are visible, including a prominent yellow one in the upper left and a blue one with a yellow stripe on the right.

Part II: Species and species groups

Chapter 10

Vulnerability of reef-building corals on the Great Barrier Reef to climate change

Ove Hoegh-Guldberg, Ken Anthony, Ray Berkelmans, Sophie Dove, Katharina Fabricus,
Janice Lough, Paul Marshall, Madeleine JH van Oppen, Andrew Negri and Bette Willis

10.1 Introduction

10.1.1 Reef-building corals

Reef-building corals (Order Scleractinia Class Anthozoa) form extensive skeletons of calcium carbonate (limestone), depositing enough material over time to form vast reef structures that may be easily seen from space. The majority of reef-building corals are hard (stony) scleractinian corals. Many octocorals (especially soft corals in the family Alcyoniidae and the blue coral *Heliopora*) and some hydrozoan corals (such as *Millepora*) also contribute to reef-building. Corals form the framework of reef structures, while other organisms such as calcareous algae (especially red coralline algae) play a key role in cementing and consolidating the reef framework. This chapter focuses on the vulnerability of reef-building corals to climate change. The implications of climate change for macroalgae are covered in chapter 7 and a broader treatment of reef processes is provided in chapter 17.

10.1.2 The role of reef-building corals in the GBR

Major coral reefs stretch along both coastlines of the Australian continent, from Frazer Island to Torres Strait on the east coast, and from the Houtman Abrolhos reefs across the northwest coast of Australia to the western edge of the Gulf of Carpentaria on the western side of Australia. These coral reefs show a tremendous variety of structures within this broad geographical range, from poorly developed reefs that fringe inshore regions to extensive carbonate barrier reefs offshore. At more southern locations, coral populations form important communities despite the fact that temperature, light and the concentration of carbonate ions are such that there is no net accumulation of calcium carbonate. These reefs are referred to as non-carbonate coral reefs. Australian coral reefs provide critical habitat for a diversity of fauna and flora that includes over 400 species of corals, 4000 species of molluscs and over 1500 species of fish. The role of coral reefs in underpinning coastal economies in Australia is becoming increasingly recognised with the pristine nature of coral reefs being identified as the key driver of an internationally focused tourism industry. The contribution that the Great Barrier Reef (GBR) tourism industry makes, as part of regional tourism, to the Australian economy is A\$6.1 billion per annum^{86,1}.

10.1.3 Critical factors for coral survival

Corals have a symbiotic relationship with dinoflagellate protists (division Pyrrhophyta, class Dinophyceae, genus *Symbiodinium*), which are referred to loosely as zooxanthellae. The dinoflagellate cells of *Symbiodinium* exist within vacuoles in coral host cells, forming a close endosymbiotic mutualistic association. The dinoflagellates photosynthesise at rates similar to that of free-living dinoflagellate species but translocate up to 95 percent of the photosynthetic products to the host cell (reviewed in Muscatine¹⁴³). The coral receives a range of products including sugars, amino acids and larger compounds such as lipids and small peptides. In return, the dinoflagellate symbionts gain access to a rich supply of inorganic nitrogen and phosphorus from the host, which supports the primary productivity of the dinoflagellate under the otherwise low-nutrient conditions typical of sub-tropical and tropical seas. The efficiencies of the internal recycling of nutrients with corals are considered to underpin their ability to build the vast reef structures found along tropical and sub-tropical coastlines.

Examination of the environmental conditions under which corals thrive today provides valuable insight into the sensitivity of corals to key environmental variables and to how they might respond under future climate change. Kleypas et al.¹⁰⁵ explored the environmental factors underpinning 6451 reef locations and identified several factors that were correlated with the distribution of coral reefs. In particular, they noted the strong correlation of carbonate reef systems with well-lit, warm (greater than 16°C) and saline (23 parts per thousand) waters with aragonite saturation states ranging from 3.28 to 4.06. Interestingly, coral reefs are found in a range of nutrient concentrations in contrast to common dogma that coral reefs are always found in low nutrient conditions. These conditions give us insight into the evolutionary limits of reef-building corals, which is important in understanding how corals might, or might not, be able to cope with the major environmental changes projected to occur over this century. This is particularly relevant to problems associated with the acidification of ocean waters caused by rising atmospheric carbon dioxide⁹⁴. Under almost all future scenarios, changes in atmospheric carbon dioxide are likely to decrease the average aragonite saturation state of the world's oceans well below 3.0, the point at which most corals appear unable to form skeletons.

A great deal of research has been undertaken on the direct impacts of climate change on adult coral colonies. The effects on potentially sensitive reproductive processes, however, have received far less attention. Successful reproduction and recruitment is essential for ongoing survival of coral reefs, particularly following heavy disturbances such as bleaching, where recovery of coral abundance and diversity relies largely on recruitment by larvae or propagules from other coral communities⁴⁴. Corals have two distinct strategies for reproduction: broadcast spawning of gametes and brooding of larvae⁷⁹. The early life stages of corals (such as oocytes, sperm, larvae and recruits), as well as critical transitions in life history (fertilisation and larval settlement), may be just as susceptible to thermal stress as mature colonies.

There are many other factors that influence the survival of corals. Poor water quality, such as high nutrient levels and sedimentation rates, can have dramatic influences on corals and the reefs they build. Coral reefs change and diminish as they approach coastal areas typified by natural coastal runoff and flooding events¹⁸⁷. In recent times, coastal development has increased the amount of sediment flowing off the land¹³², adding agrichemicals and other pollutants. Decreasing light levels, increased sediment levels and increasing levels of pollutants can reduce coral growth and in some circumstances have removed coral communities from reefs altogether¹⁸⁸. Storm frequency and intensity also influences coral reefs, through natural events that may remove corals temporarily from some areas. Natural disturbance events like storms are considered to play an important role in mediating the strong competitive forces that may end up excluding less competitive species.

Discussion of how environmental factors determine the distribution of reef-building corals is important basis from which to explore the vulnerability of reef-building corals and their dinoflagellate symbionts to climate change. The next section focuses on such vulnerability within the context of thresholds, specifically with respect to those factors that appear to play a key role in determining the distribution of corals. In addition to dealing with issues of stress exposure, the sensitivity and potential impacts of these factors will also be considered.

10.2 Vulnerability of corals to climate change

10.2.1 Changes in water temperature

10.2.1.1 Exposure – water temperature

Average water temperatures of the GBR are now significantly warmer than at the end of the 19th century, 0.4°C warmer based on 30-year averages (Lough chapter 2). Rates of warming of Australia's tropical and sub-tropical waters are similar to that seen globally for tropical waters (+0.17°C from 1951 to 1990¹²⁶). As with changes in global temperature, these changes are unprecedented in terms of rates of change seen over the past several hundred¹²⁸ if not several thousand years. Warming seas have pushed corals ever closer to their thermal maxima, with the result that warmer than average years (part of natural variability) now push corals beyond their thermal tolerance⁸².

10.2.1.2 Sensitivity – water temperature

The most dramatic manifestation of corals being pushed beyond their thermal tolerances is coral bleaching, which is a condition in which corals lose the brown pigmentation of their dinoflagellate symbionts. Coral bleaching is essentially a stress response in corals that arises as the intricate endosymbiosis between animal and single-celled plant begins to break down.

Corals will bleach in response to a range of conditions including high or low irradiance^{186,201,88,71,121}, elevated or reduced temperatures^{97,98,40,88,76,169,90}, reduced salinity¹⁰³, the presence of some toxins (eg cyanide¹⁰⁰, copper ions⁹⁹, herbicides¹⁴⁷ and microbial infection (eg *Vibrio*¹¹⁰). Bleaching in response to isolated and local-scale (1 to 500 metres squared) stresses has been reported for at least 70 years²⁰¹.

Sensitivity of corals to thermal stress can be highly variable between species^{134,129,185}, between populations within species^{75,22,185} and at spatial scales ranging from centimetres to thousands of kilometres. Some of this variation in sensitivity in space may be due to environmental factors such as differential light regimes⁴⁰, water motion¹⁴⁴ and thermal micro-, meso- and macroclimates. However, a number of biological factors also play a significant role in the sensitivity of corals to temperature. The symbiont type associated with corals in particular has been shown to greatly influence thermal tolerance with so-called type D symbionts conferring an extra 1 to 1.5°C tolerance in *Acropora millepora* compared to type C2²².

Thermal sensitivity at the coral species level is likely to be shaped in large part by host factors that govern which symbiont types form stable symbiosis with particular species, the strength of association under stressful conditions and the flexibility of the symbiosis. Some of the differential sensitivity to thermal stress among species and populations may be due to biochemical processes. For example, enzymes involved in antioxidant functions such as copper/zinc superoxide dismutase and manganese superoxide dismutase and molecular chaperones such as heat shock proteins Hsp60 and 70 and chlorophyll Hsp have been shown to play a role in the defence against thermal stress in either or both animal hosts and symbiotic algae²⁹. Similarly, mycosporin-like amino acids produced by coral hosts have been shown to provide protection against damaging ultraviolet (UV) radiation during hot, still conditions^{54,137}. The role of fluorescent pigments in the photo-protection of corals during bleaching is less clear. These pigments are more common in corals in high light environments, such as reef flats, and are clearly involved in shading corals and their symbionts from excessive light levels^{51,167}. They are also a diverse group of pigments with a range of functions that do not necessarily include reduced

sensitivity to bleaching⁵⁰. These protective and reparative mechanisms are also evident in coral eggs and larvae¹³⁹ and may influence differences in sensitivity to thermal stress between species and life history stages.

10.2.1.3 Impacts – water temperature

Mass coral bleaching events are triggered by warmer than normal conditions, a strong relationship as seen by the fact that mass bleaching events can be predicted using simple sea surface temperature anomalies measured from satellites and time-integrated temperature curves^{21,82}. Light is an important co factor. Corals that are shaded do not bleach as severely as those under normal irradiances^{100,142,9} which is a consequence of the mechanism that involves an increase in the sensitivity of the symbionts to photoinhibition^{100,82}. The water flow field also appears to be important^{144,145} and can greatly impact the photosynthetic performance of zooxanthellae *in hospite*⁸⁴, with corals that are in still as well as warm and sunlit conditions experiencing the greatest coral bleaching. This experimental outcome supports some of the initial observations of coral bleaching, which coincided with the doldrums that are typical of El Nino years in some coral reef regions⁷⁴.

Coral bleaching is not always fatal, and the outcome for the coral is dependent on the level of stress. Bleached corals may recover their symbiotic dinoflagellate populations following a bleaching event if the stress conditions are mild and short-lived. It may take several months for the dinoflagellates to repopulate the tissues, a process that arises from populations of dinoflagellates remaining in the host tissues. Often corals that appear bleached have as many as 10,000 dinoflagellates per centimetre squared⁸⁸ which is two to three orders of magnitude less than that seen in healthy corals but more than enough to initiate re-infection from within. Mortality of corals will occur if conditions are warmer for longer periods, most likely because the symbiosis reaches a critically low energy status as the symbiont population continues to decline⁹. In some cases, mortality will increase to include most corals growing within a population, reef or region⁸².

Australia's coral reefs have bleached repeatedly over the past 30 years, with events occurring in 1980, 1982, 1983, 1987, 1992, 1994, 1998, 2002 and 2006^{150,82,20,24}. Large sections of the GBR have bleached during these years, with impact measurements supporting the conclusion that events in 1998 and then 2002 were the worst on record. Fortunately, mortality rates have been relatively low because the conditions have not been as severe as in other parts of Australia and the world (eg western Indian Ocean in 1998, 46% mortality of corals⁶⁸). Scott Reef in the northwest waters of Australia, for example, has not been so lucky. In 1998, a very warm core of water persisted above the oceanic, and normally well flushed, Scott Reef for several months. This resulted in almost total bleaching and mortality of corals down to 30 metres. Recent reports indicate that recovery of these reefs has been slow¹⁴⁰, with the percentage cover of corals still very low compared to that seen before 1997. Additional bleaching in 2003 and a category 4 cyclone in 2004 have removed further corals from the remaining populations.

Not all coral species are equally susceptible to thermal stress⁸⁷, a factor that may be important in shaping the structure of future coral reefs. Following the 1998 bleaching event on the GBR, Marshall and Baird¹³⁴ demonstrated that bleaching susceptibility varies dramatically among coral taxa on the GBR: acroporids and pocilloporids were severely affected (18 to 38% mortality), poritids and faviids were moderately affected and genera such as *Turbinaria* and *Galaxea* were largely unaffected.

Interestingly, this pattern is consistent with the general pattern of species distributions across the GBR lagoon, with acroporids and pocilloporids increasing in abundance towards offshore locations and *Turbinaria* and poritids (in particular *Goniopora*) often dominating inshore reefs⁴⁶ often characterised by higher temperatures²¹ and high turbidity⁶. Tentatively, increased frequency and intensity of thermal anomalies on the scale of the GBR may push most species of acroporids and pocilloporids beyond their thermal niche boundaries (ie threshold for sustained growth, reproduction and survival). Mid-shelf reefs may experience the largest changes in community composition as intensified runoff scenarios due to stronger cyclones mean that these reefs may occasionally experience high-turbidity regimes reminiscent of inshore reefs today.

Where thermal stress has resulted in significant mortality, coral community composition has often also radically changed as a result of the variable sensitivity of different species to stress. In the Palm Island Group in the central GBR for example, declines in coral cover of between 10 and 80 percent after the 1998 bleaching event were largely due to loss of dominant *Acropora* spp.^{20,176}. Some species such as *Acropora pulchra* suffered local extirpation and other species such as the fire coral *Millepora* spp survived only as a few colonies growing in deeper water. Macro-algae increased to become the dominant cover on some of these reefs thus bringing about a community phase shift. This is a familiar pattern of community change echoed in Indian Ocean and many other reef provinces around the world after the 1998 global bleaching episode¹⁹⁷.

Increased water temperatures have the potential to affect both the reproductive output of parental colonies and the success of early coral life stages. Photosynthetic products are critical to coral gametogenesis and larval production¹⁶⁰ and bleaching during the typical eight-month period of gamete development⁷⁹ may negatively affect reproduction. Bleaching prior to or during gametogenesis can result in low testes and egg numbers along with smaller than usual eggs¹⁹² and incomplete gametogenesis¹⁷⁷. *Acropora* spp. that were affected during the 1998 Okinawan bleaching event also exhibited reduced fertilization in laboratory experiments performed nine months later¹⁵¹. Soft corals bleached in the laboratory were affected in a similar way, exhibiting reduced fecundity and fertilization failure over two reproductive cycles¹³⁸. Larvae from these bleached colonies were lower in lipids, proteins and carotenoids compared with unbleached individuals¹³⁹. Coral reproduction can also be directly affected by increased water temperature, with laboratory experiments indicating incomplete fertilization and more rapid (but often abnormal) embryogenesis as temperatures increase^{19,18,147}. High water temperature can negatively impact larval development rates and the symbiont density in zooxanthellate larvae⁵⁸ and the settlement and survival of azooxanthellate larvae¹⁸. Interestingly, high water temperature in the Virgin Islands was shown to correlate with higher numbers of juvenile corals, but this was accompanied by greater mortality rates⁵⁷.

10.2.1.4 Adaptive capacity – water temperature

The preceding discussion is built on the premise that the behaviour of corals to thermal stress does not change on the same time scale of anthropogenic climate change. In this regard, it is important to consider the potential for corals to acclimatise (a phenotypic change within the individual) or to adapt (a genetic response at the population level) to thermal stress. There is no doubt that corals, like other animals and plants, acclimatise to changes in their environment including seasonal temperature changes^{27,66,39}. Berkelmans and Willis²³, for example, found that the winter maximum upper thermal limit for the ubiquitous coral *Pocillopora damicornis* was 1°C lower than the threshold for the same

species of coral in summer. Nakamura et al.¹⁴⁶ have made similar observations for corals on reefs in Okinawa. Acclimatisation in this regard can occur in a range of cellular mechanisms and at a series of time frames³⁹. As with any physiological trait, however, there are limits to the extent to which organisms can acclimatise to environmental change. Berkelmans and Willis²³ observed that corals have some potential to acclimate to seasonal differences in temperature. However, they have little capacity to acclimate to temperatures greater than 2–3°C above mean summer maxima, at least in experimental heating trials²⁰. The observation of increasing (as opposed to decreasing) mortality rates among coral communities over the past 25 years also suggests that acclimatisation by corals to higher temperatures in the summer may have already been largely exhausted^{82,68,69}.

One of the ways in which reef-building corals may be able to acclimatise is by changing a thermally sensitive *Symbiodinium* type for one that is more thermally tolerant, an idea first put forward by Buddemeier and Fautin³² as the Adaptive Bleaching Hypothesis. There are various interpretations of this hypothesis, and there has been active discussion in the literature over its definitions and whether or not there are data to support the elements of the hypothesis⁸⁹. As yet, there is no evidence of exogenous uptake of new symbiont types by adult scleractinian corals although Lewis and Coffroth¹²³ provided some evidence for exogenous uptake by adult octocoral colonies (note: problems with the contamination of controls in this study throws some doubt on the conclusions however).

There are, however, several examples of multi-cladal associations (coral hosts that contain more than one genetic variety of *Symbiodinium*) that shift the dominance of one genetic variety over another^{15,179,178,22}. These shifts in dominant genotypes as a function of environmental conditions suggest that some genotypes may be more suited to new environmental conditions. For example, Berkelmans and van Oppen²² provided experimental evidence that *Acropora millepora* corals with multi-cladal assemblages can change the dominant symbiont type from *Symbiodinium* type C2 to D and can increase their thermal tolerance as a result. This type of change is a form of acclimatisation, because it represents a shift in the dominance of dinoflagellates that have had a pre-existing endosymbiotic relationship rather than the evolution of new symbiotic associations and also because in most instances the changes on the dominant *Symbiodinium* are not passed on from one generation to the next.

A distinction is drawn between *shuffling* and *switching* of symbiont types where the mechanism of acclimatization is due to the flexibility of coral-*Symbiodinium* symbiosis. Shuffling is a quantitative (compositional) change in the relative abundance of symbionts within a colony whereas switching is a qualitative change involving symbionts acquired from the environment. The latter exogenous symbionts may represent types that are new to the colony but not the species, or may be truly novel to the host species. In the latter case, the term 'evolutionary switching' is appropriate. The latter is used to explain changes in the symbiont distribution within hosts in response to stress. Evolutionary switching, however, is considered an extremely rare event and hence is unlikely to play the ecological role that some authors have claimed (eg Baker¹⁵).

In addition to understanding the limits to the flexibility of coral-*Symbiodinium* symbioses relative to ecological timescales, there has been a growing interest in defining the functional nature of the differences between *Symbiodinium* genotypes. In this respect, the range of genotypes of *Symbiodinium* dinoflagellates that inhabit corals^{181,182,16,125,164,117} is correlated in some instances with light, temperature and stress. Some genetic varieties such as clade D are clearly correlated with warmer and putatively

more stressful habitats than most types of clade C^{183,166,185}. Growth in corals is also clearly influenced by symbiont type. Little et al.¹²⁴ showed that juvenile *Acropora millepora* and *A. tenuis* corals grow faster with *Symbiodinium* clade C compared to those associating with clade D. These types of studies are important in that they explore the functional responses of *Symbiodinium* strains that are otherwise only distinguished by the non-coding segments of their genomes. Future studies need to focus on how the growth, reproduction, thermal tolerance and mortality of corals are influenced by the strain or sub-cladal level of symbiotic dinoflagellates that they contain.

10.2.1.5 Vulnerability and thresholds – water temperature

Isolated examples of coral bleaching have been recorded for many years. Reports, however, of entire communities and reefs bleaching (otherwise known as mass coral bleaching) have only been reported in the scientific literature over the past 30 years. In these cases, coral bleaching may affect up to 100 percent of the reef-building corals in a community. The first examples of mass coral bleaching occur in the scientific literature in the early 1980s^{200,72,150}, and since that time, mass coral bleaching has increased in frequency, intensity and geographical extent⁸².

Some of the most spectacular examples of how mass coral bleaching can eliminate corals from a reef or region occurred during the 1997–1998 global event. In this event, which began in late 1997 in the eastern Pacific and spread across the world by the end of 1998, coral reefs in most parts of the world experienced mass coral bleaching. Some reefs, however, experienced only mild effects of bleaching and recovered within a few months. Other reefs, however, experienced severe coral bleaching that was followed by mass mortality. In regions like the Seychelles, Maldives, Okinawa and Palau, mortality of corals reached over 80 percent^{82,196,77}. Some of these sites have recovered significantly. It is important to note that some regions still have much less coral than they had before the 1998 bleaching event⁶⁹ and hence the term ‘recovering’ needs to be qualified in most if not all cases.

Elevated sea temperatures are the primary cause of mass coral bleaching – a fact that is extensively supported by field and laboratory studies^{26,82,120}. These data highlight the existence of thermal thresholds that vary with geographic location, species, genotype, physical factors (eg light, salinity) and history^{41,56,99,82,23,21,28}. Despite this secondary source of variability, satellite measurements of sea surface temperature anomalies can still be used to predict bleaching events several weeks in advance with greater than 90 percent accuracy at large scales^{82,175}. There is considerable additional information that can be derived as to the severity of the outcome of thermal stress if the time-period of exposure above threshold levels for a coral reef is also considered. High resolution time-temperature curves developed from *in situ* temperature data after the 1998 bleaching event²¹ proved highly effective in predicting bleaching on the GBR in 2002 and 2006. Similarly, the Degree Heating Week (DHW) index developed by Strong et al.¹⁷⁵ is the multiple of exposure intensity (degrees above the threshold) and time, and has been highly successful in predicting mass bleaching events^a. In the 1997–1998 global bleaching event, for example, coral reefs that experienced Degree Heating Month (DHM; a variant on DHW) values of less than 1.5°C per month largely recovered while those that experienced DHM values of 3°C per month or more experienced large scale mortalities⁸³.

a Hotspot program, coordinated by the National Oceanic and Atmospheric Administration, NOAA. http://orbit-net.nesdis.noaa.gov/orad/coral_bleaching_index.html

Projections of how changing sea temperatures will impact Australia's coral reefs reveal that sea temperature may soon exceed the thresholds for coral bleaching on a yearly basis^{82,48,49}. Based on how corals respond to increased temperatures today, an increase of 2°C in the average sea temperature in tropical and subtropical Australia will lead to annual bleaching with up to 97 percent of reefs affected and will almost certainly result in regular large-scale mortality events^{82,84,24}. This is confirmed if one integrates the DHW index of Strong et al.¹⁷⁵ into the projections of how communities of corals will respond to thermal stress events that are hotter and longer in the future. Most evidence indicates that, for the majority of corals, huge increases in mortality will almost certainly ensue⁸⁵.

Models of how the expected changes in mortality will impact the abundance of coral communities indicate that even small changes in mortality regime may lead to large changes in the distribution and abundance of corals on the GBR. These changes have been examined geographically on the GBR by Done et al.⁴⁸, who modelled the probability of mild to severe bleaching events, and how recovery of such aspects as the aesthetic appeal of coral reefs interact within mild and severe climate change scenarios. Done et al.⁴⁸ found that the return time of devastating mass coral bleaching events even under mild warming scenarios was such that the ability of coral reefs to recover and maintain significant coral communities was severely compromised. The conclusions of their study support those of Hoegh-Guldberg⁸² and suggest that the deterioration of coral populations is highly likely under most of the scenarios examined by Done et al.⁴⁸. The debatable issue of rapid genetic adaptation, which may modify some of the conclusions of these two studies, will be discussed presently.

Successful reproduction and recruitment is essential to ensure the long-term survival of coral reefs, particularly following heavy disturbances such as bleaching⁴⁴. Reef-scale sub-lethal bleaching is likely to lead to the widespread failure of gametogenesis^{117,192} and a subsequent reduction in the recovery of disturbed reefs. This secondary impact may persist over several reproductive seasons and¹³⁸ as corals prioritise their energy balance towards colony repair and maintenance rather than reproduction. The only study to directly measure fecundity on GBR corals following bleaching documented widespread reductions in egg number and size across several *Acropora* and *Montipora* species¹⁹². Direct comparisons between the sensitivity of adult corals and their early life stages to thermal stress have not been made for GBR species. *Diploria strigosa* larvae from the Gulf of Mexico, however, exhibited reduced settlement and increased mortality following a weeks exposure to seawater temperatures of between 30°C and 32°C, just 1 to 3°C above the ambient seawater temperature of that region¹⁸. This result indicates that the early life histories of coral may be just as vulnerable to direct thermal stress as adult colonies, even in the absence of symbiotic dinoflagellates. The severity of response is likely to vary between species, and recruitment following bleaching events may be skewed towards those species that are more tolerant to bleaching, further accelerating phenotypic change across reefs.

10.2.2 Changes in light and ultraviolet radiation

Light is obviously of key importance to coral reefs as it drives photosynthesis and powers calcification providing both the organic matter and the calcium carbonate foundation that defines coral reefs. Photosynthesis is however a dangerous process in that it involves the capture of light energy by chlorophyll and other phytopigments and generates a flow of electrons at the same time as it generates oxygen (O₂), a ready acceptor for those electrons. The potential danger lies in the creation of singlet oxygen due to the interaction of chlorophylls that are unable to off-load their excitation

energy with O_2 , and the production of other forms of reactive oxygen species such as superoxide anions (O_2^-) as O_2 accepts electrons that are unable to be processed by electron transport to carbon dioxide (CO_2) fixation¹⁴⁸. The wavelengths of light that drive photosynthesis (photosynthetically active radiation) overlap the visible range and hence the pigments that capture this energy are also visible to humans. Shorter, more energetic wavelengths, (300 to 400 nanometres) also make it through the earth's atmosphere and are referred to as ultra violet radiation (UVR). The dangerous consequences of UVR are well known, most notoriously through the accepted causal role UV plays in the formation of skin cancers. UVR leads to indirect damage through its interaction with photosensitisers like chlorophyll leading to lipid peroxidation and DNA strand breakage. UVR can also directly damage DNA leading to structural changes that inhibit DNA replication and protein synthesis. The presence of UVR however has also been associated with positive morphogenic responses that enable plants to deal with other frequently co-occurring environmental stresses⁷⁰.

Light reaching the earth surface is attenuated in the atmosphere. Ozone plays the major role in attenuating UVR, and clouds (water vapour), dust and gases significantly attenuate photosynthetically active radiation and infrared radiation. Observations of decreases, about 3 percent per decade, in the global ozone, and increases in atmospheric CO_2 , leading to changes in weather patterns that have a potential to alter cloud patterns can therefore significantly affect the intensity and quality of light attaining the earth's surface.

10.2.2.1 Exposure – light and ultraviolet radiation

All reefs witness variability in light associated with diurnal patterns and differential cloud cover. At low latitudes, reefs are additionally affected by seasonal variability in light intensity. The water column attenuates light exponentially both by absorbing and scattering photons resulting not only in a reduction in the intensity of light with depth but also a change in quality due to the preferential absorption and scattering of red and infra-red photons. Even in crystal clear tropical waters, most of the red photons are absorbed within the first few meters of the water column with the implication that shallow water corals living in regions experiencing large tidal fluxes not only witness changes in intensity but also changes in light quality that may have substantial effects on photosynthesis. Particles in the water column such as phytoplankton and suspended sediments further attenuate and alter the spectrum of light. Highly turbid water may reduce benthic irradiance to critical light levels, compromising rates of photosynthesis for organisms like corals and marine plants^{7,8}. Conversely, given that light intensity is a measure of the number of photons passing through a fixed area in a set period of time, the shape of waves and the presence of diffuse or reflective surfaces can amplify the intensity of light by trapping or focusing photons in a specific area. This phenomenon has been shown to occur frequently in shallow lagoonal waters, and has been argued to occur between the branches or even within the tissues of reef building corals⁶⁰.

10.2.2.2 Sensitivity – light and ultraviolet radiation

The light intensity experienced by most photosynthetic organisms is neither constant in the short term (minutes to hours), nor constant in the long term (days to months). An imbalance between the amount of light energy capture and the ability to process that energy leads to the formation of damaging oxygen radicals. However, inadequate capture of light energy leads to scenarios where respiration (or metabolic activity) rates exceed photosynthetic rates impacting on growth and reproduction.

To maximise growth and limit damage, photosynthetic organisms therefore tend to optimise their ability to capture and process light energy to the prevailing environmental light regimes. The outcome is that some photosynthetic organisms are high light specialists, while others are low light specialists, with a few that are flexible enough to accommodate a large range of light intensities. The ability to accommodate a range of light intensities is genetically set by the ability to express proteins that allow for the restructuring of the antennae or the electron transport chain¹⁴⁸. A photosynthetic organism that can handle two light extremes will appear bleached under the high light environment compared to the low light environment due to having expressed proteins that bind less chlorophyll. In contrast, a low light specialist will look bleached in the high light field due to the photo-oxidation of the antennae due to the activity of accumulated singlet oxygen on the histidine ligands that bind the pigment to the protein template. Bleaching in the latter case is more likely to result in mortality².

In corals, dinoflagellates sit within the symbiosome (vacuole) membrane of the coral host cell. These symbiont-containing host vacuoles may be stacked on top of each other within the coral gastroderm leading to a highly heterogeneous light field where deeper dinoflagellates are significantly shaded⁶¹. The host cell may contain flexible pigment-proteins that modulate not only light intensity but also spectral quality⁵² (J Deckenback pers comm). The host may place dinoflagellates within tentacles that can be exposed or withdrawn based on specific spectral cues¹²². Alternatively, the host may alter its skeletal morphology to trap light effectively and reduce the effect of self-shading^{143,8,60} or even maintain fewer symbiotic dinoflagellates to limit self-shading at the expense of dinoflagellate respiration. As these mechanisms have been uncovered, there has been an increasing awareness of the multiple mechanisms that may be in operation even within a single species with no two individuals resorting necessarily to the same set of solutions.

In addition to host variability, there is considerable variability among genetically distinct varieties of *Symbiodinium*. Cultured *Symbiodinium* have been classified as high, low light specialists or generalists according to their ability to restructure their antennae⁹². Genetically distinct *Symbiodinium* have been found to occupy light associated niches within a coral branch¹⁶⁶, yet there are examples of very tight coupling between symbiont and host genotypes¹¹⁶. More often than not corals transplanted from one light environment to another undergo changes to the concentration of chlorophyll per dinoflagellate cell, rather than in the number of dinoflagellate cells present^{61,88,64}. However, this is not always the case with some host colour morphs experiencing no change in dinoflagellate chlorophyll or cell concentrations, but rather compensating changes in host pigmentation (S Dove unpublished data). In some instances, upon transplantation, coral hosts maintain a specific symbiont genotype despite the fact that conspecifics in the new light regime host a distinct symbiont genotype (E Sampayo pers comm). The flexibility associated with accommodating changing light regimes can therefore lie with a flexibility to express physiologically different *Symbiodinium* or with flexible symbiont or host gene expression.

Changes in light quality as opposed to quantity can have a significant effect not only on photosynthesis but also on a range of processes that are essential for maintaining healthy reproducing organisms. These include the setting of circadian clocks and the induction of defensive strategies. In higher plants, light quality plays an important role in balancing photosystem II and photosystem I (PSII/PSI) dynamics with the consequence that plant photosynthesis is most efficient when plants are illuminated with light of similar spectral quality to that in which they were grown^{190,189}. Pigments such as red light sensitive phytochromes and blue light sensitive cryptochromes are involved in setting

the circadian clocks. In addition to this role, phytochromes shift between active and inactive forms in response to different wavelengths of light, particularly red (which is absorbed by photosynthetic organisms) and a red irradiation. These wavelengths provide proximity meter for shade avoiding plants to grow and project into regions of un-attenuated light¹⁷³. Photolyases that repair certain types of UVB damage to DNA are induced by blue or UVA light¹⁴¹.

The role of different wavelengths in stimulating behaviour or genetic response in corals is less well characterised. Levy et al.¹²² showed that some coral species retract their tentacles in response to both blue and red light, while others only respond to blue light, and others do not respond at all. Kinzie and Hunter¹⁰⁴ showed that in comparison to red and green light, blue light stimulated increased chlorophyll a densities in corals, arguing that the relative proportion of blue light increases with depth and hence signals reductions in overall light intensities that necessitate improving the light capturing ability of the antennae. While corals and their symbionts are able to synthesis cryptochromes and photolyases (R Reef pers comm), their functional roles are yet to be elucidated. Photosynthetic action spectra have been provided for some, principally non-symbiotic, dinoflagellates¹⁵⁸. The specific action spectra of PSI, isolated from PSII has yet to be determined for *Symbiodinium* making it difficult to access whether changing spectral quality can result in an imbalance PSI/PSII dynamics.

Reductions in cloud cover and depletions in the ozone layer increase the UVR dose to which organisms are exposed. In clear tropical waters, UVR is principally attenuated by the presence of dissolved organic matter with UVB reduced to 1 percent of surface irradiance by a depth of approximately 11 metres⁵⁵. In response, most organisms have developed mechanisms to either protect themselves from UV damage, or repair DNA damage as it occurs. Protective mechanisms for organisms that are sessile usually involve the production of mycosporine like amino acids (MAAs), compounds that have high extinction coefficients in the UV. These compounds are abundant in corals above 10 metres, and are believed to originate from host diet or be translocated from their endosymbiotic dinoflagellates^{54,108}. DNA repair mechanisms either use specific enzymes (photolyase) that harness light energy to reverse DNA damage, or involve a group of genes (nuclear excision and repair genes) that cooperate in the removal and replacement of damaged DNA. The ability of corals and dinoflagellates to repair UV damaged DNA is yet to be explored. While the ability to synthesise MAAs was initially only linked to clade A *Symbiodinium*¹⁷, this may be because only a few clade C *Symbiodinium* were analysed in this study, subsequent investigation has shown that some clade C *Symbiodinium* also appear to contain MAAs⁶³.

Given that much DNA damage occurs indirectly through the creation of reactive oxygen species due to the interaction of UVR with photosensitisers in an oxygen rich environment, antioxidants play a major role in limiting damage. Both the host and the dinoflagellate may contain photosensitising pigments. Chlorophyll is the most abundant photosensitiser in photosynthetic organisms. Significantly, another fluorescent photosensitiser (named appropriately *killer red* for its ability to kill bacteria is an all protein chromophore isolated from a hydrozoan and which is structurally similar to the range of proteinaceous GFP-like compounds) that have been identified within the pigmentation of corals³³. Interestingly, pigments can also act as effective antioxidants as is best exemplified by carotenoids. As yet, the full range of antioxidants available to either host or symbiont is yet to be determined, it may even turn out that while some GFP-like compounds expressed by hosts are photosensitisers potentially mediating the appropriate defensive response to increases in photon flux density, others may act as antioxidants (M Lesser pers comm).

10.2.2.3 Impacts – light and ultraviolet radiation

Global weather patterns are changing. This is specifically true of southeast Queensland in Australia where drought conditions persist and are infrequently broken up by heavy rainfall. Correlated with these drought conditions is an observed increase in the number of cloud free days over the southern GBR (M Nunez, pers comm). Sustained insolation increases sea surface temperature and places additional stress on photosynthesis as existent pools of antioxidants and other defensive pools are used up. Infrequent and heavy rainfall is also undesirable for communities of corals as it leads to turbid freshwater flood plumes that can drastically attenuate light in the water column⁷.

Additionally, the formation of low temperature cloud particles in the stratosphere provide the surfaces required by reactions, which catalysed by light, that lead to the destruction of ozone. This phenomenon is observed every spring over Antarctica as clouds formed in the winter are exposed to solar radiation. The stratosphere is believed to be cooling as a result of climate change because green house gases trap heat in the troposphere and prevent its escape to the stratosphere. There is therefore a growing concern that climate change may result in an exponential increase in global levels of UVB.

10.2.2.4 Adaptive capacity – light and ultraviolet radiation

It is difficult to access how corals and their endosymbionts will respond to exponential increases in UVR, given that we do not know whether they have DNA repair mechanisms in addition to MAAs and an antioxidant defence mechanism. Given that increased and sustained light stress, at least in the Southern portion of the GBR, appears to co-occur with increasing temperature, it is necessary to ask how stable MAAs and this antioxidant defence system are at elevated temperatures. The answer is perhaps not so promising. Lesser et al.¹²¹ found an inverse correlation between temperature and host tissue MAA concentrations. Equally, if the flexibility to handle high light is dependent on either the symbionts or host ability to acclimatize to the changing light field then it must be hoped that elevated temperature does not interfere with this ability. Experimentally, it has been shown that increasing temperature in a low light field decreases the concentration of the xanthophyll pool, potentially limiting the ability of *Symbiodinium* to divert excess excitation energy to heat⁵³. Similarly, it has been demonstrated that while some forms of host pigmentation appear to correlate with increased photosynthetic performance at lower temperature, corals that are able to express these protein-pigments in high concentrations die as threshold temperatures are attained⁵⁰. Threshold temperatures have been correlated with a reduction in mRNA concentrations for genes encoding these proteins¹⁷¹.

Conversely, however it has been shown that corals that have been exposed in the long term to high light fields cope better (lose fewer symbionts) with increases in temperature²⁹. Closer analysis showed that the host rather than the symbiont antioxidant system was most active on the high-light surface of the coral, although dinoflagellates on the sunlit side of the coral had a significantly larger xanthophyll pool³⁰. An examination of the literature shows that few *Symbiodinium* cultures have been trialled for both heat and light tolerance. Of the few, the exclusively high-light adapted A2 *Symbiodinium* from *Zoanthus* sp. is able to tolerate relatively high temperature. The high- and low-light flexible A1 *Symbiodinium* from *Cassiopeia* sp. is intolerant of high temperatures^{92,93}. Perhaps the message is that if a symbiont is already expressing defence mechanisms that enable it to deal with increased

excitation pressure at PSII, then it can survive a limited additional amount of excitation pressure generated by temperature stress. However if the appropriate defence mechanisms have not previously been induced, then temperature stress above a given threshold will not enable them; despite having potentially enabled key enzymes in the water-water cycle¹²¹.

In this context, the massive amplification of light within the tissues of corals that is predicted to occur during a severe bleaching event, due to the trapping of unimpeded photons by the diffuse and reflective skeletal surface of a scleractinian coral may account for coral mortality⁶⁰. The scenario has been referred to as *photon hell*, which may be appropriate given the lethal doses of UVR or photosynthetically active radiation that are likely to be generated for host and remaining symbiont cells alike.

10.2.2.5 Vulnerability and thresholds – light and ultraviolet radiation

Corals show high sensitivity to light and UVR levels. This sensitivity increases under thermal stress due to blockages of electron flow through photosynthesis, essentially pushing thresholds for light exposure downwards. Increases in light and UV are occurring in tropical and subtropical Australia. These changes, however, are small. Under conditions in which climate change is not occurring, corals are only vulnerable to changes in light and UV to a small extent. This changes dramatically, however, as waters warm. Dramatic changes in the vulnerability of corals and their dinoflagellate symbionts occur as climate change occurs. The demonstration that thermally stressed corals bleach less and survive better if they are shaded during thermal stress reinforces this conclusion, and also suggests that some small scale technologies (eg shading) may successfully reduce the impact of thermal stress on local coral assemblages.

10.2.3 Changes in ocean chemistry

10.2.3.1 Exposure – ocean acidification

The present-day chemistry of the oceans is fundamental to the ability of reef-building corals to calcify and hence form the massive calcium carbonate framework of tropical coral reefs. The oceans have absorbed at least one-third of the excess CO₂ produced by human activities that has entered the atmosphere^{159,107}. On entering the ocean, CO₂ reacts with water to form carbonic acid, which dissociates to form bicarbonate ions and protons. These protons react with carbonate to form bicarbonate, moving the ionic equilibrium from carbonate to bicarbonate as more CO₂ enters the ocean¹⁵⁹. As the oceans take up CO₂, ocean pH and the saturation states of carbonate minerals (calcite, aragonite and high-magnesium calcite) decrease. These minerals are fundamental to the formation of skeletal structures in many marine calcifying organisms such as corals. The reduced carbonate ion concentration significantly reduces the ability of reef-building corals to form their skeletons and hence the reef structures that house hundreds of thousands of marine species.

10.2.3.2 Sensitivity – ocean acidification

The decrease in carbonate ions represents a major problem for calcifying organisms such as corals given that the rate of calcification varies linearly with the carbonate ion concentration^{118,159}. Various lines of evidence indicate that coral calcification rates will decrease and carbonate dissolution rates

increase as the calcium carbonate saturation state decreases. Several controlled experiments of calcification rates under elevated CO₂ levels confirm that calcification rates decrease with increasing CO₂ levels. These measurements suggest that calcification rates may decrease by up to 60 percent with a doubling of atmospheric CO₂ concentrations by end of 21st century. This may put reef structures into net erosion with long-term implications for coastal protection⁸⁵.

10.2.3.3 Impacts – ocean acidification

Cores drilled from long-lived massive corals such as massive *Porites* spp provide insight into how calcification has changed over the past centuries. Some studies^{127,25}, reported evidence of a slight increase in calcification over the decades prior to 1979 with calcification being highly correlated with average sea temperature (0.3 grams per cm² per year or 3.5% increase for each degree C of increase). Lough and Barnes¹²⁷ have proposed that the increase in calcification was probably due to the 0.25°C observed increase in sea temperature on the GBR during the same period and that, initially, some corals may increase their calcification rates as the oceans warm. There is, as yet, no observational evidence of decreases in coral calcification rates on reefs with the 0.1 drop in oceanic pH, though significant decreases have been observed in controlled laboratory experiments.

10.2.3.4 Adaptive capacity – ocean acidification

Another group of authors¹³³ have used the observation of increased calcification over the past 100 years to conclude that the ocean acidification will be counteracted by the putative increase in calcification due to future warmer conditions. This assumption is invalid given that corals start to bleach at just 1°C above today's sea temperatures, and that the physiological literature also unambiguously shows that calcification increases up to the summer sea temperature maxima but then decreases rapidly thereafter¹⁰⁶. Contrary to the predictions of the McNeil et al.¹³³ model, combinations of high sea temperatures and high CO₂ concentrations of future climate scenarios predict dramatic decreases in calcification rates. There would need to be an ever-increasing calcification rate (and a lack of negative influences from thermal stress) to enable the McNeil model to have any credibility. This and other problems with the methods and conclusions of McNeil et al.¹³³ are outlined and fully discussed in Kleypas et al.¹⁰⁶. It seems that the ability of marine calcifying organisms such as corals to adapt to the unprecedented and rapid rates of changes in ocean chemistry, combined with additional stresses resulting from climate change (eg coral bleaching and more destructive tropical cyclones) will be limited.

10.2.3.5 Vulnerability and thresholds – ocean acidification

Doubling atmospheric CO₂ above the ocean will cause the carbonate concentration to decrease to approximately 200 micromol per kg, with temperature having a small influence. A carbonate concentration of 200 micromol per kg is critical in that the calcification of corals and many other organisms declines effectively to zero at carbonate concentrations around this value. This impact is made even more significant because coral reefs are a balance between calcification and erosion and hence calcification needs to be well above zero to avoid a net erosion of coral reefs. There is overwhelming evidence that corals and the reefs they build will not be able to maintain themselves or grow if CO₂ concentrations rise above 500 parts per million^{67,105,78,85,107}. This level of CO₂ is at the lower end of the range of greenhouse scenarios for the end of this century.

10.2.4 Sea level rise

10.2.4.1 Exposure – sea level

Coral reefs of the GBR have adjusted to sea levels that have prevailed for the last 6000 years (since current level reached at end of last Ice Age). Current sea levels, therefore, are one of the controlling factors in terms of coral distribution on the GBR in terms of water depth. Global sea level is rising due to the enhanced Greenhouse effect due to both thermal expansion (of the warmer ocean waters) and contributions from the melting of continental ice sheets and glaciers. Changes to sea level have been of the order of about 20 to 25 cm over the past century^{155,36} and sea level is currently rising at 1 to 2 mm per year, an order of magnitude larger than the average rate over the previous several millennia³⁷. Current projections⁹⁴ suggest a 0.1 to 0.9 metre rise of sea level by 2100. There is however, mounting concern that this rise in sea level may be higher as the Greenland Ice Sheet has been observed to be melting faster than expected. Loss of both the Greenland Ice Sheet and West Antarctic Ice Sheet would result in global sea levels that are more than 10 metres higher than present.

10.2.4.2 Sensitivity – sea level

Previous reviews have all concluded that these changes in sea level are relatively slow when compared to the rate at which corals are able to grow (up to 20 cm per year for branching corals⁴⁷), and hence do not represent a major challenge for healthy coral populations. However, these maximum coral growth rates are rates of linear extension for individual coral branches, not the reef matrix itself. In addition, the emphasis is on healthy corals, which in turn may depend on the effect of rising sea temperature and ocean acidification, and on other stressors such as reduced water quality (eg turbidity and sedimentation).

10.2.4.3 Impacts – sea level

Due to the slowing effect of other factors on growth, there is the potential that coral populations might be left behind by rapid sea level rise. It is also important to keep in mind that these conclusions are dependent on having a slow rise in sea level. They would be invalidated in the longer term if, for example, the Greenland Ice sheet were to melt rapidly¹⁵². If this were so, then sea level rise would accelerate well above coral growth and would stabilise at 6 to 10 metres above current sea level. In this case, sea level rise would represent an extreme challenge for most marine habitats including coral reefs.

10.2.4.4 Adaptive capacity – sea level

A steady, relatively modest (eg 0.1 to 0.9 metres by 2100⁹⁴) rise in sea level is unlikely to be a major problem for corals of the GBR as reef development has been constrained by current sea levels reached several thousand years ago. Corals with high growth rates may be able to keep up with projected sea-level rises. The potential for adapting to rising sea level depends, however, on healthy coral populations which is unlikely to be the case as continued ocean warming (increasing bleaching events) and ocean acidification (reducing calcification rates) compromise the viability of corals on the GBR.

10.2.4.5 Vulnerability and thresholds – sea level

Corals of the GBR are probably less vulnerable to gradual and modest sea-level rise than to other climate change stressors. There is, however, mounting concern that the global rise in sea level is accelerating³⁶ and that the potential for catastrophic rises (of greater than 10 metres) may be triggered by loss of the Greenland Ice Sheet and, possibly the Western Antarctic Ice Sheet. Under such circumstances, extensive areas of coral communities on the GBR would be lost or compromised, as rapid changes in sea level would overwhelm the growth rates of corals pushing their communities into deeper, low-lit areas of the ocean. A massive contraction of coral distributions would almost certainly occur, in particular in coastal, turbid areas where photic zones are already compressed, until the climate stabilised once more.

10.2.5 Tropical storms, rainfall and river flood plumes

10.2.5.1 Exposure – storms and floods

The number of severe cyclones (category 4 and 5 on the Saffir-Simpson scale) has nearly doubled over the past three decades in all ocean basins^{193,59}. Using an index based on power dissipation during the life of each cyclone, Emanuel⁵⁹ showed that cyclone destructiveness has increased dramatically since 1970, correlated with the increase in tropical sea surface temperatures. The record number and intensity of storms in the Gulf of Mexico during 2005 (a record 28 storms of which 15 were classified as hurricanes with winds greater than 100 km per hour^b) underscored the conclusions of both studies. If this trend in destructive cyclone activity continues to rise and interact with other climate change stressors, coral reefs will enter an era of disturbance of unprecedented dimensions.

10.2.5.2 Sensitivity – storms and floods

Storm impacts are part of the natural disturbance regime on coral reefs, and in some areas may help maintain high species diversity by preventing monopolisation by competitively dominant species^{42,44}. However, whereas intermediate disturbance regimes can favour ecosystem health, increased frequency of severe cyclones, such as those predicted for this century, may lead to physical damage and associated stressors beyond what reefs have previously experienced. One basic premise of the intermediate disturbance hypothesis⁴² is that the disturbance frequency and/or severity are low enough to allow succession of the benthic community between events. Importantly, if the frequency or intensity of destructive storms increases beyond the reef's capacity for recovery between events, reef resilience will decline and may shift reefs into alternative, less desirable states^{47,91}.

Benthic communities reset to bare substrate and algae following severely destructive events will recover mainly through the slow process of colonisation by sexual recruits⁴³. Milder cyclone impacts, on the other hand, often allow survival of some adult colonies that can recolonise bare patches by regrowth⁴⁴. Communities of corals in coastal areas may be particularly sensitive to intensified cyclone regimes as associated secondary impacts such as terrestrial runoff and sediment resuspension will also escalate under intensified cyclone regimes (section 10.2.5.3). Interestingly, however, the shading and cooling effects of the often dense cloud cover¹⁴² and enhanced surface convection associated

b <http://www.nhc.noaa.gov/2005atlan.shtml>

with storms in regions beyond their primary impact area may alleviate risks of coral bleaching. For example, during late 2005, coral reefs in the southeastern Caribbean experienced the warmest sea surface temperatures and associated mass bleaching in history^c. The passing of Hurricanes Katrina and Rita in the northern Caribbean in August to September, prior to substantial heating of the southern Caribbean, led to significantly reduced sea surface temperatures, solar irradiance, and thereby lowered bleaching risks (M Eakin pers comm). It is important to note, however, that such lowered bleaching risks on reefs in marginal impact areas are likely to be counteracted by the increased mortality risk from secondary stressors (eg runoff and sedimentation) in coastal areas subjected to major flooding events.

10.2.5.3 Impacts – storms and floods

The impacts of tropical storms extend well beyond the direct physical impact of the wind waves they generate. Secondary impacts following storms like Hurricane Andrew were more important than the physical impacts during the storm through changes in coastal runoff and reduced water quality in nearshore areas¹⁵⁶. In coastal areas, tropical storms often lead to heavy rainfall and associated runoff on the scale of 100s of kilometres⁶², whereas the destructive wind forces occur on a scale of 10s of kilometres. Major flooding events are runoff of freshwater and dissolved nutrients from coastal catchments is perhaps the biggest threat to corals in nearshore waters⁴⁵. Freshwater plumes³⁴ and increased nutrient loading⁴⁵ may inundate reefs within 50 km of major river mouths. Although terrestrial discharges of suspended solids are deposited within a few kilometres of river mouths⁶⁵, resuspension of sediment due to wind waves¹¹⁴ may reduce benthic light regimes dramatically⁸, compromising coral energy budgets⁷. As these secondary impacts may persist for weeks following a cyclone⁴⁵, and may extend over a larger area than the physical impact area, they may cause far more damage to reefs than the structural impact *per se*. Given the recent tropical cyclone activity around Australia's coral reef coastlines, changes in storm intensity on Australian reefs are likely to be similar to those seen for other coral reef regions.

10.2.5.4 Adaptive capacity – storms and floods

Given that coral reefs have evolved under a stochastic, natural regime of storms, they undoubtedly have some capacity for adapting to locally intensified storm regimes. The more critical question is perhaps whether reefs can tolerate an intensified storm regime as well as impacts from multiple other stressors that are also predicted to intensify in the future. Perhaps most importantly, ocean acidification through increasing CO₂ levels (section 10.2.3) will severely reduce the capacity of corals to build skeletons¹⁰⁵ and potentially the ability of crustose coralline algae to consolidate the reef matrix (Diaz-Pulido et al chapter 7). Since increased erosion of calcium carbonate will increase the susceptibility of reefs to storm damage, the adaptive capacity of coral reefs to physical disturbances is likely to be rapidly exceeded. Future communities of corals will most likely lack high-diversity assemblages of branching *Acropora*, but may enter a phase of largely massive and/or semi-encrusting morphologies that have higher resistance to wave impacts.

c <http://coralreefwatch.noaa.gov/caribbean2005>

10.2.5.5 Vulnerability and thresholds – storms and floods

The vulnerability of coral reefs to increased storm intensity and flooding is highly interactive with the other side of the equilibrium within which coral communities sit. Major disturbances like category 5 storms can have a major impact on sections of coral reef yet are (currently) fairly infrequent events. Recovery from these natural events occurs over several decades and in past climate regimes has not led to any persistent decrease in coral community abundance. This equilibrium may shift as the frequency of catastrophic storms increase and recovery processes become increasingly compromised through ocean warming and acidification. This suggests that coral communities will become increasingly vulnerable as storm activity increases and recovery processes decline. Specific thresholds have not been identified. However, several modelling studies⁹⁶ have revealed that coral populations are highly sensitive to small changes in mortality or recruitment. This suggests that thresholds should be relatively easy to identify.

10.2.6 Changes in ocean circulation

10.2.6.1 Exposure – ocean circulation

One of the ways the planet copes with differential heating patterns is to balance the energy budget by transporting heat from the tropics to the poles, which is achieved by both large-scale air and ocean currents. Ocean currents are driven by wind as well as fluxes of heat and freshwater, the latter referred to as thermohaline circulation. In our present climate, the sinking of cold water near Antarctica and in the northern Atlantic Ocean are drivers for a major conveyor system known as the Atlantic meridional overturning circulation³¹. Cold, dense water in these regions sinks to the bottom of the ocean from where dense flows spread toward the equator at great depth eventually rising to the surface and being returned to the poles. The Gulf Stream is the major surface current that closes the northern arm of the meridional overturning circulation and runs from the Caribbean, along the east coast of the USA to the Greenland-Norwegian Sea. It is this current that has the greatest sensitivity to climate change. At the edge of the GBR, the East Australian Current plays a major role in determining many of the environmental conditions discussed above that can influence coral condition. In addition to influencing basic water quality, the behaviour of these currents affect whether communities of corals are connected or not, and aspects of coastal weather (such as storms and doldrums) which in turn drive parameters that affect corals. Steinberg (chapter 3) discusses these large-scale variations.

10.2.6.2 Sensitivity – ocean circulation

Since the drivers for the meridional overturning circulation are primarily the Arctic and Antarctic ice sheets and to a lesser extent tropical heating, any change to the volume of ice at high latitudes, their melting rate, or heat input at low latitudes could affect the speed of this current. Melting of the Greenland and Antarctic ice sheets is happening at much faster rates than previously thought¹⁵² and the resultant freshwater influx has the potential to slow down or even halt the North Atlantic meridional overturning circulation. The warm surface water of this conveyor forms the Gulf Stream, which normally provides northern Europe its relatively mild climate. A slowing down of the Gulf Stream is likely to abruptly and profoundly influence the climate of the northern USA and Europe with likely flow-on effects to the climate of the rest of the world. To a large extent, our understanding

of the impact of climate change on ocean circulation is still rapidly evolving. It is clear, however, that many parts of the ecosystem are highly sensitive to changes in global temperature, and that coral reefs are highly sensitive to these changes.

10.2.6.3 Impacts – ocean circulation

Paleo-proxy records of the northern hemisphere show that a slowing down or halting of the North Atlantic meridional overturning circulation has occurred on a number of occasions in the past. The last major abrupt climate change occurred some 8200 years ago when two glacial lakes melted and drained into Hudson Bay, Canada^{38,119}. This event is recorded in the $\delta^{18}\text{O}$ signature of Greenland ice cores and is estimated to have caused a 3 to 6°C decrease in northern European temperatures within a few years^{4,161}. Bryden et al.³¹ provide observational evidence that the oceanic density fields in the North Atlantic have changed considerably resulting in a weakening of the circulation of more than 30 percent between 1957 and 2004. A repeat breakdown of the circulation would have devastating effects on the socio-economic condition of countries bordering the eastern North Atlantic. The flow on effects to coral reef regions under such a scenario are uncertain, but could include enhanced warming and tropical storm activity in the Caribbean and global sea level rise⁹⁴, the consequences of which are discussed in sections 10.2.1.4, 10.2.4.3 and 10.2.5.3.

Although projecting the precise details of how ocean circulation will change is difficult, it is quite clear from current evidence that it is changing and that coral communities are highly sensitive to change. Currents determine aspects of the environment such as temperature and to an extent local weather. To see the effects of relatively minor changes in ocean currents on coral communities one has only to examine the large scale changes that have resulted during El Niño-Southern Oscillation (ENSO) disturbances to the Indo-Pacific in the 1982–1983⁷³ or 1997–1998 global ocean-atmosphere events⁸². The latter event involved changes (as was the 1982–1983 event) to ocean circulation and led to the loss of 16 percent of reef-building corals globally.

10.2.6.4 Adaptive capacity – ocean circulation

Forcing of ocean currents are subject to physical laws. As such there is little scope for ‘adaptation’ in the same sense as biological and human systems can adapt to changes. Ocean currents change in response to regional changes in heat fluxes, freshwater input, wind forcing and sea ice volume. These forcing factors interact in complex ways and themselves are a response to local and regional climate variation. For this reason anticipating the timing and dynamics of ocean currents is difficult to predict.

10.2.6.5 Vulnerability and thresholds – ocean circulation

Under present climate change models, the likelihood of a shutdown or slowdown in the North Atlantic meridional overturning circulation of sufficient magnitude to cause a cooling in the Europe is considered small (despite the large-scale changes it would bring). Meehl et al.¹³⁶ modelled the latent response of our climate system using two independent climate models and showed that even under a high-end A2 climate scenario, there was no cooling over northern Europe despite significant slowing of the meridional overturning circulation. This is principally because increases in greenhouse gas emissions and resultant warming overwhelmed any tendency to high-latitude cooling. The IPCC⁹⁴ notes that it is too early to say with confidence whether an irreversible collapse in the Atlantic

meridional overturning circulation is likely or not and at what threshold it might take place. However, none of the coupled models predict a complete shutdown of the current under any of the climate scenarios by 2100.

10.2.7 Linkages with other components

10.2.7.1 Constraints to adaptation

Evidence for past adaptation of corals to distinct thermal regimes comes from the observation that populations from warmer locations can withstand higher temperatures compared to conspecific or congeneric populations that live in cooler water, and that those differences are maintained after laboratory acclimation^{41,82,185,22,171,173}. These results suggest that variation in bleaching resistance of corals has a significant genetic component, which is a prerequisite for selection to lead to adaptive change. In other words, if all of the observed variation in bleaching resistance reflected phenotypic plasticity, corals would be unable to respond to selection for increased temperature resistance and hence would not adapt.

To predict the rate at which corals and their algal endosymbionts can potentially adapt given the most likely warming scenarios, it is useful to quantify the extent to which the observed variance in bleaching resistance is genetically determined using quantitative genetic approaches. This information is currently unavailable. A second important factor in estimating potential rates of adaptation of corals is the generation time, that is, the time period from birth to average age of reproduction. The longer the generation time, the slower the process of adaptation. Generation times in corals depend on their growth rates, as reproductive maturity is related to size¹². The age at first reproduction is probably on the order of three to eight years, but because corals are iteroparous, the generation time should be a weighted average of the age of a maternal colony at which each of her offspring was produced¹⁵⁴. Generation times for long-lived coral species that grow to large sizes are therefore expected to be significantly longer than three to eight years, as most offspring will be produced when the maternal colonies are large (ie at an older age) and after adult polyp fecundity has been reached¹².

Symbiodinium populations, on the other hand, are asexual in *hospite*, but population genetic studies show that sexual reproduction does occur although it may be infrequent^{13,14,115,168}. *Symbiodinium* occurs at extremely large population sizes (probably on the order of several billion cells per coral colony). Therefore, even in the absence of frequent sexual reproduction, infrequent somatic mutations may become relevant in such huge populations. Aided by clonal reproduction, selection may lead to the rapid dominance of cells that have undergone a mutation, which enhances thermal tolerance. This is very hypothetical, and experimental work should be directed to explore the likelihood that such evolutionary processes play a role in the evolution of *Symbiodinium*. Furthermore, it is unknown whether *Symbiodinium* with enhanced thermal tolerance will also increase the thermal tolerance of the holobiont.

In any of these discussions about the adaptation of populations of corals to climate change, it is important to note that climate change does not involve a step change but rather, is (and will continue to be) characterised by continuous change. 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 stabilise global temperatures at 2°C above present day conditions, 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 northern genotypes to migrate to southern locations on the reef over time (probably over decades), assuming that levels of gene flow are sufficient to accomplish this, and to flourish at these southern locations as conditions stabilised. The key part of this preceding statement is the stabilisation of climate, which is highly dependent on the rate of greenhouse gas emissions achieved over the next few decades. Stabilisation of climate becomes increasingly unlikely with anything less than aggressive reductions of greenhouse gas emissions (greater than 80% by 2050). Given that stabilisation is unlikely, notions of rapid adaptation changing the thermal thresholds of corals and their symbionts in whole communities are also unlikely. In the unlikely event that we could stop all greenhouse gas emissions today, we are still committed to significant climate change and disruption to habitats like coral reefs^{136,195} before stabilisation is reached.

10.2.7.2 Interactions between stressors

There are a large number of interactions between stressors, producing either muted or enhanced outcomes for corals and *Symbiodinium* as two or more factors coincide. These interactions have not been exhaustively pursued and should be the subject of future research work. Interactions between thermal stress and light have been explored at both physiological¹⁰¹ and ecological¹⁴² levels and via modelling⁸². As discussed above, the flow of water around corals also has an important effect on thermal and photic stress^{144,145} and effects on the photosynthetic performance of zooxanthellae in hospite have also been documented¹⁸⁴. Anthony et al.⁹ explored the interaction between water quality, light and temperature, on coral bleaching and mortality and found that the complex interactions between these variables are largely explained by their effects on coral energetics. These interactions ultimately define environmental limits to growth⁷ and are ultimately related to common variables within the energy budgets of corals that are attempting to undergo photosynthesis in the challenging conditions associated with life in coastal water.

Despite the fact that much is known about the interaction of some variables, we have only a hint of how factors such as thermal stress and acidification will interact under future oceanic conditions. As discussed above, the poorly constructed conclusions of McNeil et al.¹³³ stemmed from inaccurate assumptions about how coral calcification might fair in a warmer more acidic ocean. This highlights the importance with which we must address the questions of how different drivers will interact as the world changes. For example, the process of recovery of coral reefs following bleaching events is surprisingly poorly described despite the importance given to the concept of resilience. How fishing pressure affects reef recovery, or how poor water quality affects mortality following thermal stress need to be determined if we are to understand and better manage the impacts that appear almost certain as the global ocean warms and acidifies.

10.2.7.3 Coral disease

Recognition that coral disease can be a major force in structuring coral communities has emerged only recently and has been based primarily on studies of Caribbean reefs in the past two decades^{11,157}. The first record of a coral disease was in the early 1970s¹⁰, but since then, more than 30 coral diseases have been described, the majority from the Caribbean (reviewed in Weil¹⁹⁴). Disease is commonly defined as a deviance from the normal physiological functioning of an organism, but the distinction

between health and disease is not always clear-cut. The distinction is typically based on the extent of the dysfunction; mild dysfunctions of behaviour, growth and reproduction generally fall within the realm of relative health, whereas severe dysfunctions and mortality are classified as disease. Coral diseases may be either infectious or non-infectious (eg environmentally induced). Infectious diseases of corals are associated with a variety of pathogens, including bacteria, cyanobacteria, ciliate protists, and fungi, although causative agents (as verified using Koch's postulates) have been identified for only a few coral diseases (reviewed in Weil¹⁹⁴). Surveys of coral disease reveal generally low (less than 5%) disease prevalence on reefs in the GBR¹⁹⁸. Overall, seven disease types have been recorded: black band disease (BBD), skeletal eroding band (SEB), white syndrome (WS), brown band disease (BrBD), coral tumors, atramentous necrosis, and cyanobacteria syndromes (other than BBD), although current understanding of the majority of these is limited to field descriptions of lesions. All seven of these coral diseases are widespread throughout the GBR. For example, BBD occurs on more than 70 percent of reefs surveyed (n = 19) throughout the northern, central and southern sectors, although its prevalence is typically low (affecting about 0.1% of scleractinian corals)¹⁵³. Black band disease has been recorded to infect at least 32 coral species in 10 families on the GBR, with branching pocilloporid and acroporid corals being important hosts¹⁹⁸. Abundance of WS increased 20-fold in the 2001 and 2002 period, around the time of the most severe bleaching event so far recorded on the GBR, and increased further in 2002 and 2003¹⁹⁸ but has since declined to low levels in all regions (B Willis and C Page unpublished data). Detection of some of the more common and infectious Caribbean diseases (BBD and potentially some of the white diseases), in combination with discovery of diseases unique to the region (brown band disease¹⁹⁸), suggest that coral diseases are common on Indo-Pacific reefs and may have a greater role in structuring Indo-Pacific coral communities than previously thought. Diseases are ubiquitous in all plant and animal populations, thus such contributions to the dynamics of coral populations are not unexpected. Increases in white syndrome abundance¹⁹⁸ and atramentous necrosis in the summer of 2001–2002¹⁰² are the only disease outbreaks so far documented on the GBR. At present, diseases have had a comparatively low impact on GBR coral populations in comparison to those in the Caribbean. However, the impacts of coral disease in other reef areas highlight the potential for increased risk in the future, especially in a warming climate.

Increasing reports of diseases in many marine organisms globally in the past few decades are postulated to be linked to ocean warming^{80,113,191,170}. Increasing sea water temperatures have the potential to increase not only host susceptibility to disease, but also virulence of the pathogens themselves^{80,163}. It is difficult to separate the effects of ocean warming from concurrent increases in stressors such as nutrients, toxic chemicals and other pollutants, based solely on reports of disease¹¹³. However, a number of additional lines of evidence support a link between elevated temperatures and disease. For example, the role of high temperatures in summer outbreaks of bacterially induced bleaching in Mediterranean populations of the coral, *Oculina patagonica*, appears to be well established^{180,95}. These outbreaks have been linked to increased expression of virulence genes by the bacterium, *Vibrio shiloi*, at higher temperatures (reviewed in Rosenberg and Ben-Haim¹⁸⁰). Seasonal patterns in coral disease prevalence on the GBR¹⁹⁸ and spatial patterns in black band disease abundance in the Caribbean¹¹¹ support a link between elevated temperatures and the prevalence of a number of coral diseases (eg white syndrome), black band disease, skeletal eroding band and brown band disease on the GBR¹⁹⁸. Recent analyses of the relationship between annual patterns in the abundance of white syndrome on the GBR and warm thermal anomalies also corroborate a link between elevated seawater

temperatures and coral disease¹⁷⁰. Speculation that warmer winter temperatures will favour pathogen populations and therefore not provide a winter reprieve from pathogen load associated with current mean winter minima⁸¹ represents another potential way in which climate change may affect disease dynamics in GBR coral populations.

It is noteworthy that, in addition to temperature and environmental stressors, biological factors may also affect disease incidence, thus predicting the vulnerability of coral populations to disease as a consequence of climate change is complex. Host density is known to affect pathogen transmission⁵ therefore reduced cover of dominant coral species may lower the spread of disease once low host density thresholds are reached. It is also possible that pathogens, which are currently positively affected by summer temperatures, will be negatively affected at higher sea water temperatures associated with climate change. Furthermore, there may be reduced coral disease under climate change scenarios as elevated sea water temperatures negatively affected some pathogens¹¹². Evidence that an acroporid tissue loss syndrome decreases in abundance during the summer months at Heron Island^{162,3} supports this possibility. These studies have documented programmed cell death (apoptosis) as the mechanism underlying tissue loss, although the trigger (eg environmental stress or microbial pathogens) for cell death is unknown. The greater disease abundance in winter may relate to dwindling energy resources (perhaps due to thermal stress in the preceding summer) prior to entering the colder, darker months. In summary, the impact of ocean warming will depend on relative thermal optima of coral hosts and pathogens. However, the potential for rapid spread of pathogens throughout marine populations, as demonstrated by the rapid spread of herpes virus throughout Australian pilchard populations and of morbillivirus throughout seal and dolphin populations¹³⁰, highlights the need for greater understanding of mechanisms of coral pathogen transmission and virulence, as well as mechanisms of disease resistance of corals, to better evaluate the vulnerability of corals to disease as a consequence of climate change.

10.2.7.4 Threats to resilience

This chapter is devoted to the impacts of climate change on reef-building corals. It is important to note, however, that impacts on corals are likely to reverberate throughout the GBR ecosystem. Corals are responsible for the physical and ecological foundations that underpin reefs, making the fate of coral communities a critical determinant of ecosystem resilience. The many chapters in this book provide important insights into how impacts to coral communities from climate change will affect particular species or habitats. Emerging as important to understanding how impacts on corals might affect resilience more generally, is an awareness of the dependency between corals and other habitat components.

Corals support tens if not hundreds of thousands of other organisms. Many of these are totally dependent on corals for food, shelter and reproduction. Many others rely only partly on corals, while nearly every organism has some sort of indirect dependency on the goods and services provided by corals. Where direct and strong dependencies occur, changes in coral cover or composition can have obvious and immediate impacts on other species. Coral obligates like the orange-spotted filefish (*Oxymonacanthus longirostris*), for example, rapidly disappeared from Okinawan reefs after the 1998 bleaching event¹⁰⁹. In contrast, less direct or facultative relationships can result in complicated, delayed or minor responses to changes in coral communities. In the Seychelles, for example, Spalding and Jarvis¹⁷⁴ found that the overall structure of fish communities had changed very little despite massive decreases (3 to 20 fold) in living coral cover after the 1997–1998 bleaching event. This effect



is amplified further up the trophic pyramid, as exemplified by the difficulty in detecting impacts on reef-based fisheries after major coral mortality events caused by bleaching³⁵. Competitive interactions involving corals are also important to the composition and dynamics of coral reefs. The ability of corals to dominate available hard substrate to the exclusion of algae, for example, is fundamental to the long-term resilience of the ecosystem¹³¹.

These illustrations highlight the complex web of relationships that centres on corals. Changes in the abundance or composition of coral communities will necessarily have impacts on other parts of the ecosystem, with the potential to severely undermine resilience. This emphasises the importance of measures that take into account the complex responses that are likely from inter-dependent ecosystems such as the GBR, rather than a focus on any one species, group or habitat. In the context of climate change, more than any other issue, understanding the connections between different parts of the ecosystem, and the role of species or groups in ecosystem resilience is critically important when formulating management responses. In particular, taking a resilience-based approach to the management of tropical marine ecosystems (McCook et al. chapter 4, Marshall and Johnson chapter 24) is critical to address the issue of climate change, where impacts are certain to occur, but their scale, intensity and frequency is largely unknown.

10.3 Summary and recommendations

10.3.1 Major vulnerabilities to climate change

The vulnerability of coral and the reefs they build to climate change was brought into sharp focus after 1998, when an estimated 16 percent of the world's coral communities died. Analysing the literature since that time reveals that rapidly rising sea temperatures and increasing levels of acidity in the ocean remain the major threat to coral reefs. Successive studies of the potential impacts of thermal stress on coral reefs^{82,48,49} have supported the notion that coral dominated reefs are likely to largely disappear with a 2°C rise in sea temperature over the next 100 years. This, coupled with the additional vulnerability of coral reefs to high levels of acidification once the atmosphere reaches 500 parts per million^{105,78,107}, suggests that coral dominated reefs will be rare or non-existent in the near future. In this regard, we conclude that communities of Australian corals are extremely vulnerable to the effects of ocean warming and ocean acidification. While new assemblages will certainly form in the absence of coral-dominated reefs, the diversity and structure of these communities as well as the types of fishing and tourist industries they might support are completely unknown.

Changes to other factors such as storm intensity, water quality and light intensity will have a lower, yet significant, impact on coral reefs. Although coral reefs are less vulnerable to these particular factors, and hence they are likely to interact with climate change and ocean acidification in some important ways. Increased storm activity, for example, may reduce the effects of climate change locally by mixing the water column and cooling the overlying waters. Stronger storms, however, will accelerate the breakage of increasingly fragile coral skeletons caused by ocean acidification and will cause larger coral mortality events in coastal areas due to more intense flooding. Other factors such as increasing sunlight days as the Australian coastal areas undergo drying will exacerbate the effects of warming. Although a full understanding of the many interactions with secondary variables has not been achieved, their role in the vulnerability of coral reefs is likely to grow.

10.3.2 Vulnerability and thresholds (extinction risk and irreversibility)

As outlined above, 500 parts per million is the highest CO₂ concentration under which any semblances to the communities of corals we have today can survive. It is also the only scenario in which the climate will eventually stabilise. Above this point (500 parts per million), coral reefs will also change irreversibly and be lost for many thousands of years. To contemplate any higher CO₂ is untenable given the huge likelihood of such catastrophic events as runaway greenhouse effects and the flooding of the planet as the Greenland and Western Antarctic Ice Sheets melt. Even though 500 parts per million is seen as an ambitious greenhouse target, effects on ocean temperature and acidity will mean that coral calcification will decrease to 40 percent of today's value and major (1998 level) bleaching events will occur every 2 to 4 years^{82,48,49}. Under these conditions, Australian reefs will have the following characteristics:

- Major increase in the frequency and intensity of coral bleaching, mortality events and recruitment failure with increased incidences and outbreaks of coral disease.
- Coral dominated reefs will contract to less than 20 percent of today's distribution and corals will be rare on most coral reefs. Benthic microalgae, macroalgae and cyanobacteria communities will dominate these reefs although it is uncertain which species or taxa will dominate.
- Reef carbonate frameworks are likely to slowly disintegrate under vastly reduced calcification (due to elevated temperatures and decreasing pH) and the possible acceleration of bioerosion. Reefs will have less structure and hence reduced habitat complexity and holding capacity for reef organisms. It is not known how long these processes will take to have an effect on coral reefs.
- Reduced coral communities and reef structure will lead to a major reduction in reef biodiversity with some coral-dependent species going extinct.
- At longer time frames, negative reef maintenance and growth will mean that sections of the Australian coastline that are currently protected by reef structures like the GBR will gradually become more exposed to ocean wave stress. This may eventually have ramifications for the current distribution of coastal seagrass and mangrove communities.
- Intensified cyclone regime will increase physical impacts on coral communities and will accelerate the shift from high-diversity communities to assemblages dominated by few resistant massive/encrusting species. Reduced vitality of corals will mean that recovery will be compromised; further accelerating the shift of reefs away from coral dominated reefs.
- The increased intensity of flood events along with prolonged drought along east Australia will lead to periods of reduced water quality and flooding (with associated sediment, nutrients, and freshwater impacts) that will affect reefs further offshore.

10.3.3 Potential management responses

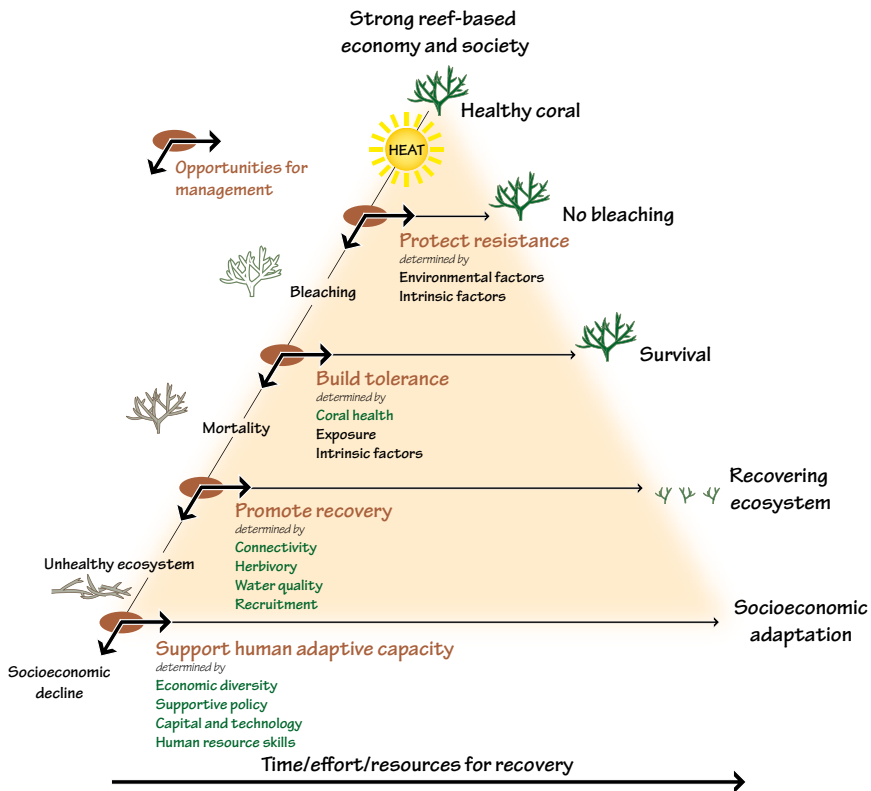
The most serious threats to corals in the context of climate change are coral bleaching caused by warming sea temperatures, and decreased calcification due to ocean acidification. Neither water temperature nor ocean chemistry is amenable to mitigation at the scale of local reef management. However, there is a variety of local factors that can influence the susceptibility of corals to global stressors. An understanding of the process of coral bleaching, and the factors that influence outcomes

at various steps along the causal pathway, provides the basis for scientifically-based management strategies that aim to reduce the impacts of climate change on corals^{149,135}.

A similar analysis may be possible for ocean acidification in the future, once more is known about the interactions between aragonite saturation state and other (more local) factors that influence calcification in corals. Possible management strategies at the local scale could be measures to (1) increase pH to shift the aragonite saturation state, or (2) reduce wave regimes locally to protect patches of more susceptible morphologies from breakage. This could probably only be achieved in enclosed reef areas (eg micro atolls). However, it is unlikely that such attempts would be cost effective as a conservation strategy or as a rescue operation for four operators.

Three conditions determine the outcome of stressful temperatures on corals: resistance, tolerance and reef recovery. Each of these offers a potential focus for management action aimed at reducing the impacts of coral bleaching (Figure 10.1). Damage to a coral community might be reduced if managers can influence or somehow enhance the effects of factors that determine the ability of corals to maintain their symbiotic dinoflagellates even when exposed to high temperatures (protecting resistance). Experiments to test the effectiveness of shading corals during periods of hot,

Figure 10.1 The coral bleaching process, showing opportunities for management action to reduce the impacts of stressful sea temperatures on coral communities (from Marshall and Schuttenberg 2006)



still conditions are an example of efforts to protect resistance at a very limited spatial scale. Managers may also be able to build the ability of corals to tolerate bleaching. In particular, recent research has shown that the lipid content of corals affects their ability to endure bleaching⁹, suggesting that management strategies aimed at maintaining coral health (such as improving water quality) may play an important role in reducing the severity of coral bleaching. The part of the bleaching process most amenable to management action is the potential for coral communities to rapidly recover following coral mortality. Healthy habitats are better able to provide the conditions required for recruitment, survival and growth of new corals after bleaching has killed established colonies. In particular, good water quality, an abundant and diverse community of herbivores, and high coral cover are key aspects of ecosystem quality that should be priorities for reef management that aims to minimise the impacts of climate change on coral communities¹⁹⁹.

Although there are management actions that can reduce the impacts of coral bleaching, ultimately the fate of coral reefs will be determined by a combination of the rate of climate change, and their resilience to these changes. This suggests that immediate steps must be taken to reduce the sources of emissions that are driving climate change. In addition, the interaction of climate change impacts with secondary factors (eg water quality and fishing pressure) suggests some important strategies that need to be undertaken as climate change continues. These would build on the significant steps that have already been taken to improve the resilience of the GBR ecosystem, such as increasing the area of no-take zones from 5 to 33 percent, and developing a Reef Water Quality Protection Plan. Together, these measures have been hailed as being of international conservation significance. However, climate change poses additional and new challenges to tropical marine ecosystems, requiring further management efforts. Based on what is currently known about the risks from climate change, we offer the following recommendations:

- To minimise the risk of major degradation of coral reefs, global emissions need to be reduced so that atmospheric concentrations of CO₂ stabilise at levels no higher than 500 parts per million.
- Management effectiveness will benefit from a thorough understanding of regional differences in vulnerability across all stresses. Hence, a more detailed understanding of the basis of tolerance in organisms like corals and their symbionts as well as a detailed 'vulnerability map' for the GBR can contribute substantially to resilience-building efforts.
- Reef resilience will also be improved through effective management of river catchments (ie reduced erosion potential of particulates, nutrients and toxicants) so as to improve coastal water quality and prepare for the impacts of more intense storms on an increasingly drought ridden coastline.
- Continued protection of healthy herbivore populations will help maintain and promote coral recruitment into disturbed areas.
- Explore the pros and cons of artificial structures to maintain reef species in areas where corals have been removed and the reef framework has disintegrated, or as stepping-stones between source and sink reefs in areas of low connectivity.
- Efforts to explore the effectiveness and costs of technologies to reduce climate impacts (shade structures, restoration technologies) should be facilitated for small areas of high natural or industry (tourism) value.



10.3.1 Further research

Our analysis reveals numerous gaps in our understanding of how corals and their dinoflagellate symbionts will survive under rapid climate warming and ocean acidification. Although we are rapidly improving our understanding of how corals are affected by thermal stress and acidification, we need to improve our understanding of how these conditions affect other important reef species, especially those that are important reef calcifying organisms (eg calcareous red algae). It is imperative that we pursue an understanding of the molecular basis for stress tolerance in corals and their symbionts. As the tools of the later exist, engaging in a national research program to achieve this must be a priority. We need to also expand our understanding of how climate change and ocean acidification will interact, both together and with other climate related factors (eg storm intensity). At higher levels of organisation, we need to improve our understanding of the consequences of the loss of corals as major community members on Australian reefs. In this regard, a regional ‘vulnerability map’ would be a valuable tool for understanding the interplay between local and global stresses in complex ecosystems like the GBR. Assessments are also needed of how reef biodiversity is tied to, and affected by, the abundance of reef-building corals. Equally, we need to know how projected changes in benthic community structure will affect commercial fish stocks, and to explore ways that we might ameliorate these changes (eg artificial reef structures). Other industries such as marine tourism (one of Australia’s largest industries and export earners) will be affected by severely degraded coral reefs. Some analyses of this problem have been undertaken. Projections of vulnerability of these industries and reef usages, however, need to be coupled with socio-economic studies that examine strategies to reduce the impact and spread the risk to these industries of major changes in the appeal of coral reefs to visitors. Lastly, we need to understand better how changes in the health of tropical marine ecosystems in Australia’s backyard (southeast Asia and the western Pacific) will affect the status of societies that depend on coral reefs for food and resources. In this respect, Australia needs to understand and be ready for potential impacts on the social and economic well-being of millions of people who depend for subsistence on the coral reefs in neighbouring countries.

References

- 1 Access Economics (2007) *Measuring the economic and financial value of the GBR Marine Park 2005/06*. Report by Access Economics Pty Limited for GBR Marine Park Authority. GBR Marine Park Authority.
- 2 Adamska I, Kloppstech K and Ohad I (1993) Early light inducible protein in pea is stable during light stress but is degraded during recovery at low light intensity. *Journal of Biological Chemistry* 268, 5438–5444.
- 3 Ainsworth TD, Kvennefors EC, Blackall L, Fine M and Hoegh-Guldberg O (2007) Disease and cell death in White Syndrome of Acroporid corals on the Great Barrier Reef. *Marine Biology* 151, 19–29.
- 4 Alley RB and Ágústsdóttir AM (2005) The 8k event: cause and consequences of a major Holocene abrupt climate change. *Quarterly Scientific Reviews* 24, 1103–1149.
- 5 Anderson RM and May RM (1986) The invasion, persistence and spread of infectious diseases within animal and plant populations. *Philosophical Transactions of the Royal Society London B Biological Science* 314, 533–70.
- 6 Anthony KRN (2006) Enhanced energy status of corals on coastal, high-turbidity reefs. *Marine Ecology Progress Series* 319, 111–116.
- 7 Anthony KRN and Connolly SR (2004) Environmental limits to growth: physiological niche boundaries of corals along turbidity-light gradients. *Oecologia* 141, 373–384.
- 8 Anthony KRN, Ridd PV, Orpin A, Larcombe P and Lough JM (2004) Temporal variation in light availability in coastal benthic habitats: effects of clouds, turbidity and tides. *Limnology and Oceanography* 49, 2201–2211.
- 9 Anthony KRN, Connolly SR and Hoegh-Guldberg O (2007) Bleaching, energetics and coral mortality risk: Effects of temperature, light, and sediment regime. *Limnology and Oceanography* 52, 716–726.
- 10 Antonius A (1973) New observations on coral destruction in reefs. Association of Island Marine Laboratories of the Caribbean 10, 3.
- 11 Aronson RB and Precht WF (2001) White band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460, 25–38.
- 12 Babcock R (1991) Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. *Ecological Monographs* 61, 225–244.
- 13 Baillie BK, Belda-Baillie CA and Maruyama T (2000a) Conspecificity and Indo-Pacific distribution of Symbiodinium genotypes (Dinophyceae) from giant clams. *Journal of Phycology* 36, 1153–1161.
- 14 Baillie BK, Belda-Baillie CA, Silvestre V, Sison M, Gomez AV, Gomez ED and Monje V (2000b) Genetic variation in *Symbiodinium* isolates from giant clams based on random-amplified-polymorphic DNA (RAPD) patterns. *Marine Biology* 136, 829–836.
- 15 Baker AC (2001) Reef corals bleach to survive change. *Nature* 411, 765–766.
- 16 Baker AC and Rowan R (1997). Diversity of symbiotic dinoflagellates (zooxanthellae) in scleractinian corals of the Caribbean and eastern Pacific. *Proceedings of the 8th International Coral Reef Symposium* 2, 1301–1305.
- 17 Banaszak AT, Lajeunesse TC and Trench RK (2000) The synthesis of mycosporine-like amino acids (MAAs) by cultured, symbiotic dinoflagellates. *Journal Experimental Marine Biology and Ecology* 249, 219–233.
- 18 Bassim KM and Sammarco PW (2003) Effects of temperature and ammonium on larval development and survivorship in a scleractinian coral *Diploria strigosa*. *Marine Biology* 142, 241–252.
- 19 Bassim KM, Sammarco PW and Snell TL (2002) Effects of temperature on success of (self and non-self) fertilization and embryogenesis in *Diploria strigosa* (Cnidaria, Scleractinia). *Marine Biology* 140, 479–488.
- 20 Berkelmans R (2001) Bleaching, upper thermal limits and temperature adaptation in reef corals. PhD Thesis, James Cook University, Townsville.
- 21 Berkelmans R (2002) Time-integrated thermal bleaching thresholds of reefs and their variation on the Great Barrier Reef. *Marine Ecology Progress Series* 229, 73–82.
- 22 Berkelmans R and van Oppen MJH (2006) The role of zooxanthellae in the thermal tolerance of corals: a ‘nugget of hope’ for coral reefs in an era of climate change. *Proceedings Of The Royal Society Of London B Biological Sciences* 273, 2305–2312.
- 23 Berkelmans R and Willis BL (1999) Seasonal and local spatial patterns in the upper thermal limits of corals on the inshore Central Great Barrier Reef. *Coral Reefs* 18, 219–228.
- 24 Berkelmans R, De’ath G, Kininmonth S and Skirving WJ (2004) A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: Spatial correlation, patterns and predictions. *Coral Reefs* 23, 74–83.
- 25 Bessat F and Buigues D (2001) Two centuries of variation in coral growth in a massive *Porites* colony from Moorea (French Polynesia): a response of ocean-atmosphere variability from south central Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology* 175, 381–392.

- 26 Brown BE (1997a) Coral bleaching: causes and consequences. *Coral Reefs* 16, Supplement: S109–S138.
- 27 Brown BE (1997b) Adaptations of reef corals to physical environmental stress. *Advances in Marine Biology* 31, 221–299.
- 28 Brown BE, Dunne RP, Goodson MS and Douglas A. (2000) Bleaching patterns in reef corals. *Nature* 404, 142–43.
- 29 Brown BE, Downs CA, Dunne RP and Gibb SW (2002a) Exploring the basis of thermotolerance in the reef coral *Goniastrea aspera*. *Marine Ecology Progress Series* 242, 119–129.
- 30 Brown BE, Dunne RP, Goodson MS and Douglas AE (2002b) Experience shapes the susceptibility of a reef coral to bleaching. *Coral Reefs* 21, 119–106.
- 31 Bryden HL, Longworth HR and Cunningham SA (2005) Slowing of the Atlantic meridional overturning circulation at 25° N. *Nature* 438, 655–657.
- 32 Buddemeier RW and Fautin DG (1993) Coral bleaching as an adaptive mechanism. *Bioscience* 43, 320–326.
- 33 Bulina ME, Chudakov DM, Britanova OV, Yanushevich YG, Staroverov DB, Chepurmykh TV, Merzlyak EM, Shkrob MA, Lukyanov S and Lukyanov K (2005) A genetically encoded photosensitizer. *Nature Biotechnology* 24, 95–99.
- 34 Burrage DM, Heron ML, Hacker JM, Stieglitz TC, Steinberg CR and Prytz A (2002). Evolution and dynamics of tropical river plumes in the Great Barrier Reef: An integrated remote sensing and *in situ* study. *Journal of Geophysical Research* 107(C12): doi: 10.1029/2001JC001024..
- 35 Cesar HSJ (ed) (2000) *Collected Essays on the Economics of Coral Reefs*. Coral Reef Degradation in the Indian Ocean, Department for Biology and Environmental Sciences, Kalmar University, Sweden.
- 36 Church JA and White NJ (2006) A 20th century acceleration in global sea-level rise. *Geophysical Research Letters* 33, L01602, doi:10.1029/2005GL024826.
- 37 Church JA, Gregory JM, Huybrechts P, Kuhn M, Lambeck K, Nhuan MT, Qin D and Woodworth P (2001) Changes in Sea Level. In: JT Houghton, Y Ding, DJ Griggs, M Noguer, P van der Linden, X Dai, K Maskell and CI Johnson, (eds) *Climate Change The Scientific Basis*. Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, pp. 639–694.
- 38 Clarke GKC, Leverington DW, Teller JT and Dyke AS (2004) Paleohydrology of the last outburst flood from glacial Lake Agassiz and the 8200 BP cold event. *Quarterly Science Reviews* 23, 389–407.
- 39 Coles SL and Brown BE (2003) Coral Bleaching? Capacity for Acclimatization and Adaptation. *Advances in Marine Biology* 46, 183–223.
- 40 Coles SL and Jokiel PL (1978) Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. *Marine Biology* 49, 187–195.
- 41 Coles SL, Jokiel PL and Lewis CR (1976) Thermal tolerance in tropical versus subtropical Pacific coral reefs. *Pacific Science* 30, 159–166.
- 42 Connell JH (1978) Diversity in tropical rainforests and coral reefs. *Science* 199, 1302–1320.
- 43 Connell JH and Keough MJ (1985) Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: STA Pickett and PS White (eds) *The Ecology of Natural Disturbance and Patch Dynamics*, Academic Press, Orlando pp. 125–147.
- 44 Connell JH, Hughes TP and Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs* 67, 461–488.
- 45 Devlin MJ and Brodie J (2005) Terrestrial discharge into the Great Barrier Reef Lagoon: nutrient behavior in coastal waters. *Marine Pollution Bulletin* 51, 9–22.
- 46 Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1, 95–107.
- 47 Done TJ (1999). Coral community adaptability to environmental change at the scales of regions, reefs, and reef zones. *American Zoologist* 39, 66–79.
- 48 Done TJ, Whetton P, Jones R, Berkelmans R, Lough J, Skirving W and Wooldridge S (2003) *Global Climate Change and Coral Bleaching on the Great Barrier Reef*. Final report to the State of Queensland Greenhouse Taskforce through the Department of Natural Resources and Mining, Townsville.
- 49 Donner SD, Skirving WJ, Little CM, Oppenheimer M and Hoegh-Guldberg O (2005) Global assessment of coral bleaching and required rates of adaptation under climate change. *Global Change Biology* 11, 1–15
- 50 Dove S (2004) Scleractinian corals with photoprotective host pigments are hypersensitive to thermal bleaching. *Marine Ecology Progress Series* 272, 99–116.
- 51 Dove S, Takabayashi M and Hoegh-Guldberg O (1995) Isolation and partial characterisation of the pink and blue pigments of pocilloporid and acroporid corals. *Biological Bulletin* 189, 288–297.

- 52 Dove S, Hoegh-Guldberg O and Ranganathan S (2001) Major colour patterns of reef-building corals are due to a family of GFP-like proteins. *Coral Reefs* 19, 197–204.
- 53 Dove S, Ortiz JC, Enríquez S, Fine M, Fisher P, Iglesias-Prieto R, Thornhill D and Hoegh-Guldberg O (2006) Response of holosymbiotic pigments from the scleractinian coral *Montipora monasteriata* to short term heat stress. *Limnology and Oceanography* 51, 1149–1158.
- 54 Dunlap WC and Chalker BE (1986) Identification and quantification of near UV absorbing compounds (S-320) in a hermatypic scleractinian. *Coral Reefs* 5, 155–159.
- 55 Dunne RP and Brown BE (1996) The penetration of solar UV-B radiation in shallow tropical waters and its potential biological effects on coral reefs; results from the central Indian Ocean and Andaman Sea. *Marine Ecology Progress Series* 144, 109–118.
- 56 Edmunds PJ (1994) Evidence that reef-wide patterns of coral bleaching may be the result of the distribution of bleaching-susceptible clones. *Marine Biology* 101, 107–142.
- 57 Edmunds PJ (2004) Juvenile coral population dynamics track rising seawater temperature on a Caribbean reef. *Marine Ecology Progress Series* 269, 111–119.
- 58 Edmunds PJ, Gates RD, Leggat W, Hoegh-Guldberg O and Allen-Requa L (2005) The effect of temperature on the size and population density of dinoflagellates in larvae of the reef coral *Porites astreoides*. *Invertebrate Biology* 124, 185–193.
- 59 Emanuel K (2005) Increasing destructiveness of tropical cyclones over the past 30 years. *Nature* 436, 686–687.
- 60 Enríquez S, Méndez ER and Iglesias-Prieto R (2005) Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. *Limnology and Oceanography* 50, 1025–1032.
- 61 Falkowski P and Dubinsky Z (1981) Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. *Nature* 289, 172–174.
- 62 Furnas M (2003) *Catchments and Corals: Terrestrial Runoff to the Great Barrier Reef*. Australian Institute of Marine Science and CRC Reef Research Centre, Townsville.
- 63 Fisher P (2006) Investigating the photo-physiology of *Symbiodinium* sub-clades and its relationship to coral bleaching. PhD thesis, University of Queensland, St. Lucia.
- 64 Fitt W, Brown B, Warner M, and Dunne R (2001) Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* 20, 51–65.
- 65 Gagan MK., Sandstrom MW and Chivas AR (1987) Restricted terrestrial carbon input to the continental shelf during cyclone Winifred: implications for terrestrial runoff to the Great Barrier Reef province. *Coral Reefs* 6, 113–119.
- 66 Gates RD and Edmunds PJ (1999) The physiological mechanisms of acclimatization in tropical reef corals. *American Zoologist* 39, 30–43.
- 67 Gattuso J-P, Frankignoulle M, Bourge I, Romaine S and Buddemeier RW (1998) Effect of calcium carbonate saturation of seawater on coral calcification. *Global Planetary Change* 18, 37–47.
- 68 GCRMN (2000) In: CR Wilkinson (ed) *Global Coral Reef Monitoring Network: Status of coral reefs of the world in 2000*. Published by the Australian Institute of Marine Science, Townsville.
- 69 GCRMN (2004) In: CR Wilkinson (ed) *Global Coral Reef Monitoring Network: Status of coral reefs of the world in 2004*. Published by the Australian Institute of Marine Science, Townsville.
- 70 Gitz DC and Liu-Gitz L (2003) How do UV Photomorphogenic Responses Confer Water Stress Tolerance? *Photochemistry and Photobiology* 78, 529–534.
- 71 Gleason DF and Wellington GM (1993) Ultraviolet radiation and coral bleaching. *Nature* 365, 836–838.
- 72 Glynn PW (1984) Widespread coral mortality and the 1982–83 El Niño warming event. *Environmental Conservation* 11, 133–146.
- 73 Glynn PW (1988) El Niño–Southern Oscillation 1982–1983: nearshore population, community, and ecosystem responses. *Annual Review of Ecology and Systematics* 19, 309–345.
- 74 Glynn PW (1993), Coral reef bleaching ecological perspectives. *Coral Reefs* 10, 1–17.
- 75 Glynn PW (2001) History of significant coral bleaching events and insights regarding amelioration. In: RV Salm and SL Coles (eds) *Coral Bleaching and Marine Protected Areas. Proceedings of the Workshop on Mitigating Coral Bleaching Impact Through MPA Design*. Bishop Museum, Honolulu, Hawaii.
- 76 Glynn PW and D'Croz L (1990) Experimental evidence for high temperature stress as the cause of El Niño coincident coral mortality. *Coral Reefs* 8, 181–191.
- 77 Goreau TJ, McClanahan T, Hayes RL and Strong AL (2000) Conservation of coral reefs after the 1998 global bleaching event. *Conservation Biology* 14, 5–15.

- 78 Guinotte JM, Buddemeier RW and Kleypas JA (2003) Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. *Coral Reefs* 22, 551–558.
- 79 Harrison PL and Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Z Dubinsky (ed) *Coral Reefs Ecosystems of the World* Volume 25. Elsevier Science Publishing Company, Amsterdam, pp. 133–207.
- 80 Harvell CD, Kim K, Burkholder J, Colwell RR, Epstein PR, Grimes J, Hofmann EE, Lipp EK, Osterhaus ADME, Overstreet R, Porter JW, Smith GW and Vasta GR (1999) Emerging marine diseases - climate links and anthropogenic factors. *Science* 285, 1505–1510.
- 81 Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, Ostfeld RS and Samuel MD (2002) Climate warming and disease risk for terrestrial and marine biota. *Science* 296, 2158–2162.
- 82 Hoegh-Guldberg O (1999) Coral bleaching, Climate Change and the Future of the World's Coral Reefs. *Marine and Freshwater Research* 50, 839–866.
- 83 Hoegh-Guldberg O (2001) The future of coral reefs: Integrating climate model projections and the recent behaviour of corals and their dinoflagellates. *Proceedings of the 9th International coral reef symposium*. October 23–27, 2000, Bali, Indonesia.
- 84 Hoegh-Guldberg O (2004) Coral reefs in a century of rapid environmental change. *Symbiosis* 37, 1–31.
- 85 Hoegh-Guldberg O (2005) Low coral cover in a high-CO₂ world, *Journal Of Geophysical Research* 110, C09S06, doi:10.1029/2004JC002528.
- 86 Hoegh-Guldberg H and Hoegh-Guldberg O (2004) *Biological, Economic and Social Impacts of Climate Change on the Great Barrier Reef*. World Wide Fund for Nature.
- 87 Hoegh-Guldberg O and Salvat B (1995) Periodic mass-bleaching and elevated sea temperatures: Bleaching of outer reef slope communities in Moorea, French Polynesia. *Marine Ecology Progress Series* 121, 181–190.
- 88 Hoegh-Guldberg O and Smith GJ (1989) The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. *Journal Experimental Marine Biology and Ecology* 109, 279–303.
- 89 Hoegh-Guldberg O, Jones RJ, Ward S and Loh WK (2002) Is coral bleaching really adaptive? *Nature* 415, 601–602.
- 90 Hoegh-Guldberg O, Fine M, Skirving W, Johnstone R, Dove S and Strong A (2005) Coral bleaching following wintry weather. *Limnology and Oceanography* 50, 265–271.
- 91 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, Nyström M, Palumbi SR, Pandolfi JM, Rosen B and Roughgarden J (2003) Climate change, human impacts and the resilience of coral reefs. *Science* 301, 929–933.
- 92 Iglesias-Prieto R and Trench RK (1997) Acclimation and adaptation to irradiance in symbiotic dinoflagellates. II. Response of chlorophyll-protein complexes to different photon-flux densities. *Marine Biology* 130, 23–33.
- 93 Iglesias-Prieto R, Matta JL, Robins WA and Trench RK (1992) Photosynthetic response to elevated-temperature in the symbiotic dinoflagellate *Symbiodinium microadriaticum* in culture. *Proceedings of the National Academy of Science* 89, 302–305.
- 94 IPCC (Intergovernmental Panel on climate Change) (2001) Climate Change 2001. The Scientific Basis. In: JT Houghton, Y Ding, DJ Griggs, N Noguer, PJ van der Linden, X Dai, K Maskell, and CA Johnson (eds) *Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge United Kingdom and New York, NY, USA.
- 95 Israely T, Banin E and Rosenberg E (2001) Growth, differentiation and death of *Vibrio shiloi* in coral tissues as a function of seawater temperatures. *Aquatic Microbial Ecology* 24, 1–8.
- 96 Johnson CR, Dunstan PK and Hoegh-Guldberg O (2002) Predicting the long term effects of coral bleaching and climate change on the structure of coral communities. *Workshop of the National Center for Coral Reef Research*, October 3–5, Miami, USA.
- 97 Jokiel PL and Coles SL (1977) Effects of temperature on photosynthesis and respiration in hermatypic corals. *Marine Biology* 43, 209–216.
- 98 Jokiel PL and Coles SL (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperatures. *Coral Reefs* 8, 155–161
- 99 Jones RJ (1997) Changes in zooxanthellar densities and chlorophyll concentrations in corals during and after a bleaching event. *Marine Ecology Progress Series* 158, 51–59
- 100 Jones RJ and Hoegh-Guldberg O (1999) Effects of cyanide on coral photosynthesis: implications for identifying the cause of coral bleaching and for assessing the environmental effects of cyanide fishing. *Marine Ecology Progress Series* 177, 83–91.

- 101 Jones R, Hoegh-Guldberg O, Larkum AWL and Schreiber U (1998) Temperature induced bleaching of corals begins with impairment of dark metabolism in zooxanthellae. *Plant Cell and Environment* 21, 1019–1030.
- 102 Jones RJ, Bowyer J, Hoegh-Guldberg O and Blackhall L (2004) Dynamics of a temperature-related coral disease outbreak. *Marine Ecology Progress Series* 281, 63–77.
- 103 Kerswell AP and Jones RJ (2003) Effects of hypo-osmosis on the coral *Stylophora pistillata*: nature and cause of ‘low-salinity bleaching’. *Marine Ecology Progress Series* 253, 145–154.
- 104 Kinzie RA III and Hunter T (1987) Effect of light quality on photosynthesis of the reef coral {*Montipora*} {*verrucosa*}. *Marine Biology* 94, 95–109.
- 105 Kleypas JA, Buddemeier RW, Archer D, Gattuso J-P, Langdon C and Opdyke BN (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284, 118–120.
- 106 Kleypas JA, Buddemeier RW, Eakin M, Gattuso J-P, Guinotte J, Hoegh-Guldberg O, Iglesias-Prieto R, Jokiel P, Langdon C, Skirving W. and Strong AE (2005) Comment on “Coral reef calcification and climate change: The effect of ocean warming”. Response to McNeil et al. 2004. *Geophysical Research Letters* 32, No. 8, L08601.
- 107 Kleypas JA, Feely RA, Fabry VJ, Langdon C, Sabine CL and Robbins LL (2006) *Impacts of Ocean Acidification on Coral Reefs and Other Marine Calcifiers: A Guide for Future Research*. Report of a workshop held 18–20 April 2005, St. Petersburg, FL, sponsored by NSF, NOAA, and the U.S. Geological Survey, 88pp (<http://www.isse.ucar.edu/florida/>).
- 108 Kluter A (2002) Pigmentation as a strategy for reducing solar damage in reef-building corals. PhD Thesis, The University of Queensland, St. Lucia.
- 109 Kokita T and Nakazono A (2001) Rapid response of an obligately corallivorous filefish *Oxymonacanthus longirostris* (Monacanthidae) to a mass coral bleaching event. *Coral Reefs* 20, 155–158.
- 110 Kushmaro A, Loya Y, Fine M and Rosenberg M (1996) Bacterial infection and coral bleaching. *Nature* 380, 396.
- 111 Kuta KC and Richardson LL (2002) Ecological aspects of black band disease of corals: relationships between disease incidence and environmental factors. *Coral Reefs* 21, 393–398.
- 112 Lafferty KD (1997) Environmental parasitology: What can parasites tell us about human impacts on the environment? *Parasitology Today* 13, 251–55.
- 113 Lafferty KD, Porter JW and Ford SE (2004) Are diseases increasing in the ocean? *Annual Reviews of Ecological and Evolutionary Systematics* 35, 31–54.
- 114 Larcombe P, Ridd PV, Prytz A and Wilson B (1995) Factors controlling suspended sediment on inner-shelf coral reefs, Townsville, Australia. *Coral Reefs* 14, 163–171.
- 115 Lajeunesse TC (2001) Investigating the biodiversity, ecology and phylogeny of endosymbiotic dinoflagellates in the genus *Symbiodinium* using the ITS region: In search of a “species” level marker. *Journal of Phycology* 37, 866–880.
- 116 Lajeunesse TC (2005) “Species” radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. *Molecular Biology and Evolution* 22, 570–581.
- 117 Lajeunesse TC, Loh WKW, van Woessik R, Hoegh-Guldberg O, Schmidt GW and Fitt WK (2003) Low symbiont diversity in southern Great Barrier Reef corals relative to those of the Caribbean. *Limnology and Oceanography* 48, 2046–2054.
- 118 Langdon C, Takahashi T, Sweeney C, Chipman D, Goddard J, Marubini F, Aceves H, Barnett H and Atkinson MJ (2000) Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochemical Cycles* 14, 639–654.
- 119 LeGrande AN, Schmidt GA, Shindell DT, Field CV, Miller RL, Koch DM, Faluvegi G and Hoffman G (2006) Consistent simulations of multiple proxy responses to an abrupt climate change event. *Proceedings of the National Academy of Science* 103, 837–842.
- 120 Lesser MP (2004) Experimental Biology of coral reef ecosystems. *Journal of Experimental Marine Biology and Ecology* 300, 217–252.
- 121 Lesser MP, Stochaj WR, Tapley DW and Shick JM (1990) Bleaching in coral reef anthozoans: effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. *Coral Reefs* 8, 225–232.
- 122 Levy O, Dubinsky Z and Achituv Y (2003) Photobehavior of stony corals: responses to light spectra and intensity. *Journal of Experimental Biology* 206, 4041–4049.
- 123 Lewis CL and Coffroth MA (2004) The acquisition of exogenous algal symbionts by an octocoral after bleaching. *Science* 304, 1490–1492.
- 124 Little AF, van Oppen MJH and Willis BL (2004) Flexibility in algal endosymbiosis shapes growth in reef corals. *Science* 304, 1492–1494.
- 125 Loh W, Carter DA and Hoegh-Guldberg O (1997) Diversity of zooxanthellae from scleractinian corals of One Tree Island (Great Barrier Reef). *Proceedings of Australian Coral Reef Society 75th Annual Conference*, pp. 141–150.

- 126 Lough JM (2004) A strategy to improve the contribution of coral data to high-resolution paleoclimatology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 204, 115–143.
- 127 Lough JM and Barnes DJ (2000) Environmental controls on growth of the massive coral *Porites*. *Journal Experimental Marine Biology and Ecology* 245, 225–243.
- 128 Lough J, Berkelmans R, van Oppen M, Wooldridge S and Steinberg C (2006) The Great Barrier Reef and Climate Change. *Bulletin of the Australian Meteorological and Oceanographic Society* 19, 53–58.
- 129 Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H and Van Woesik R (2001) Coral bleaching: the winners and the losers. *Ecology Letters* 4, 102–131.
- 130 McCallum H, Harvell CD and Dobson A (2003) Rates of spread of marine pathogens. *Ecology Letters* 6, 1062–1067.
- 131 McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18, 357–367.
- 132 McCulloch M, Fallon S, Wyndham T, Hendy E, Lough J and Barnes D. (2003) Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. *Nature* 421, 727–730.
- 133 McNeil BI, Matear RJ and Barnes DJ (2004) Coral reef calcification and climate change: The effect of ocean warming. *Geophysical Research Letters* 31, L22309, doi:10.1029/2004GL021541.
- 134 Marshall PA and Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* 19, 155–163.
- 135 Marshall PM and Schuttenberg HZ (2006) *A reef manager's guide to coral bleaching*. Great Barrier Reef Marine Park Authority, Townsville.
- 136 Meehl GA, Washington WM, Collins WD, Arblaster JM, Hu A, Buja LE, Strand WG and Teng H (2005) How much more climate change and sea level rise? *Science* 307, 1769–1772.
- 137 Michalek-Wagner K (2001) Seasonal and sex-specific variations in the levels of photo-protecting mycosporine-like amino acids (MAAs) in soft corals. *Marine Biology* 139, 651–660.
- 138 Michalek-Wagner K and Willis BL (2001a) Impacts of bleaching on the soft coral *Lobophytum compactum*. I. Fecundity, fertilization and offspring viability. *Coral Reefs* 19, 231–239.
- 139 Michalek-Wagner K and Willis BL (2001b) Impacts of bleaching on the soft coral *Lobophytum compactum*. II. Biochemical changes in adults and their eggs. *Coral Reefs* 19, 240–246.
- 140 Miller I and Sweatman H (eds) (2004) Status Of Coral Reefs In Australia And Papua New Guinea In: C Wilkinson (ed) *Status of coral reefs of the world: 2004* Volume 2. Australian Institute of Marine Science, Townsville, pp. 303–336.
- 141 Mitani H, Uchida N and Shima A (1996) Induction of cyclobutane pyrimidine dimer photolyase in cultured fish cells by UVA and blue light. *Photochemistry and Photobiology* 64, 943–948.
- 142 Mumby PJ, Chisholm JRM, Edwards AJ, Andréfouët S and Jaubert J (2001) Cloudy weather may have saved Society Islands coral reefs during the 1998 ENSO event. *Marine Ecology Progress Series* 222, 209–216.
- 143 Muscatine L (1990) The role of symbiotic algae in carbon and energy flux in reef corals. In: Z Dubinsky (ed) *Coral Reefs Ecosystems of the World* Volume 25. Elsevier Science Publishing Company, Amsterdam pp. 75–87.
- 144 Nakamura T and van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. *Marine Ecology Progress Series* 210, 301–304.
- 145 Nakamura T, Yamasaki H and van Woesik R. (2003) Water flow facilitates recovery from bleaching in the coral *Stylophora pistillata*. *Marine Ecology Progress Series* 256, 287–291.
- 146 Nakamura E, Yokohama Y and Tanaka J (2004) Photosynthetic activity of a temperate coral *Acropora pruinosa* (Scleractinia, Anthozoa) with symbiotic algae in Japan. *Phycological Research* 52, 38–44.
- 147 Negri AP, Marshall PA and Heyward AJ (2007) Differing effects of thermal stress on coral fertilization and early embryogenesis in four Indo Pacific species. *Coral Reefs in press*.
- 148 Niyogi KK (1999) Photoprotection revisited. Genetic and molecular approaches. *Annual Review of Plant Physiology and Plant Molecular Biology* 50, 333–359.
- 149 Obura D (2005) Resilience and climate change: lessons from coral reefs and bleaching in the Western Indian Ocean. *Estuarine and Coastal Marine Science* 63, 353–372.
- 150 Oliver J (1985) Recurrent seasonal bleaching and mortality of corals on the Great Barrier Reef. *Proceedings of the 5th International Coral Reef Symposium*, 4, 201–206.
- 151 Omori M, Fukami H, Kobinata H and Hatta M (2001) Significant drop in fertilization of *Acropora* corals in 1999: An after effect of coral bleaching? *Limnology and Oceanography* 46, 704–706.
- 152 Overpeck JT, Otto-Bliessner BL, Miller GH, Muhs DR, Alley RB and Kiehl JT (2006) Paleoclimatic Evidence for Future Ice-Sheet Instability and Rapid Sea-Level Rise. *Science* 311, 1747–1750.

- 153 Page C and Willis BL (2006) Distribution, host range and large-scale spatial variability in black band disease prevalence on the Great Barrier Reef, Australia. *Diseases of Aquatic Organisms* 69, 41–51.
- 154 Pianka ER (1978) *Evolutionary Ecology*, Second Edition Harper and Rowe Publishers, New York, USA.
- 155 Pittcock BA (1999) Coral reefs and environmental change: Adaptation to what? *American Zoologist* 1999, 10–29.
- 156 Porter JW and Meier OW (1992) Quantification of loss and change in Floridian reef coral populations. *American Zoologist* 32, 625–640.
- 157 Porter JW, Dustan P, Jaap WC, Patterson KP, Kosmyrin V, Meier OW, Patterson ME and Parsons M (2001) Patterns of spread of coral disease in the Florida Keys. *Hydrobiologia* 460, 1–24.
- 158 Prezelin BB, Ley AC and Haxo FT (1976) Effect of growth irradiance on the photosynthetic action spectra of the marine dinoflagellate, *Glenodinium* sp. *Planta* 130, 251–256.
- 159 Raven J, Caldeira K, Elderfield H, Hoegh-Guldberg O, Liss P, Riebesell U, Shepherd J, Turley C and Watson A (2005) *Ocean acidification due to increasing atmospheric carbon dioxide*. Royal Society Special Report, ISBN 0 85403 617 2.
- 160 Rinkevich B (1989) The contribution of photosynthetic products to coral reproduction. *Marine Biology* 101, 259–263.
- 161 Risebrobakken B, Jansen E, Andersson C, Mjelde E and Hevroy K (2003) A high-resolution study of Holocene paleoclimatic and paleoceanographic changes in the Nordic Seas. *Paleoceanography* 18, doi 10.1029/2002PA000764.
- 162 Roff G (2004) Epizootiology of the Tabulate Acropora White Syndrome. Honours Thesis, The University of Queensland, St. Lucia.
- 163 Rosenberg E and Ben-Haim Y (2002) Microbial diseases of corals and climate change. *Environmental Microbiology* 4, 318–326.
- 164 Rowan R (1998) Diversity and ecology of zooxanthellae on coral reefs. *Journal of Phycology* 34, 407–417.
- 165 Rowan R (2004) Thermal adaptation in reef coral symbionts. *Nature* 430, 742.
- 166 Rowan R, Knowlton N, Baker A and Jara J (1997) Landscape ecology of algal symbionts creates variation in episodes of bleaching. *Nature* 388, 265–269.
- 167 Salih A, Larkum AWD, Cox G, Kuhl M and Hoegh-Guldberg O (2000) Fluorescent pigments in corals are photoprotective. *Nature* 408, 850–853.
- 168 Santos SR, Gutierrez-Rodriguez C, Lasker HR and Coffroth MA (2003) *Symbiodinium* sp. associations in the gorgonian *Pseudopterogorgia elisabethae* in the Bahamas: high levels of genetic variability and population structure in symbiotic dinoflagellates. *Marine Biology* 143, 111–100.
- 169 Saxby T, Dennison WC and Hoegh-Guldberg O (2003) Photosynthetic responses of the coral *Montipora digitata* cold temperature stress. *Marine Ecology Progress Series* 248, 85–97.
- 170 Selig ER, Harvell CD, Bruno JF, Willis BL, Page CA, Casey KS and Sweatman H (2006) Analyzing the relationship between ocean temperature anomalies and coral disease outbreaks at broad spatial scales. In: J Phinney, O Hoegh-Guldberg, J Kleypas, W Skirving, A Strong (eds) *Coral Reefs and Climate Change: Science and Management*. American Geophysical Union, Coastal and Estuarine Series 61.
- 171 Smith C (2005) The role of genetic and environmental variation on the thermal tolerance of a reef building coral *Acropora millepora*. PhD Thesis, The University of Queensland, St. Lucia.
- 172 Smith-Keune C and van Oppen MJH (2006) Genetic structure of a reef-building coral from thermally distinct environments on the Great Barrier Reef. *Coral Reefs* 25, 493–502.
- 173 Smith H (2000) Phytochromes and light signal perception by plants—an emerging synthesis. *Nature* 407, 585–591.
- 174 Spalding MD and Jarvis GE (2002) The impact of the 1998 coral mortality on reef fish communities in the Seychelles. *Marine Pollution Bulletin* 44, 309–321.
- 175 Strong AE, Barrientos CS, Duda C and Saper J (1997) Improved satellite techniques for monitoring coral reef bleaching. In: HA Lessios and IG Macintyre (eds) *Proceedings of the 8th International Coral Reef Symposium Vol. 2*. Smithsonian Tropical Research Institute, Panama, pp. 1495–1498.
- 176 Sweatman H, Burgess S, Cheal A, Coleman G, Delean S, Ermslie M, Miller I, Osborne K, McDonald A and Thompson A (2005) *Long term monitoring of the Great Barrier Reef. Status Report No. 7*. Australian Institute of Marine Science, Townsville.
- 177 Szmant AM and Gassman NJ (1990) The effects of prolonged “bleaching” on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. *Coral Reefs* 8, 217–224.
- 178 Thornhill DJ, Fitt WK and Schmidt GW (2006) Highly stable symbioses among western Atlantic brooding corals. *Coral Reefs* 25, 515–519.
- 179 Toller WW, Rowan R and Knowlton N (2001) Repopulation of zooxanthellae in the Caribbean corals *Montastraea annularis* and *M. faveolata* following experimental and disease-associated bleaching. *Biological Bulletin* 201, 360–373.

- 180 Torren A, Landau L, Kushmaro A, Loya Y and Rosenberg E (1998) Effect of temperature on adhesion of *Vibrio* strain AK-1 to *Oculina patagonica* and on coral bleaching. *Applied Environmental Microbiology* 64, 1347–1384.
- 181 Trench RK (1979) The cell biology of plant-animal symbiosis. *Annual Review of Plant Physiology* 30, 485–531.
- 182 Trench RK (1997) Diversity of symbiotic dinoflagellates and the evolution of microalgal-invertebrate symbiosis. *Proceedings of the 8th International Coral Reef Symposium* 2, 1075–1086.
- 183 Ulstrup KE and van Oppen MJH (2003) Geographic and habitat partitioning of genetically distinct zooxanthellae (Symbiodinium) in *Acropora* corals on the Great Barrier Reef. *Molecular Ecology* 10, 3477–3484.
- 184 Ulstrup KE, Hill R and Ralph PJ (2005) Photosynthetic impact of hypoxia on *in hospite* zooxanthellae in the scleractinian coral *Pocillopora damicornis*. *Marine Ecology Progress Series* 286, 105–132.
- 185 Ulstrup KE, Berkelmans R, Ralph PJ and van Oppen MJH (2006) Variation in bleaching sensitivity of two coral species with contrasting bleaching thresholds across a latitudinal gradient on the Great Barrier Reef. *Marine Ecology Progress Series* 314, 135–148.
- 186 Vaughan TW (1914) Reef corals of the Bahamas and of southern Florida. Carnegie Institution of Washington, Year Book for 1914.
- 187 Veron J (2000) *Corals of the World*. Australian Institute of Marine Science, Townsville.
- 188 Wachenfeld D (1997) Long-term trends in the status of coral reef-flat benthos - The use of historical photographs in "State of the Great Barrier Reef World Heritage Area". In: D Wachenfeld, J Oliver and K Davis K (eds) *Proceedings of State of the Great Barrier Reef World Heritage Area Workshop, Townsville, November 27-29, 1995*.
- 189 Walters RG (2004) Towards an understanding of photosynthetic acclimation. *Journal of Experimental Botany* 56, 411 doi:10.1093/jxb/eri060.
- 190 Walters RG, Rogers J, Shephard F and Horton P (1999) Acclimation of *Arabidopsis thaliana* to the light environment: the role of photoreceptors. *Planta* 209, 517–527.
- 191 Ward JR and Lafferty KD (2004) The elusive baseline of marine disease: Are diseases in ocean ecosystems increasing? *Public Library of Science, Biology* 2, 542–547.
- 192 Ward S, Harrison P and Hoegh-Guldberg O (2002) Coral bleaching reduces reproduction of scleractinian corals and increases susceptibility to future stress. In: MK Moosa, S Soemodihardjo, A Soegiarto, K Romimohartarto, A Nontji and S Suharsono (eds) *Proceedings of the 9th International Coral Reef Symposium*, pp. 1123–1128.
- 193 Webster PJ, Holland GJ, Curry JA and Chang HR (2006) Changes in Tropical Cyclone Number, Duration, and Intensity in a Warming Environment. *Science* 309, 1844–1846.
- 194 Weil E (2004) Coral reef disease in the wider Caribbean: Status and Prognosis. In: E Rosenberg and Y Loya (eds) *Coral Health and Disease*, Springer, Berlin, pp 35–68.
- 195 Wigley TML (2005) The climate change commitment. *Science* 307, 1766–1769.
- 196 Wilkinson CR (1999) Global and local threats to coral reef functioning and existence: review and predictions. *Marine and Freshwater Research* 50, 867–878.
- 197 Wilkinson CR (ed) (2004) *Global Coral Reef Monitoring Network: Status of coral reefs of the world in 2004*. Published by the Australian Institute of Marine Science, Townsville.
- 198 Willis BL, Page CA and Dinsdale EA (2004) Coral disease on the Great Barrier Reef. In: E Rosenberg and Y Loya (eds) *Coral Health and Disease*, Springer, Berlin, pp 69–104.
- 199 Wooldridge S, Done T, Berkelmans R, Jones R and Marshall P (2005) Precursors for resilience in coral communities in a warming climate: a belief network approach. *Marine Ecology Progress Series* 295, 157–169.
- 200 Yamazato K (1981) A note on the expulsion of zooxanthellae during summer 1980 by the Okinawan reef-building corals. *Sesoko Marine Science Laboratory Technical Reports* 8, 9–18.
- 201 Yonge CM and 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* 1, 177–211.

