

Climate change, coral bleaching and the future of the world's coral reefs

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Abstract. Sea temperatures in many tropical regions have increased by almost 1°C over the past 100 years, and are currently increasing at ~1–2°C per century. Coral bleaching occurs when the thermal tolerance of corals and their photosynthetic symbionts (zooxanthellae) is exceeded. Mass coral bleaching has occurred in association with episodes of elevated sea temperatures over the past 20 years and involves the loss of the zooxanthellae following chronic photoinhibition. Mass bleaching has resulted in significant losses of live coral in many parts of the world. This paper considers the biochemical, physiological and ecological perspectives of coral bleaching. It also uses the outputs of four runs from three models of global climate change which simulate changes in sea temperature and hence how the frequency and intensity of bleaching events will change over the next 100 years. The results suggest that the thermal tolerances of reef-building corals are likely to be exceeded every year within the next few decades. Events as severe as the 1998 event, the worst on record, are likely to become commonplace within 20 years. Most information suggests that the capacity for acclimation by corals has already been exceeded, and that adaptation will be too slow to avert a decline in the quality of the world's reefs. The rapidity of the changes that are predicted indicates a major problem for tropical marine ecosystems and suggests that unrestrained warming cannot occur without the loss and degradation of coral reefs on a global scale.

Extra keywords: global climate change, zooxanthellae, temperature, photoinhibition

Environmental and economic importance of the world's coral reefs

Coral reefs are the most spectacular and diverse marine ecosystems on the planet. Complex and productive, coral reefs boast hundreds of thousands of species, many of which are undescribed by science. They are renowned for their beauty, biological diversity and high productivity.

Coral reefs have had a crucial role in shaping the ecosystems that have dominated tropical oceans over the past 200 million years. Early scientists such as Charles Darwin puzzled over the unusual positioning of these highly productive ecosystems in waters that are very low in the nutrients necessary for primary production (Darwin 1842; Odum and Odum 1955). Consequently, coral reefs are often likened to 'oases' within marine nutrient deserts. In the open sea surrounding coral reefs, productivity may fall as low as 0.01 gC m⁻² day⁻¹ Hatcher (1988) and yet may be many thousands of times higher within associated coral reef systems (e.g. algal turfs: 280 gC m⁻² day⁻¹; corals: 40 gC m⁻² day⁻¹; benthic microalgae: 363 gC m⁻² day⁻¹; reviewed by Hatcher 1988). Their high productivity within these otherwise unproductive waters makes coral reefs critical to the survival of tropical marine ecosystems and hence of local people.

The elimination of coral reefs would have dire consequences. Coral reefs represent crucial sources of income and resources through their role in tourism, fishing, building materials, coastal protection and the discovery of new drugs and biochemicals (Carte 1996). Globally, many people

depend in part or wholly on coral reefs for their livelihood, and ~15% (0.5 billion people) of the world's population live within 100 km of coral reef ecosystems (Pomeroy 1999). Tourism alone generates billions of dollars for countries associated with coral reefs; \$US1 billion is generated annually by the Great Barrier Reef (Australia: Done *et al.* 1996), \$US1.6 billion by Floridean reefs (USA: Birkeland 1997) and ~\$US90 billion by reefs throughout the Caribbean (Jameson *et al.* 1995).

Tourism is the fastest growing economic sector associated with coral reefs and is set to double in the very near future. One hundred million tourists visit the Caribbean each year and SCUBA diving in the Caribbean alone is projected to generate almost \$US1 billion by the year 2005 (US Department of State 1998). The fisheries associated with coral reefs also generate significant wealth for countries with coral reef coastlines. Annually, fisheries in coral reef ecosystems yield at least 6 million metric tonnes of fish catches world-wide (Munro 1996) and provide employment for millions of fishers (Roberts *et al.* 1998). Fisheries in coral reef areas also have importance beyond the mere generation of monetary wealth and are an essential source of protein for many millions of the world's poorer societies. For example, 25% of the fish catch in developing countries is provided from fisheries associated with coral reefs (Bryant *et al.* 1998).

Coral reefs also protect coastlines from storm damage, erosion and flooding by reducing wave action across tropical coastlines. The protection offered by coral reefs also enables

the formation of associated ecosystems (e.g. seagrass beds and mangroves) which allow the formation of essential habitats, fisheries and livelihoods. The cost of totally losing coral reefs would run into hundreds of billions of dollars each year. For example, the cost of losing 58% of the world's coral reefs has been estimated as \$US90 billion in lost tourism alone (Bryant *et al.* 1998). If these direct costs are added to the indirect losses generated by losing the protection of tropical coastlines, the economic effect of losing coral reefs becomes truly staggering.

Despite their importance and persistence over geological time, coral reefs appear to be one of the most vulnerable marine ecosystems. Dramatic reversals in their health have been reported from every part of the world. Between 50% and 70% of all coral reefs are under direct threat from human activities (Goreau 1992; Sebens 1994; Wilkinson and Buddemeier 1994; Bryant *et al.* 1998; Wilkinson 1999 this volume). Like their terrestrial counterparts—rainforests—coral reefs are being endangered by a diverse range of human-related threats. Eutrophication and increased sedimentation flowing from disturbed terrestrial environments, over-exploitation of marine species, mining and physical destruction by reef users are the main causes of reef destruction (Sebens 1994). Mass coral 'bleaching' is yet another major contributing factor to decline of coral reefs (Glynn 1993; Brown 1997a; Hoegh-Guldberg *et al.* 1997). Six major episodes of coral bleaching have occurred since 1979, with the associated coral mortality affecting reefs in every part of the world. Entire reef systems have lost almost all their living reef-building corals following bleaching events (e.g. Brown and Suharsono 1990).

The decline in reef systems world-wide has begun to receive attention at the top levels of world governments. Actions such as the recent formation of the US and International Coral Reef Initiatives and US President William J. Clinton's Executive Order 13089 on 11 June 1998 emphasize this point. The latter states at one point that 'All Federal agencies whose actions may affect U.S. coral reef ecosystems ... should seek or secure implementation of measures necessary to reduce and mitigate coral reef ecosystem degradation and to restore damaged coral reefs'.

The size and scale of coral bleaching, the most recent addition to the barrage of human-related assaults on coral reefs, has attracted considerable social, political and scientific comment. Despite this, there are many questions that remain unanswered. For example, is coral bleaching a natural signal that has been misinterpreted as a sign of climate change? Has the incidence of coral bleaching increased since 1979 or has it simply been overlooked before 1979? Are bleaching events likely to increase or decrease in intensity in the next 100 years? These questions lie at the heart of debate associated with human-induced climate change and the cost that may be borne by both developed and developing countries world-wide.

This article reviews what we know about coral bleaching and its effect on coral reef ecosystems. It reviews the scientific evidence that coral bleaching is a sign of climate change and builds a case for the prediction that thermally triggered coral bleaching events will increase in frequency and severity in the next few decades. In particular, this article rationalizes known thermal thresholds of coral reefs with the output of the main global circulation models used internationally, which all predict rapid rises in tropical sea temperature over the next 100 years if greenhouse gas concentrations continue to increase. The present understanding of coral bleaching suggests that corals are not keeping up with the rate of warming and that they may be the single largest casualty of 'business-as-usual' greenhouse policies. Although reef-building corals are not likely to become extinct in the long term, their health and distribution will be severely compromised for many hundreds of years unless warming is mitigated. The implications of this 'future' are enormous and should be avoided with all the resources at our disposal.

Central role of symbioses in coral reefs

The central feature of shallow-water coastal ecosystems is the predominance of symbioses between invertebrates and dinoflagellate microalgae (zooxanthellae; Odum and Odum 1955). Coral reefs depend on an array of symbioses that serve to restrict the outward flow of life-supporting nutrients to the water column; corals and their zooxanthellae live by limiting the flow of nitrogen and other essential nutrients to the nutrient "desert" represented by tropical seas.

Muscatine and Porter (1977) emphasize this point with respect to the endosymbiosis (one organism living inside the cells of the other) between dinoflagellates and invertebrates. Reef-building corals, the heart of coral reefs, are all symbiotic with a diverse range of dinoflagellates. Close association of primary producer and consumer makes possible the tight nutrient recycling that is thought to explain the high productivity of coral reefs.

Corals are central to coral reef ecosystems. The vigorous growth of reef-building corals in tropical seas is responsible for the framework of coral reef systems. While other organisms serve to weld the structure together (e.g. calcareous red algae) and populate it (e.g. fish, algae, invertebrates and bacteria), corals have been the underlying reason for the structure of coral reef ecosystems for at least 200 million years; they have built the primary structure of entire reefs, islands and such massive oceanic barriers as the Great Barrier Reef.

The symbiosis between corals and zooxanthellae (Fig. 1) has been the subject of considerable interest since the odd brown cells of corals and other symbiotic invertebrates were classified as separate organisms by Brandt (1881). The symbiotic dinoflagellates of corals and invertebrates from at least five other phyla live symbiotically within the cells of their hosts. Representatives are found in the Mollusca (snails and

clams), Platyhelminthes (flatworms), Cnidaria (corals and anemones), Porifera (sponges) and Protista (e.g. single-celled ciliates).

Histology and physiology

Except in giant clams (Norton and Jones 1992; Norton *et al.* 1992), zooxanthellae are intracellular (Trench 1979) and are found within membrane-bound vacuoles in the cells of the host. Until recently, most zooxanthellae were considered to be members of a single pandemic species, *Symbiodinium microadriaticum*. Pioneering studies by Trench (Trench 1979; Schoenberg and Trench 1980a, 1980b) and Rowan (Rowan and Powers 1991, 1992) have revealed that zooxanthellae are a highly diverse group of organisms which may include hundreds of taxa with perhaps as many as two or three species per host in some invertebrate species (Rowan *et al.* 1997; Loh *et al.* 1997).

Zooxanthellae photosynthesize while residing inside their hosts, and provide energy and nutrients for the invertebrate host by translocating up to 95% of their photosynthetic production to it (Muscatine 1990). Zooxanthellae selectively leak amino acids, sugars, complex carbohydrates and small peptides across the host–symbiont barrier. These compounds provide the host with a supply of energy and essential compounds (Muscatine 1973; Trench 1979; Swanson and Hoegh-Guldberg 1998). Corals and their zooxanthellae form a mutualistic symbiosis, as both partners appear to derive benefit from the association. Corals receive photosynthetic products (sugars and amino acids) in return for supplying zooxanthellae with crucial plant nutrients (ammonia and phosphate) from their waste metabolism (Trench 1979). The latter appear to be crucial for the survival of these primary producers in a water column that is normally devoid of these essential inorganic nutrients.

Corals and the associated organisms that make up coral reefs contribute heavily to the primary production of coral reefs. The benefits of this production flow down a complex food chain (Odum and Odum 1955) and provide the basis of the most diverse marine ecosystem on the planet. Fish, bird, marine reptile and mammal communities within coral reefs are substantial and contrast the usually clear and unpopulated waters that surround most coral reef ecosystems.

Mass coral bleaching and the role of temperature

Environmental factors affecting reef-building corals and their zooxanthellae

Coral reefs dominate coastal tropical environments between the latitudes 25°S and 25°N and roughly coincide with water temperatures between 18°C and 30°C (Veron 1986). Below 18°C (generally at latitudes greater than 30°), the number of reef-building coral species declines rapidly and reefs do not form. Reefs at these temperatures are dominated by forests of kelp and other macroalgae. While low water temperature is

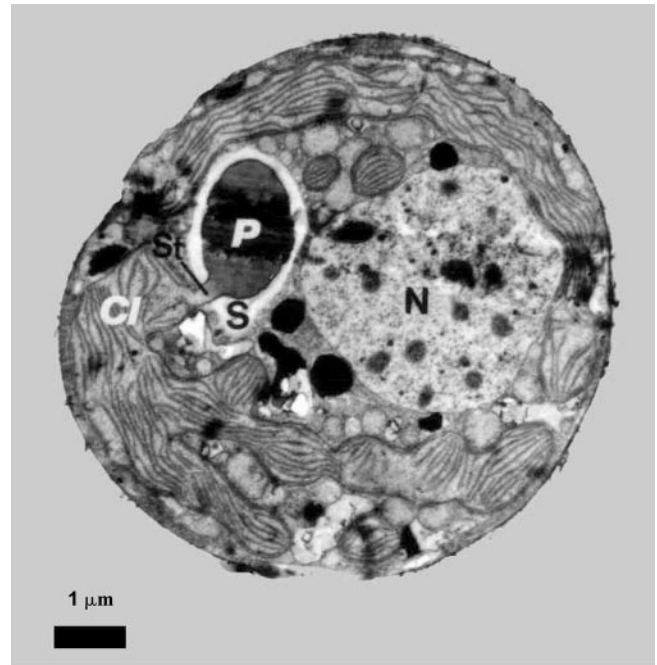


Fig. 1. Symbiotic alga or zooxanthella from a reef-building coral. P, pyrenoid; N, nucleus; Cl, chloroplast; S, starch. (Photographer: Misaki Takabayashi.)

correlated with the decline of coral reefs in a poleward direction, other variables such as light and the carbonate alkalinity of seawater (Gattuso *et al.* 1999; Kleypas *et al.* 1999a) may also play significant roles in determining the distribution of reefs. The combined influence of these factors determines how well corals compete with macroalgae and other organisms that flourish at higher latitudes.

Reef-building corals are greatly influenced by the biological and physical factors of their environment. Predators such as the crown-of-thorns starfish *Acanthaster planci* (Moran 1986) and disease greatly affect the survivorship of reef-building corals and a range of other coral-associated invertebrates. Temperature, salinity and light have major effects on where reef-building corals grow. Environments in which coral reefs prosper are also typified by a high degree of stability. Not only are seasonal and diurnal fluctuations in tropical sea temperature generally small, but evidence suggests that mean sea temperatures in tropical oceans may have varied by less than 2°C over the past 18 000 years (Thunnell *et al.* 1994). Corals exist naturally at salinities that range from 32 to 40 (Veron 1986). Rapid decreases in salinity cause corals to die (Hoegh-Guldberg and Smith 1989a), an effect that probably underlies the mass mortalities of corals after severe rain storms or flood events (Goreau 1964; Egana and DiSalvo 1982). Fluctuations in salinity are thought to play an important role in limiting the distribution of reef-building corals in coastal regions. The proximity of rivers to coral reefs is a very important determinant of reef distribution; not only are rivers

the principal source of sediments, nutrients and salinity stress along tropical coastlines, but they now carry a range of other substances that may affect corals and coral reef organisms (e.g. pesticides, herbicides: Goreau 1992; Wilkinson and Buddemeier 1994).

Light plays a major role in providing the energy that drives the photosynthetic activity of the zooxanthellae (Chalker *et al.* 1988). Consequently, light has a profound effect on determining where corals may grow, and in influencing other aspects such as colony morphology (Muscatine 1990). Reef-building corals are found within the top 100 m of tropical oceans, except in the case of some deeper-water corals in which pigment adaptations increase the ability of the zooxanthellae to collect light for photosynthesis (Schlichter *et al.* 1985). Limits to coral growth are much shallower in areas where sedimentation reduces the transmission of light through the water column or smothers corals. Corals may be eliminated altogether in areas where large amounts of sediment enter the sea, such as those close to river mouths (Veron 1986). In the latter case, sediment may have additional effects such as causing the smothering of corals.

Corals and their zooxanthellae have some versatility with respect to their ability to acclimatize to low or high light intensity. Concentrations of chlorophyll and other photosynthetic pigments within zooxanthellae increase under low light intensity (Falkowski and Dubinsky 1981; Porter *et al.* 1984) and decrease under high light intensity. Under extremely high light intensity the photoinhibition of zooxanthellae can be a significant problem, and reef-building corals and their zooxanthellae appear to have a series of 'quenching' mechanisms to reduce the impact of excess light (Hoegh-Guldberg and Jones 1999; Ralph *et al.* 1999). These protective measures against high light intensity have even been reported for corals growing on reefs at high latitudes in winter (Hoegh-Guldberg and Jones 1999), suggesting that light intensity over the geographic range of corals is usually higher than these organisms require for growth. The mechanisms by which quenching is achieved appear to involve changes in xanthophyll pigments (Brown *et al.* 1999), as has been described for sometime in higher plants (Bilger *et al.* 1987; Demmig-Adams 1990) and marine algae (Franklin *et al.* 1996).

In addition to visible light (photosynthetically active radiation, PAR), short-wavelength radiation (290–400 nm) such as ultra-violet radiation (UVR) strongly influences both the distribution and physiology of marine plants and animals (Jokiel 1980). It also has destructive effects on marine organisms (Jokiel 1980) including corals and their symbiotic dinoflagellates (Lesser 1996; Shick *et al.* 1996). Effects of UVR on cultured symbiotic dinoflagellates include decreased growth rates, cellular chlorophyll *a* concentrations, carbon : nitrogen ratios, photosynthetic oxygen evolution and ribulose biphosphate carboxylase/oxygenase (Rubisco) activities (Banaszak and Trench 1995; Lesser 1996). Similar effects have been reported for symbiotic dinoflagellates living within cnidarian tissues

(Jokiel and York 1982; Lesser and Shick 1989; Shick *et al.* 1991, 1995; Gleason 1993; Gleason and Wellington 1993; Kinzie 1993; Banaszak and Trench 1995). Both host and symbiont have been reported to have a range of protective mechanisms to counteract the direct and indirect influences of UVR. These include the production of mycosporine-like amino acids, which are natural sunscreen (UVR blocking) compounds, and a range of active oxygen scavenging systems (for review, Shick *et al.* 1996).

Mass coral bleaching and its causes

Population densities of zooxanthellae in reef-building corals range between 0.5×10^6 and 5×10^6 cells cm^{-2} (Drew 1972; Porter *et al.* 1984; Hoegh-Guldberg and Smith 1989a, 1989b). Zooxanthellae inhabiting the tissues of corals normally show low rates of migration or expulsion to the water column (Hoegh-Guldberg *et al.* 1987). Despite these low rates, population densities have been reported to undergo seasonal changes (Jones 1995; Fagoonee *et al.* 1999; W. K. Fitt personal communication). These seasonal changes are far from uniform and probably depend on changes in the physical variables of the immediate environment. Changes are gradual and probably represent slow adjustments of symbioses that optimize the physiological performance of the two-genome syncytium as the environment changes. Under a range of physical and chemical conditions, however, sudden reductions in the density of zooxanthellae may lead to greater rates of loss from symbiotic corals and other invertebrate hosts (Brown and Howard 1985; Hoegh-Guldberg and Smith 1989a).

Reduced salinity (Goreau 1964; Egana and DiSalvo 1982), increased or decreased light (Vaughan 1914; Yonge and Nichols 1931; Hoegh-Guldberg and Smith 1989a; Gleason and Wellington 1993; Lesser *et al.* 1990) or temperature (Jokiel and Coles 1977, 1990; Coles and Jokiel 1978; Hoegh-Guldberg and Smith 1989a; Glynn and D'Croz 1990) can cause corals and other symbiotic invertebrates to rapidly pale. Chemical factors such as copper ions (Jones 1997a), cyanide (Jones and Steven 1997; Jones and Hoegh-Guldberg 1999), herbicides, pesticides and biological factors (e.g. bacteria, Kushmaro *et al.* 1996) can also cause the loss of algal pigments from symbiotic invertebrates. Because corals rapidly lose colour and turn a brilliant white, this phenomenon has been referred to as 'bleaching'. In most cases the rapid bleaching of corals, especially during mass bleaching events, is found to be due to the loss of zooxanthellae and/or the loss of the pigments of the zooxanthellae (Hoegh-Guldberg and Smith 1989a).

Bleaching may occur at local scales (e.g. parts of reefs: Goreau 1964; Egana and DiSalvo 1982) or at geographic scales that may involve entire reef systems and geographic realms ('mass bleaching': Glynn 1984; Goreau 1990; Williams and Williams 1990; Hoegh-Guldberg and Salvat 1995; Brown 1997a). Because of the intensity and geographic scale of recent bleaching events and associated coral mortalities, mass

bleaching is considered by most reef scientists to be a serious and relatively new challenge to the health of the world's coral reef (e.g. Glynn 1993, Goreau and Hayes 1994, Hoegh-Guldberg and Salvat 1995, Brown 1997a).

Increased water temperature and mass bleaching events

Most evidence indicates that elevated temperature is the cause of mass bleaching events. Increasing water temperature rapidly causes zooxanthellae to leave the tissues of reef-building corals and other invertebrates resulting in a reduced number of zooxanthellae in the tissues of the host (Coles and Jokiel 1977, 1978; Hoegh-Guldberg and Smith 1989a; Glynn and D'Croz 1990; Lesser *et al.* 1990). Changes to PAR or UVR aggravate the effect of temperature (Hoegh-Guldberg and Smith 1989a; Gleason and Wellington 1993; Lesser 1996). But as pointed out by Hoegh-Guldberg and Smith (1989), the effect of changes in PAR or UVR alone does not closely match the characteristics in corals collected during mass bleaching events. During recent global bleaching corals were characterized by reduced population densities of zooxanthellae (with or without a decrease in zooxanthellae-specific pigments). The changes associated with mass coral bleaching have never been reported as solely due to the loss of photosynthetic pigments, as sometimes occurs under extremely high PAR and UVR (e.g. Hoegh-Guldberg and Smith 1989a; Lesser 1996).

Other factors such as reduced salinity may cause colour loss but do not resemble corals after mass bleaching events (Hoegh-Guldberg and Smith 1989a). For example, in some cases of 'bleaching' caused by reduced salinity, loss of coral tissue may be confused with the loss of zooxanthellae that is characteristic of mass bleaching. Corals survive salinities down to 23 (two-thirds the strength of seawater) but then die, with tissue sloughing off to reveal the white skeleton below (Hoegh-Guldberg and Smith 1989a). Although superficially the same (i.e. whitened corals), the physiological mechanism and the lack of tissue do not generally resemble those of corals collected during mass bleaching events. A key characteristic of mass bleaching events (Fig. 2A) is that the host tissue remains on the skeleton but is relatively free of zooxanthellae (Fig. 2B).

Correlative field studies have pointed to warmer-than-normal conditions as being responsible for triggering mass bleaching events (reviews: Glynn 1993; Brown 1997a; Hoegh-Guldberg *et al.* 1997; Winter *et al.* 1998). Glynn (1984, 1988) was the first to provide substantial evidence of the association of mass coral bleaching and mortality with higher-than-normal sea temperature. Glynn (1993) indicated that 70% of the many reports of coral bleaching were associated with reports of warmer-than-normal conditions. Goreau (1990), Glynn (1991) and Hayes and Goreau (1991) were among the first to suggest that the projected increases in sea temperature associated with global climate change were likely to push corals beyond their thermal limits. The associ-

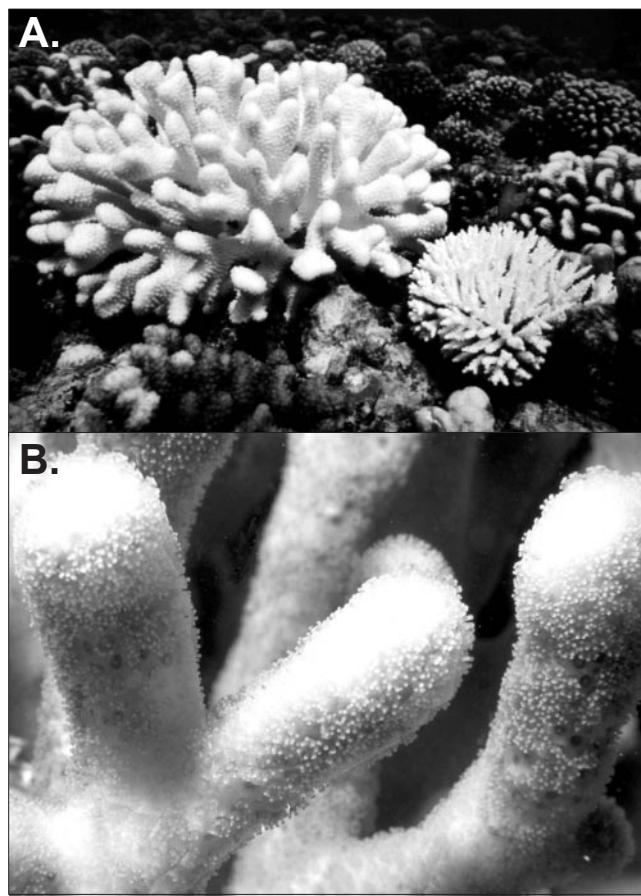


Fig. 2. (A) Bleached corals on northern reef slope of Moorea, French Polynesia, 1994. (Photographer: R. Grace/Greenpeace International.) (B) Close-up of bleached corals from Lizard Island, central Great Barrier Reef; note fully extended polyps despite the conspicuous lack of zooxanthellae. (Photographer: O. Hoegh-Guldberg.)

ation of bleaching and higher-than-normal sea temperatures has become even stronger with a proliferation of correlative studies for different parts of the world (e.g. Goreau *et al.* 1993; Goreau and Hayes 1994; Hoegh-Guldberg and Salvat 1995; Brown 1997a; Hoegh-Guldberg *et al.* 1997; Jones 1997b; Jones *et al.* 1997; Winter *et al.* 1998). These studies show a tight association between warmer-than-normal conditions (at least 1°C higher than the summer maximum) and the incidence of coral bleaching.

The severe bleaching event in 1998 have added further weight to the argument that elevated temperature is the primary variable triggering coral bleaching. Not only were most incidents of bleaching in 1998 associated with reports of warmer-than-normal conditions, but the 'Hotspot' program (Goreau and Hayes 1994) run by the US National Oceanic and Atmospheric Administration (NOAA) predicted (days or weeks in advance) bleaching for most geographic regions where bleaching occurred during 1998. NOAA/NESDIS (NOAA/National Environmental Satellite Data and

Information Service) established in January 1997 an interactive Web site based on the use of 'hotspots' (when sea surface temperatures (SSTs) exceed the monthly maximum climatological value by 1°C) to predict bleaching. One of the most graphic examples of the success of this program was the prediction of the record bleaching event on the Great Barrier Reef sent by email to the CHAMP (Coral Health and Monitoring Program: coral-list@coral.aoml.noaa.gov) network email list (Hendee 1998) by A. E. Strong on 10 February 1998: 'SSTs have warmed considerably off the eastern coast of Australia during the past few weeks. Our "HotSpot" chart indicates bleaching may have begun in the southernmost region of the Great Barrier Reef. To my knowledge, our SSTs from 1984 have not seen anything quite this warm'.

What happened next was truly remarkable. The CHAMP Network (Hendee 1998) received the first reports of bleaching on the Great Barrier Reef four days later (M. Huber, Townsville, 14 February 1998). By 27 February, reports (B. Willis, Bundaberg, Qld; D. Bucher, Lismore, NSW; R. Berkelmans, Townsville, Qld) had been returned from both the southern and northern regions of the Great Barrier Reef that heavy bleaching was occurring on a number of inshore reefs. By mid March, extensive surveys run by the Great Barrier Reef Marine Park Authority (GBRMPA) (Berkelmans and Oliver 1999) and the Australian Institute of Marine Sciences (AIMS) revealed that the inner reefs along the entire length of the Great Barrier Reef had experienced a major bleaching event. More than 100 observational reports from other areas across the globe during 1998 that documented the tight correlation between positive thermal anomalies and bleaching can be obtained from the NOAA web site (<http://coral.aoml.noaa.gov>, April 1999). Similar conclusions can be drawn from events occurring during 1995–97 (Goreau *et al.* 1997).

Global patterns of coral bleaching

The mass coral bleaching event of 1998 is considered to be the most severe on record (NOAA 1998; ISRS 1998a), with bleaching affecting every geographic coral-reef realm in the world (Fig. 3). This was the sixth major episode of coral bleaching since 1979 to affect coral reefs across a significant portion of the world's oceans.

Strong bleaching episodes coincide with periods of high SST and are associated with disturbances to the El Niño–Southern Oscillation (ENSO; Fig. 3). Most occur during strong El Niño periods, when the Southern Oscillation Index (SOI) is negative (< -5). However, some regions such as the southern parts of the Cook Islands experience bleaching in strong La Niña periods due to southward shifts in the position of the south Pacific Convergence zone and associated water masses. In 1997–98 the most extensive and intense bleaching event on record coincided with (by some indices) the strongest ENSO disturbance on record (Kerr 1999). For the first time, coral reefs in every region of the

world recorded severe bleaching events (Fig. 3). In some places (e.g. Singapore, ISRS 1998a), bleaching was recorded for the first time. Many massive corals (which may live for well over 1000 years) have died as a result of the 1998 event, including some with an age of up to 700 years (ISRS 1998a); this, although in need of study, suggests that for these corals at least, conditions in 1998 were extreme relative to the previous 700 years.

Bleaching began in 1997–98 in the Southern Hemisphere during summer. Incidents of bleaching in the 1997–98 episode were first reported on the CHAMP Network (Hendee 1998) in the eastern Pacific (Galapagos) and parts of the Caribbean (Grand Cayman) in late 1997, and spread across the Pacific to French Polynesia, Samoa and Australia by early February 1998. Soon afterwards (March and April 1998), bleaching was being reported at sites across the Indian Ocean, with reports being received from South-east Asia in May 1998. As summer began in the Northern Hemisphere, north-east Asian and Caribbean coral reefs began to bleach in June, with bleaching continuing until early September 1998 (Fig. 4). Reports supplied to CHAMP Network on the 1997–98 bleaching episode have been archived by NOAA (<http://coral.aoml.noaa.gov>, April 1999; Hendee 1998) and have been collated by Wilkinson (1999).

The pattern associated with the 1997–98 bleaching episode strongly resembles patterns seen during the strong 1982–83, 1987–88 and 1994–95 bleaching episodes. Southern Hemisphere reefs (both Pacific and Indian Oceans) tend to experience the major episodes of bleaching during February–April, South-east Asian reefs in May, and Caribbean reefs during July–August (CHAMP Network 1997–99, Hendee 1998). Bleaching in the Northern Hemisphere tends to occur after the appearance of bleaching in the Southern Hemisphere, although this is not always the case.

Importance of light: the photoinhibition model of coral bleaching

Elevated sea temperatures explain most incidents of mass bleaching. It is pertinent to point out, however, that there is still variability associated with mass bleaching events that is not completely explained by sea temperature anomalies. At a local scale, there is often a gradation of bleaching intensity within colonies (Fig. 5), with the upper sides of colonies tending to bleach first and with the greatest intensity (Goenaga *et al.* 1988). Given that temperature is unlikely to differ between the top and sides of a coral colony (mostly because of the high thermal capacity of water), other explanations are needed.

The extent of bleaching can also differ between colonies that are located side by side. At a geographic scale, the intensity of bleaching does not always correlate perfectly with anomalies in SST. Aside from arguments based on instrument precision and accuracy (e.g. Atwood *et al.* 1992), several other factors have been evoked to clarify patterns not

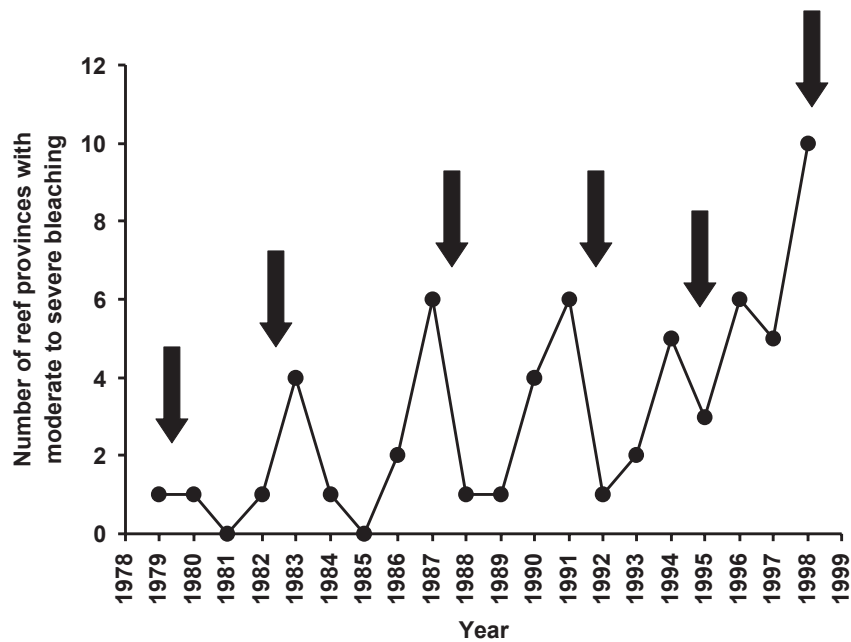


Fig. 3. Number of reef provinces bleaching since 1979. (Graph modified from Goreau and Hayes (1994) with data added for 1992 onwards.) Arrows indicate strong El Niño years.

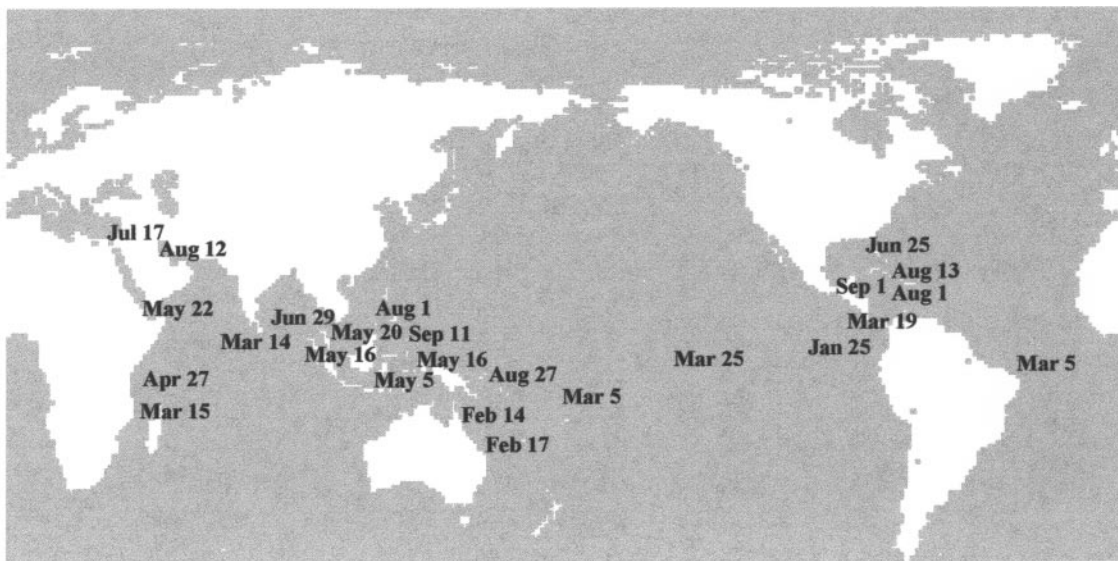


Fig. 4. Dates and locations of when severe bleaching began in 1988. Data obtained from Coral Health and Monitoring Network e-mail list (<http://coral.aoml.noaa.gov>).

completely explained by increased water temperature. These are principally the proximal factors light intensity and the genotype of the coral and zooxanthellae. Consideration of these factors provides important insight into the physiological basis of mass bleaching.

The intensity of various forms of solar radiation has long been suspected to play a role in bleaching events. Several

investigators have also proposed that elevated levels of UVR have been instrumental in causing bleaching in corals (Jokiel 1980; Fisk and Done 1985; Harriott 1985; Oliver 1985; Goenaga *et al.* 1988; Lesser *et al.* 1990; Gleason and Wellington 1993). Evidence, however, for a primary role of UVR has been circumstantial and has been restricted to the observations that (1) doldrum periods (when waters are clear and

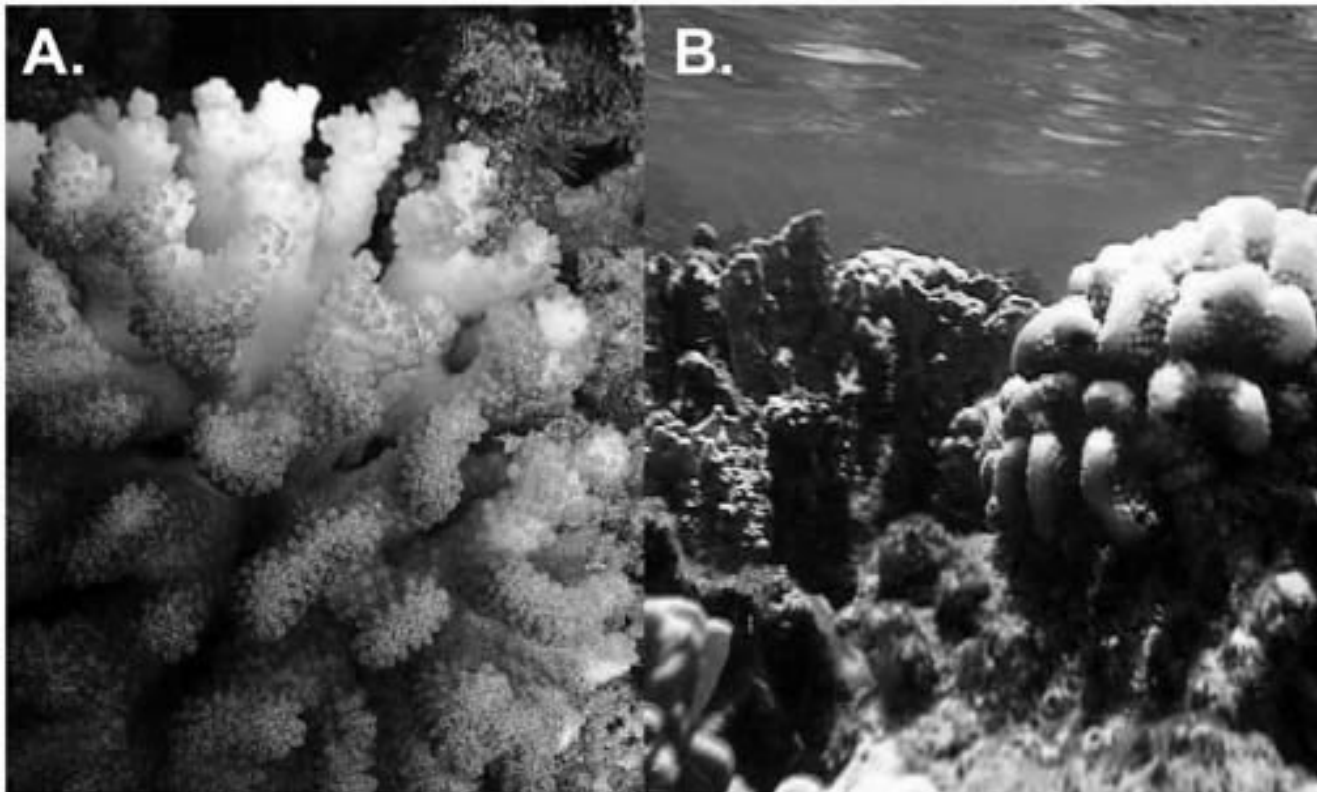


Fig. 5. (Left) Coral showing normally pigmented regions and bleached regions to the upper (more sunlit) side of colony. (Right) Coral in shallows showing similar pattern. (Photographer: O. Hoegh-Guldberg.)

calm and the penetration of UVR is high) have preceded some bleaching events (e.g. Great Barrier Reef 1982–83, Harriott 1985; French Polynesia 1994, Drollet *et al.* 1994), (2) corals tend to bleach on their upper, most-sunlit surfaces first, and (3) experimental manipulation of the UVR and PAR above reef-building corals and symbiotic anemones can also cause a bleaching response (Gleason and Wellington 1993).

The complete absence, however, of mass bleaching events occurring in the presence of high UVR intensity and normal temperatures argues against high UVR intensity being a primary factor in causing mass bleaching. The statement that bleaching events are solely caused by UVR has not been the claim of recent authors (e.g. Lesser 1996), who now consider that a combination of high temperature and UVR may be involved. Certainly, the observation that corals bleach on the upper surfaces first during exposure to elevated temperature argues that the quality and quantity of solar radiation are important secondary factors (Hoegh-Guldberg 1989). Work by Fitt (Fitt and Warner 1995) has reinforced the importance of light quality, finding that blue light enhances temperature-related bleaching.

Recent evidence suggests that the fact that the upper surfaces of corals bleach before their shaded bases is more related to presence of PAR as opposed to UVR (Jones *et al.*

1998; Hoegh-Guldberg and Jones 1999). The explanation for the role that PAR plays came from a series of studies aiming to decipher the specific site of action of heat stress on the metabolism of the symbiotic algae. Hoegh-Guldberg and Smith (1989) confirmed that the photosynthetic activity of heat-stressed corals is drastically reduced, an observation first made by Coles and Jokiel (1977) for corals affected by the heat effluent flowing from a power plant in Hawaii. Some of the reduced photosynthetic output seen by Coles and Jokiel (1977) was due to the reduced population density of zooxanthellae in the heat-stressed corals, but subsequent studies have found that heat stress also acts to reduce the photosynthetic rate of the zooxanthellae (Hoegh-Guldberg and Smith 1989a; Iglesias-Prieto *et al.* 1992; Fitt and Warner 1995; Iglesias-Prieto 1995; Warner *et al.* 1996).

The application of pulse amplitude modulated (PAM) fluorometry (Schreiber and Bilger 1987) to heat-stressed corals has initiated the identification of the component of the photosynthetic metabolism that fails when zooxanthellae are exposed to heat stress. Variable fluorescence (measured by the PAM fluorometer) is a relative measure of the rate at which one of two photosystems (PS II) can use light to process electrons flowing from the water-splitting reactions of photosynthesis. This affords a measure of the efficiency (activity) of the

light reactions of photosynthesis. Complete inhibition of photosynthetic oxygen evolution and a loss of variable fluorescence has been reported in cultured zooxanthellae exposed to temperatures of 34–36°C (Iglesias-Prieto *et al.* 1992), and in zooxanthellae within Caribbean corals exposed to 32° and 34°C (Fitt and Warner 1995; Warner *et al.* 1996). These studies demonstrated a decrease in the efficiency of PS II when corals and their zooxanthellae were exposed to heat and led to the suggestion that the primary effect of temperature was to cause a malfunction of the light reactions of photosynthesis.

However, when a PAM fluorometer was used to trace the effects of experimental manipulations of corals from One Tree Island on the southern Great Barrier Reef, Jones *et al.* (1998) showed that first site of damage due to thermal stress in zooxanthellae was the dark reactions of photosynthesis and not the light reactions as previously thought (Fig. 6). A second important observation by Jones *et al.* (1998) was that light amplified the extent of damage caused by thermal stress, almost perfectly replicating the many field reports of corals bleaching on their upper, most-sunlit surfaces (Goenaga *et al.* 1988).

The key observation of this work is that coral bleaching is related to the general phenomenon of photoinhibition (Walker 1992) and to the general response shown by terrestrial plants and other photosynthetic organisms to heat stress (Schreiber and Bilger 1987). Normally, increasing light intensity will lead to an increased photosynthetic rate up to a point at which the relationship between photosynthesis and light saturates. At relatively high light intensities, increasing light levels lead to the over-reduction of the light reactions and the production of potentially harmful products such as oxygen free radicals. Oxygen free radicals, if not detoxified by several enzyme systems found in higher plants (and zooxanthellae, Lesser 1996) will rapidly lead to cellular damage. In the case of higher plants, failure of the ability of the dark reactions to process photosynthetic energy results in an increased sensitivity of these organisms to photoinhibition. The overriding conclusion of the work of Jones *et al.* (1998) and Hoegh-Guldberg and Jones (1999) is that bleaching is due to a lowering of the sensitivity of zooxanthellae to photoinhibition. Basically, light, which is essential for the high productivity of coral reefs under normal conditions, becomes a liability under conditions of higher than normal temperatures.

The model presented in Fig. 6 has a number of properties that lead to predictions and explanations outlined in Table 1. Firstly, PAR assumes an important secondary role to that of UVR. Although temperature has to be higher than normal for a mass bleaching event to occur, light will cause damage to the photosystems even at normal intensities when water temperature is elevated above a critical maximum (Property 1, Table 1). This explains the frequent observation that the extent of damage is light dependent (Goenaga *et al.* 1988, Salih *et al.* 1997a) and that most coral bleaching starts on the upper, more-sunlit surfaces of corals. It also links thermal-stress-related

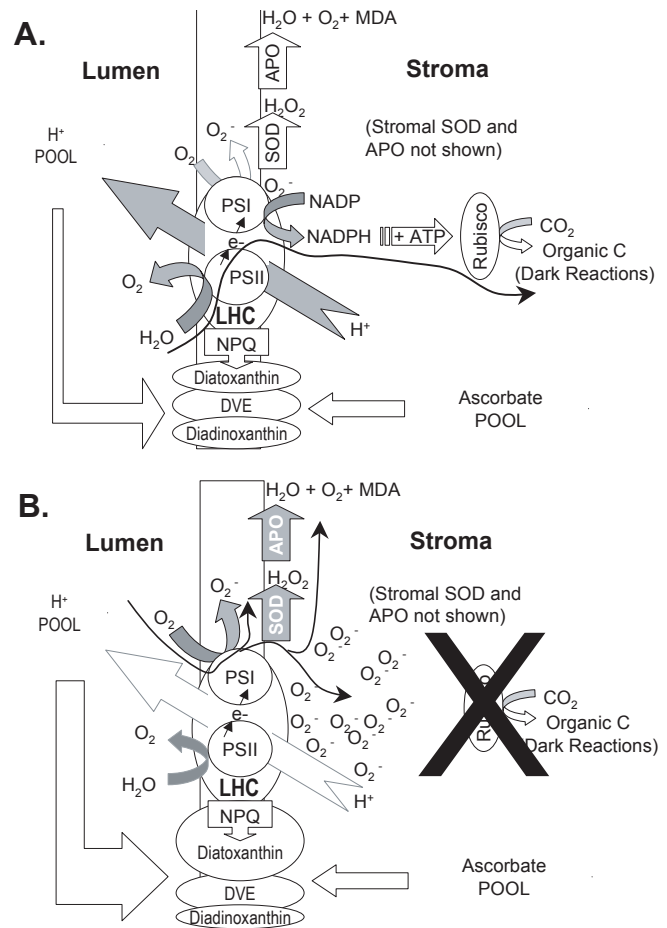


Fig. 6. Photoinhibition model of coral bleaching (Jones *et al.* 1998). Detail of events occurring on the thylakoid membrane of the chloroplast of zooxanthellae. (A) Under normal circumstances, the two photosystems (PSI and PSII) pass light energy to the dark reactions where CO₂ is fixed by the enzyme Rubisco. The amount of light energy flowing to the dark reactions is regulated by the interconversion of the two pigments diatoxanthin and diadinoxanthin. Any active oxygen (O₂⁻) is soaked up by the SOD and APO enzyme systems. (B) Heat stress interrupts the flow of energy to the dark reactions. The light reactions are then destroyed by the buildup of light energy which is passed to oxygen rather than the dark reactions, creating active oxygen that then begins to denature the proteins that make up the photosynthetic components of the zooxanthellae. Not shown are the singlet oxygen species that are generated in PSII, by triplet chlorophyll in the reaction centre, and which are more abundant when PSII is over-reduced in high light under heat stress. SOD, superoxide dismutase; APO, ascorbate peroxidase; VDE, violaxanthin de-epoxidase.

bleaching directly to the solar bleaching studied by Brown and co-workers (Brown *et al.* 1994a; Brown 1997a).

Brown (1997a) has already made the important link between photo-protective measures adopted by zooxanthellae and coral bleaching, and suggests that photo-protective measures are likely to play an important part in the way that corals and their zooxanthellae may be able to limit the effect of bleaching stresses arising from a combination of increased temperature and irradiance in the field. This linkage also

explains several unusual bleaching patterns, such as when the bases but not the tips bleached in relatively shallow populations of *Montastrea* spp. in Panama in 1995. In this case, more light-tolerant zooxanthellae (found in the tips) were actually more resistant to thermal stress than shade-adapted genotypes living in other places within the same colonies (Rowan *et al.* 1997). Property 2 (Table 1) emphasizes the fact that zooxanthellae that are able to evoke protective measures by acclimation (phenotype) or through adaptation (genotype) should be more tolerant of anomalous high sea temperature. Property 3 predicts that any stress (chemical or physical) that blocks the energy flow to the dark reactions will lead to photoinhibitory stresses at lower light intensities. Symptoms similar to bleaching will follow. So far, the response of corals and their zooxanthellae to cyanide appears to conform to the same model, as discussed by Jones and Hoegh-Guldberg (1999). One might expect other factors that block the dark reactions or lead to the over-energization of the light reactions of photosynthesis to exhibit similar symptoms (e.g. herbicides, UVR, high PAR stress).

Climate change and coral bleaching

Why is the incidence of bleaching increasing?

One of the most important questions facing scientists, policy makers and the general public is the question of why there has been an apparent increase in the incidence of coral

bleaching and mortality since 1979. Since 1979, scores of reports of mass bleaching events have been made in the primary literature. Prior to 1979, reports of bleaching events in the primary literature are virtually non-existent and are restricted to largely unpublished observations or recollections (e.g. Puerto Rican bleaching in 1969, Winter *et al.* 1998). Some commentators have suggested that the answer lies in the increase in the number of reef observers and the ease with which these reports can be brought to the attention of the scientific community (e.g. Internet). Although this argument is probably true to some extent, it does not explain the absence of scientific reports of mass coral bleaching around intensively studied sites such as those around research stations (e.g. Heron Island, Australia; Florida Keys, USA) and tourist resorts prior to 1979. Underwater film makers who filmed extensively on the Great Barrier Reef during the 1960s and 1970s never saw coral bleaching on the scale seen since 1979 (e.g. Valerie Taylor, personal communication). It seems certain that brilliant white coral as far as the eye could see, plus the associated mortality and stench from bleached reefs that had died would have been noticed. Similarly, indigenous fishers, who have an extensive knowledge of coral reefs, seem to have been unaware of coral bleaching in the past and do not appear to have a traditional terminology to describe it (e.g. French Polynesia, Hoegh-Guldberg unpublished; Okinawa, Y. Laya, pers. comm.).

Table 1. Predictions or explanations stemming from the Photoinhibition model of coral bleaching proposed by Jones *et al.* (1998)

Prediction or Explanation	Support or Further prediction
(1) Light (PAR) is required for elevated temperature to trigger bleaching. The extent of damage during bleaching will be directly correlated with the intensity of light. Elevated temperature will have a reduced effect if corals are shielded from normal sunlight. May indicate possible ways to effect small-scale amelioration during bleaching conditions (e.g. small-scale shading of sections of reef with high tourist or other value).	(a) Upper surfaces of corals bleach preferentially in most cases (Goenaga <i>et al.</i> 1988; Jones <i>et al.</i> 1998). But see complication outlined in Prediction 2. (b) Species with deeper tissues (hence more shade) are more resistant to bleaching. Hence, the deeper tissues of <i>Porites</i> spp. are less susceptible to bleaching than the veneer tissue configuration of <i>Acropora</i> spp. or <i>Pocillopora</i> spp. (Salvat 1991; Gleason 1993; Glynn 1993; Hoegh-Guldberg and Salvat 1995). This explains some of the variability among sites and depths in coral communities (e.g. Hoegh-Guldberg and Salvat 1995) (c) Tissue retraction may be an important mechanism that some species use to reduce damage during thermal bleaching stress as suggested for solar bleaching by Brown <i>et al.</i> (1994b). (d) Coral species have mechanisms (pigmentation) by which they shade their zooxanthellae during bleaching stress (Salih <i>et al.</i> 1997a; Hoegh-Guldberg and Jones 1999). Enhanced fluorescence of stressed corals may represent attempts to bolster this strategy.
(2) Coral and zooxanthella species that are better able to photo-acclimatize may be better able to resist bleaching stress. Differences in the ability to resist bleaching stress will be related to the ability to produce and regulate accessory pigments such as the xanthophylls (Brown 1997a; Hoegh-Guldberg and Jones 1999; Brown <i>et al.</i> 1999).	(a) Light-adapted zooxanthellae (putatively Clade A) are better able to resist thermal stress in <i>Montastrea</i> spp. than shade-adapted genotypes (Clade C, Rowan <i>et al.</i> 1997). (b) Patterns associated with bleaching will be complicated by genotype, acclimatory state and environment interactions. This may explain some depth gradients that show greater frequencies of bleaching in deeper water but communities with similar species compositions.
(3) Any stress that blocks the dark reactions before the light reactions of photosynthesis will result in similar bleaching phenomena.	(a) Cyanide stress results in a series of responses that are identical to those seen during temperature-related bleaching (Jones and Hoegh-Guldberg 1999). (b) UVR enhances bleaching. Lesser <i>et al.</i> (1990) speculated that a similar blocking of the principal carboxylation enzyme in zooxanthellae could lead to a buildup of redox energy within the light reactions of zooxanthellae. This is essentially consistent with Jones <i>et al.</i> (1998).

Although rigorous analysis is needed, it appears that the case for regular yet unnoticed massive bleaching events prior to 1979 is extremely scant at best.

So why have bleaching events increased in frequency since 1979? Given the strong correlation between bleaching events and high sea surface temperatures (Goreau and Hayes 1994), recent and historic SSTs should provide insight into the triggers of the recent series of strong mass bleaching episodes. The following analysis reveals the answers to both these questions.

Tropical seas have undergone warming in the past 100 years (Bottomley *et al.* 1990; Brown 1997a; Cane *et al.* 1997; Winter *et al.* 1998; see also historic temperature data for seven tropical sites, Table 2). Coral cores from the central Pacific confirm this warming trend (Wellington, Linsley and Hoegh-Guldberg, unpublished). Increases of 1–2°C in sea temperature are expected by 2100 in response to enhanced concentrations of atmospheric greenhouse gases (Bijlsma *et al.* 1995). Goreau (1990), Glynn (1991) and many others (e.g. Hoegh-Guldberg and Salvat 1995; Brown 1997a) have pointed to the significance of this trend for reef-building corals and have stated

variously that global climate change is likely to increase the frequency and intensity of bleaching.

Trends in SST can also be used to shed light on the apparent advent of mass coral bleaching since 1979 and on how the frequency of mass coral bleaching will change in the next few decades. Sea temperatures over the past 20 years, extensively measured and cross-compared by instruments on satellites, ships and buoys, have shown upward trends in all regions, and blended data from the three sources have shown that rates of change are now greater than 2°C per century in many tropical seas (Table 3; IGOSS-nmc blended data, Integrated Global Ocean Services System, <http://ioc.unesco.org/igossweb/igoshome.htm>). Simple correlations ($P \leq 0.05$ in all cases, most with $P < 0.001$) through IGOSS-nmc blended data reveal rates of change in SST that range from 0.46°C per century (northern Great Barrier Reef) to 2.59°C per century (central Great Barrier Reef, waters off Townsville, Qld).

These trends may reflect longer-term cycles of change. However, they have been confirmed by a growing number studies of SST trends that go back at least 40–150 years using

Table 2. Rates of warming detected by regression analysis within Trimmed Monthly Summaries from the Comprehensive Ocean-Atmosphere Data Set (COADS, up to Dec 1992) and IGOSS-nmc blended data (January 1993–April 1999)

Data obtained from the Lamont Doherty Earth Observatory server (<http://rainbow.ligo.columbia.edu/>). Data were included only if all months were recorded (hence shorter periods for some parts of the world). All trends were highly significant with the possible exception of Rarotonga. GBR, Great Barrier Reef

Locality	Position	Period of data examined	Rate (°C per 100 years)	Significance of trend
Jamaica	17.5°N, 76.5°W	1903–99	1.25	< 0.001
Phuket	7.5°N, 98.5°E	1904–99	1.54	< 0.001
Tahiti	17.5°S, 149.5°W	1926–99	0.69	0.003
Rarotonga	21.5°S, 159.5°W	1926–99	0.84	0.05
Southern GBR	23.5°S, 149.5°E	1902–99	1.68	< 0.001
Central GBR	18°S, 147.5°E	1902–99	1.55	< 0.001
Northern GBR	11°S, 143°E	1903–99	1.25	< 0.001

Table 3. Rates of warming in tropical oceans for period 1981–99

Rates determined from regressions done on Integrated Global Ocean Services System (IGOSS) nmc blended weekly sea surface temperature data obtained from data sets available at the Lamont Doherty Earth Observatory server (<http://rainbow.ligo.columbia.edu/>). Seasonal variability within the data was removed by applying a 12-month moving-point average before the regression analysis. GBR, Great Barrier Reef

Locality	Position	Rate (°C per 100 years)	Significant of trend	Other data
Jamaica	17.5°N, 76.5°W	2.29	< 0.001	2.53, Winter <i>et al.</i> (1998)
Phuket	7.5°N, 98.5°E	2.30	< 0.001	1.26, Brown (1997a)
Tahiti	17.5°S, 149.5°W	1.44	< 0.001	
Rarotonga	21.5°S, 159.5°W	2.27	< 0.001	
Southern GBR	23.5°S, 149.5°E	2.54	< 0.001	
Central GBR	18°S, 147.5°E	2.59	< 0.001	
Northern GBR	11°S, 143°E	0.47	< 0.001	

other data sets and such sources as coral cores (e.g. Brown 1997a; Winter *et al.* 1998). For example, measurements made by researchers at the research station at La Parguera in Puerto Rico registered a rate of change of 2.53°C per century (Winter *et al.* 1998) while the IGOSS-nmc data for the same area records a rate of increase of SST of 2.29°C per century (Table 3). Similar comparisons can be made between rates of change reported by Brown (1997a) using different data (MOHSST 6) going back to 1946 (Brown 1997a: 1.26°C per century v. 2.30°C per century reported here). There is no evidence of a slowing or reversing of this rate of change.

Whereas small errors have been noted for pure satellite SST data (Hurrell and Trenberth 1997), blended data have the advantage that bias is reduced or eliminated as data are generally confirmed (usually) by several sources. Correlations between *in situ* instrument readings at study sites on coral reefs and blended SST data are high, as shown by numerous authors including Wellington and Dunbar (1995) and Lough (1999). For example, Lough has shown that regressions between IGOSS-nmc blended data and *in situ* data have regression coefficients that range between 0.93 and 0.98 for five sites on the Great Barrier Reef.

Will the frequency and intensity of coral bleaching continue to increase?

An important question follows from the fact that sea surface temperatures in the tropics are increasing: How will increases in SST affect the frequency and severity of bleaching events in the future? We can deduce the thermal thresholds of corals and their zooxanthellae from the past behaviour of corals during bleaching events over the past 20 years. This is the basis for the highly successful predictions of the 'Hotspot' program (Strong *et al.* 1998). If this is combined with projections of future SSTs then the number of times that thermal thresholds are exceeded can be predicted. If corals are not adapting or acclimating fast enough, then each of these points will translate as a bleaching event. The issue of adaptation or acclimation is discussed below. Corals have acclimatory abilities in many circumstances (Gates and Edmunds 1999), but evidence from the past 20 years suggests that corals and their zooxanthellae are not able to acclimatize or adapt fast enough to the short, sporadic thermal events typical of recent 'bleaching' episodes.

Projecting future changes to sea temperatures can not be based solely on what has happened in the past. Seasonality and differences between years due to variation in the strength of the El Niño–Southern Oscillation complicates attempts to predict future tropical sea temperatures. Additionally, use of data from the past 20 years to predict the future has the problem that stochastic and improbable events (e.g. the cooling effects of two major volcanic eruptions over the past 20 years) would be extrapolated at a high frequency to future temperature trends. Global Circulation Models (GCMs), that show an increasing level of accuracy and coherence, however,

provide an opportunity to examine how sea temperatures are likely to change in the future.

SST data for this study were simulated using the following Global Circulation Models (GCM):

(A) *ECHAM4/OPYC3 IS92a*. The global coupled atmosphere–ocean–ice model (Roeckner *et al.* 1996) was developed by the Max-Planck-Institut für Meteorologie and is used by the United Nations for climatology simulations. Data from this model run and those described below in *B* and *C* were kindly provided by Dr Axel Timmermann of KNMI, Netherlands. Horizontal resolution is roughly equivalent to 2.8° × 2.8° latitude–longitude. This model has been used in studies of climate variability (Roeckner *et al.* 1996; Bacher *et al.* 1997; Christoph *et al.* 1999), climate prediction (Oberhuber *et al.* 1998) and climate change with a high degree of accuracy (Timmermann *et al.* 1999; Roeckner *et al.* in press). In order to reduce the drift of the unforced-coupled model, a yearly flux correction for heat and freshwater flux was employed. Simulation of the El Niño–Southern Oscillation is essential for approximating tropical climate variability and is handled well by the ECHAM4/OPYC3 model (Roeckner *et al.* 1996; Oberhuber *et al.* 1998; Timmermann 1999). Changes in greenhouse gases that were used in the model were derived as follows: Observed concentrations of greenhouse gases were used up to 1990, and changes outlined in the IPCC scenario IS92a (IPCC 1992) were implemented thereafter. The mid-range emission scenario (IS92a) is one of six specified by the Intergovernmental Panel on Climate Change (IPCC) in 1992. It is the central estimate of climate forcing by greenhouse gases and assumes a doubling of 1975 CO₂ levels by the year 2100, with sulfate aerosol emissions, which have a cooling effect, remaining at 1990 levels. Greenhouse gases are prescribed as a function of time: CO₂, CH₄, N₂O and also a series of industrial gases including CFCs and HCFCs.

(B) *ECHAM4/OPYC3 IS92a (with aerosol integration)*, the global coupled atmosphere–ocean–ice model (Roeckner *et al.* 1996) but with the influence of aerosols added. Horizontal resolution is also roughly equivalent to 2.8° × 2.8° latitude–longitude. Changes in greenhouse gases and aerosols were prescribed as follows. Observed concentrations of greenhouse gases and sulfate aerosols were used up to 1990, and changes outlined in the IPCC scenario IS92a (IPCC 1992) were implemented thereafter. Greenhouse gases are prescribed as a function of time: CO₂, CH₄, N₂O and also a series of industrial gases including CFCs and HCFCs. The tropospheric sulfur cycle was also incorporated but with only the influence of anthropogenic sources considered. Natural biogenic and volcanic sulfur emissions are neglected, and the aerosol radiative forcing is generated through the anthropogenic part of the sulfur cycle only.

(C) *ECHAM3/LSG IS92a*. This earlier model differs substantially from its descendant ECHAM4/OPYC3. The LSG ocean model and the ECHAM3 atmosphere model are coupled via the heat, freshwater and momentum fluxes.

Ocean SSTs plus a few correction terms are taken as boundary conditions for the atmosphere. In order to avoid climate drift in the coupled mode, the flux-correction technique (Sausen *et al.* 1988) is applied, which is equivalent to coupling both subsystems by their individual flux-anomalies relative to their equilibrium states. Horizontal resolution is approximately equivalent to $5.6^\circ \times 5.6^\circ$ latitude–longitude. ECHAM3/LSG is built on a different ocean model to ECHAM4, and only crudely captures thermocline processes. El Niño-related variability is underestimated by a factor of three. Further details of the model and the coupling strategy can be found in Voss *et al.* (1998) and Maier-Reimer *et al.* (1993). Changes in greenhouse gases were derived as in *A* (above).

(*D*) *CSIRO DAR Model.* This coupled model with dynamic sea ice is run by the Division of Atmospheric Research at Australia's Commonwealth Scientific and Industrial Research Organisation (CSIRO). It is a comprehensive coupled model that contains atmospheric, oceanic, sea-ice and biospheric submodels. The resolution is to 5.6° longitude by 3.2° latitude. The model is described in full by Gordon and O'Farrell (1997). Greenhouse gas concentrations were derived for use as follows. Historic concentrations (CO_2 equivalents) from the IPCC combined historic data were used up to 1990. After that, emissions specified by the IS92a scenario were used (IPCC 1992).

Temperatures were generated for each month from 1860 to 2100 (2060 in the case of model *B*). Data generated by all four models for past sea temperatures show a close correspondence to actual sea temperature records. The later-generation model runs (ECHAM4, *A* and *B*) performed the best with respect to this criterion. Model *C* simulates El Niño with a high degree of realism (Timmermann *et al.* 1999) and shows similar mean and maximal values as well as range of sea temperatures (Table 4). Mean sea temperatures predicted for the period November 1981 to December 1994 were approximately 0.05° and 1.22°C greater than the temperatures in the IGOSS-nmc data set. As outlined above, summer maximum

temperatures are the key factors that predict when corals will bleach. Maximum temperatures predicted by model *A* were only -0.15° to 0.46°C different from the summer maxima reported in the IGOSS-nmc data set (Table 4). A similar situation held for SST data in the other three models (Table 5*A*, 5*B*). In this case, the predicted mean summer temperatures (calculated from the average of the sea temperatures over three months) were generally within 0.5°C of the observed mean summer temperatures for data from 1903 to 1999. Only model *D* delivered a few of the larger differences on a consistent basis.

The thermal thresholds of corals were derived by using the IGOSS-nmc data set and both literature and Internet reports of bleaching events (Glynn 1993; Goreau and Hayes 1994; Hoegh-Guldberg and Salvat 1995; Brown 1997*a*; Hoegh-Guldberg *et al.* 1997; Hendee 1998; Jones *et al.* 1998; CHAMP Network 1999). For example (Fig. 7), bleaching events were reported in French Polynesia ($17.5^\circ\text{S}, 149.5^\circ\text{W}$) in 1983, 1986, 1991, 1994, 1996 and 1998 and correspond to periods when SSTs rose above 29.2°C . This temperature was consequently selected as the presumed thermal trigger for corals at this locality (Hoegh-Guldberg and Salvat 1995, see also Brown 1997*a*, Hoegh-Guldberg *et al.* 1997). This was repeated for the south coast of Jamaica ($17.5^\circ\text{N}, 76.5^\circ\text{W}$), Phuket ($7.5^\circ\text{N}, 98.5^\circ\text{E}$), Rarotonga ($21.5^\circ\text{S}, 159.5^\circ\text{W}$), and three sites on the Great Barrier Reef—in the southern ($23.5^\circ\text{S}, 149.5^\circ\text{E}$), central ($18^\circ\text{S}, 147.5^\circ\text{E}$) and northern ($11^\circ\text{S}, 143^\circ\text{E}$) sections. Thermal thresholds (Figs 8 and 10; Rarotonga not shown) ranged from 28.3°C at Rarotonga to 30.2°C at Phuket (previously reported by Brown 1997*a*). Table 6 lists the thermal thresholds derived and used in this study.

The sea temperature data generated by the GCM model runs were used with the threshold values to predict the frequency and intensity of coral bleaching. Differences between predicted and observed sea temperature data (although minor) were subtracted from model data prior to analysis (using data from 1903–94, Table 5*b*). An example of the

Table 4. Comparison between Integrated Global Ocean Services System (IGOSS) nmc blended monthly sea surface temperature data and output from the global coupled atmosphere–ocean–ice model (ECHAM4/OPYC3, Roeckner *et al.* 1996)

IGOSS-nmc data available from Lamont Doherty Earth Observatory (<http://rainbow.ldeo.columbia.edu/>) and model data kindly provided by Dr Axel Timmermann of KNMI, Netherlands. All data are in $^\circ\text{C}$. GBR, Great Barrier Reef

Locality	Mean (IGOSS-nmc)	Mean ECHAM4/OOPYC3a	Difference	Max (IGOSS-nmc)	Max ECHAM4/OPYC3a	Difference	Range (IGOSS-nmc)	Range ECHAM4/OPYC3a
Jamaica (S coast)	27.95	28.36	0.41	29.40	29.25	-0.15	3.24	1.95
Phuket	29.08	29.13	0.05	30.48	30.87	0.39	2.70	3.00
Tahiti	27.51	27.85	0.34	29.57	29.96	0.39	3.92	3.46
Rarotonga	25.43	26.35	0.92	28.49	28.88	0.39	5.59	4.42
GBR (S)	25.04	26.25	1.21	28.51	28.87	0.36	8.27	5.08
GBR (C)	26.21	27.43	1.22	29.61	30.07	0.46	7.28	4.76
GBR (N)	27.39	28.38	0.99	29.89	30.38	0.48	5.45	3.62

Table 5. Differences between summer sea surface temperatures (Integrated Global Ocean Services System (IGOSS) nmc blended monthly sea surface temperature data) and summer sea surface temperatures calculated from the global coupled atmosphere–ocean–ice model (ECHAM4/OPYC3, Roeckner *et al.* 1996) with and without the influence of aerosols

IGOSS-nmc data obtained from Lamont Doherty Earth Observatory (<http://rainbow.ldeo.columbia.edu/>) and model data kindly provided by Dr Axel Timmermann of KNMI, Netherlands and the Commonwealth Scientific and Industry Research Organisation (CSIRO Australia). Summer temperatures were calculated using the mean SST for the three-month period (January–March, Southern Hemisphere; June–August, Northern Hemisphere) for the periods from (a) 1981–99 and (b) 1903–94. All data are in °C. GBR, Great Barrier Reef

Locality	ECHAM4/OPYC3a	ECHAM4/OPYC3a (with aerosol effect)	ECHAM3/LCG	CSIRO-DAR
<i>(a) 1981–99</i>				
Jamaica (S coast)	0.44	0.73	-0.59	0.60
Phuket	0.44	0.32	-0.28	-0.23
Tahiti	0.39	-0.10	-1.16	0.76
Rarotonga	-0.05	0.16	-1.25	0.50
GBR (S)	-0.05	0.01	-0.98	2.14
GBR (C)	-0.36	-0.34	-1.06	1.13
GBR (N)	-0.15	0.37	-0.99	0.47
<i>(b) 1903–94</i>				
Jamaica (S coast)	-0.03	-0.32	0.26	-0.54
Phuket	-0.04	0.23	-0.13	0.08
Tahiti	0.03	0.31	1.30	-0.10
Rarotonga	-0.58	-0.69	0.30	-0.98
GBR (S)	0.10	0.26	0.72	-1.20
GBR (C)	0.15	0.28	0.66	-1.19
GBR (N)	-0.15	-0.62	0.42	-0.82

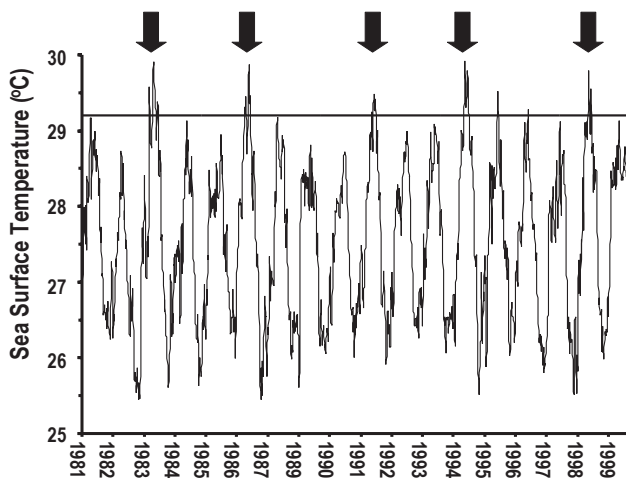


Fig. 7. Weekly sea surface temperature data for Tahiti (17.5°S,149.5°W). Arrows indicate bleaching events reported in the literature. Horizontal line indicates the minimum temperature above which bleaching events occur (threshold temperature). IGOSS-nmc blended data courtesy of the Lamont-Doherty Climate Center at Columbia University.

analysis comparing predicted sea temperature data from model *A* and the known thermal thresholds of corals for seven sites in tropical oceans is shown in Figs 8, 9, 10 and 11. Model *A*, like the other three, shows the universal trend within tropical seas of increasing sea temperature under the

Table 6. Estimated temperatures at which corals bleach (thermal thresholds) for seven sites)

GBR, Great Barrier Reef. Thermal thresholds were derived by comparing reports of when bleaching events have occurred since 1979 with weekly sea temperature records obtained from IGOSS-nmc blended data from the Lamont-Doherty Climate Center at Columbia University

Locality	Position (°C)	Thermal threshold (°C)
Jamaica	17.5°N,76.5°W	29.2
Phuket	7.5°N,98.5°E	30.2
Tahiti	17.5°S,149.5°W	29.2
Rarotonga	21.5°S,159.5°W	28.3
Southern GBR	23.5°S,149.5°E	28.3
Central GBR	18°S,147.5°E	29.2
Northern GBR	11°S,143°E	30.0

moderate global climate change scenario, IS92a. Model *A* also includes the most accurate simulation of El Niño activity (Timmermann *et al.* 1999; Roeckner *et al.* in press) and confirms that future ENSO events are likely to reach higher and higher sea temperature thresholds. By comparing simulated sea temperatures to the thermal thresholds listed in Table 6, we can estimate the frequency with which sea temperatures will exceed the thermal threshold of corals and their zooxanthellae. If corals are incapable of changing their physiology to cope with this stress, bleaching will occur. As men-

tioned previously, the key assumption here is that reef-building corals and their zooxanthellae are unable to adapt (genetically) fast enough or acclimate (phenotypically) to sporadic thermal stress.

The change in the frequency of bleaching events per decade predicted by the four models is shown in Figs 9 and 11. The trends in these graphs reveal four important points that are confirmed by all four model runs. Firstly, the frequency of bleaching is set to rise rapidly, with the rate being highest in the Caribbean and slowest in the Central Pacific. Secondly, the intensity of bleaching will increase at a rate proportional to the probability that the thermal maxima of the corals will be exceeded by future SSTs. Thirdly, most regions will be experiencing bleaching conditions every year within 30–50 years. Lastly, the reason for the relatively low frequency of bleaching events before 1979 becomes clear; tropical sea temperatures have been rising over the past 100 years (Bijlsma *et al.* 1995) and have brought corals ever closer to their upper thermal limit. The ability for an El Niño event to trigger bleaching was only reached in most oceans in the period from 1970 to 1980 (the abscissa intercept values of the rapid rise in the frequency of bleaching events in Figs 9 and 11 occurs around 1970–1980). This explains why mass bleaching events are not seen to any great extent before 1979 (Table 7). This conclusion is also supported by the actual sea temperatures records from the Comprehensive Ocean-Atmosphere Data set (COADS, up to December 1992) and IGOSS-nmc blended data set (January 1993–April 1999).

The use of a number of powerful climate models has important ramifications for the conclusion of this report. Firstly, the conclusions are not dependent on which climate model is used. A second important point can be made. The

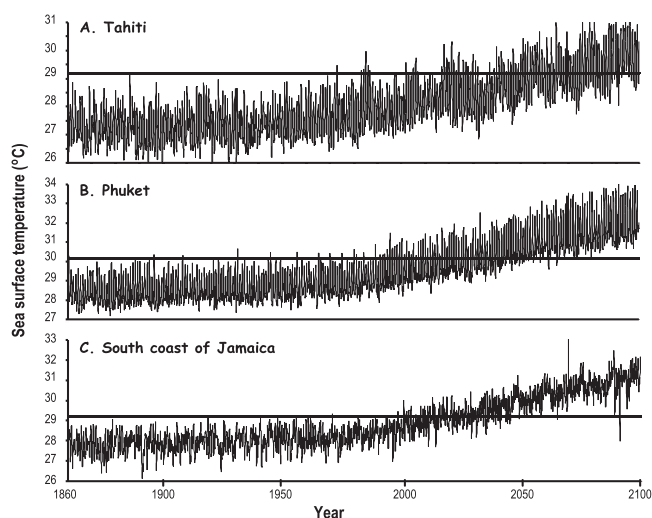


Fig. 8. Sea surface temperature data generated by the global coupled atmosphere–ocean–ice model (ECHAM4/OPYC3, Roeckner *et al.* 1996) and provided by Dr Axel Timmermann of KNMI, Netherlands. Temperatures were generated for each month from 1860 to 2100, and were forced by greenhouse gas concentrations that conform to the IPCC scenario IS92a (IPCC 1992). Effects of El Niño–Southern Oscillation (ENSO) events are included. Horizontal lines indicate the thermal thresholds of corals at each site. Data were generated for four regions: Tahiti (17.5°S, 149.5°W), Phuket (7.5°N, 98.5°E), Jamaica (17.5°N, 76.5°W), and Rarotonga (data not shown).

fact that all seven sites within the three models (4 runs) all show the same increasing trends, suggest that the trends illustrated by this analysis are a consistent feature of projected climate change over the next century. Thirdly, factors such as cooling by anthropogenic aerosols produce only

Table 7. Major issues resolved by the examination of the patterns of increasing sea temperature

(1) Why are corals growing so close to their thermal limit?	Before recent increases in sea temperature, corals and their zooxanthellae lived in water that typically never rose above their maximum thermal limits. Because of the increases in SST over the past hundred years (~1°C), corals are now just below their upper thermal limits. Before this warming, corals would always have been a degree or two below these critical level in summer. The fact that corals are so close to their thermal limits is also evidence that they have not been able to acclimatize or adapt to these increase to any real extent.
(2) Why are there few reports of coral bleaching before 1979?	Increases in sea temperatures have only become critical since the late 1970s, when El Niño events disturbances began to exceed the thermal tolerances of corals and their zooxanthellae. Before this, El Niño disturbances did not exceed the thermal limits of corals and zooxanthellae on a regular basis.
(3) Will coral bleaching increase in the future?	Bleaching events are likely to increase in frequency until they become annual by 2050 in most oceans. In some areas (e.g. south-east Asia, Caribbean, GBR) this will occur more rapidly (by 2020). In 30–50 years from now, bleaching will be triggered by seasonal changes in water temperature and will no longer depend on El Niño events to push corals over the limit. This will become critical as bleaching events exceed the frequency at which corals can recover from bleaching-related mortality. Most evidence suggests that coral reefs will not be able to sustain this stress and a phase shift to algae-dominated communities is a likely outcome.

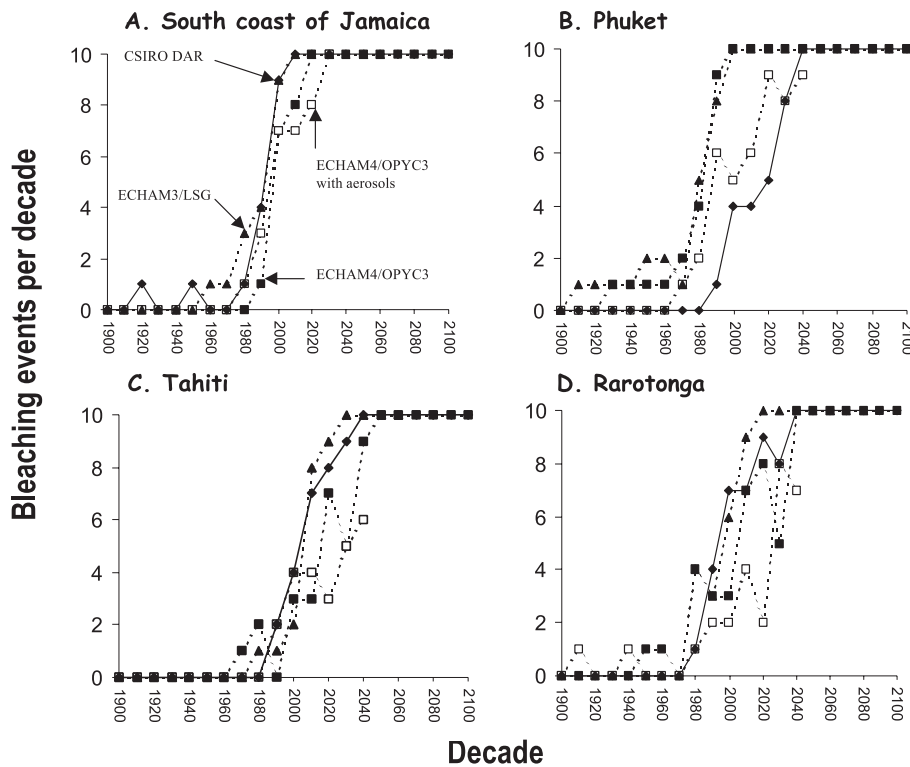


Fig. 9. Number of times per decade that predicted temperatures (see Fig. 8) exceed coral threshold levels (bleaching events) for (A) Jamaica (17.5°N, 76.5°W), (B) Phuket (7.5°N, 98.5°E), (C) Tahiti (17.5°S, 149.5°W) and (D) Rarotonga (21.5°S, 159.5°W). Key to models: ■ ECHAM4/OPYC3; □ ECHAM4/OPYC3 with aerosol effect added; ▲ ECHAM3/LSG; and ◆ CSIRO DAR GCM.

minor delays (mostly ~20–40 years) in the rate of warming of tropical seas. If the critical point for coral reefs occurs when bleaching occurs every two years with the intensity of the 1998 event, then these delays will be less (10–20 years; compare with and without aerosols in Figs 9 and 11).

The conclusions of this analysis are a matter of great concern. If sea temperatures continue to increase with time and corals continue to show an inability to acclimatize or adapt fast enough to these changes, coral bleaching events will increase in frequency and intensity (proportional to the size of the thermal anomaly) with serious consequences. It is hard to believe that coral reefs will be able to survive *yearly* bleaching events (let alone events every two years) of the same scale and intensity of the bleaching episode in 1998. By approximately 2050, however, sea temperatures in tropical oceans will experience anomalies every year that will be several times those seen in 1998.

Biotic responses to changes in sea temperature: acclimation v. adaptation

A crucial part of what will happen to reef-building corals depends on how they and their zooxanthellae will respond to the increases in sea temperature outlined here and by leading climate physicists (e.g. 1–2°C by 2100, IPCC 1992, Bijlsma

et al. 1995). There are two broad ways that marine biota can respond to temperature change (Clarke 1983). Firstly, marine organisms can ‘acclimatize’ by modifying the various component processes that make up their cellular metabolism to perform better at the new temperatures; for example, corals might be able to change their physiology such that they are more tolerant of higher temperatures. Secondly, marine biota may ‘adapt’ via the selection of individuals within populations that are better able to cope with the new temperatures; these individuals survive while others that are less temperature tolerant either do not survive or do not breed. In the case of corals and zooxanthellae, populations would evolve new ‘adaptations’ to cope with the higher temperature regimes over time.

The question of whether corals and their zooxanthellae will acclimatize and/or adapt to temperature change is dependent on the time-scale of the predicted changes. The time required for plants and animals to acclimatize to temperature change is likely to be on the order of hours or days, irrespective of such aspects as their generation times. In contrast, the adaptation of plants and animals to temperature change may require hundreds or even thousands of years, and depends on the generation time of the organism. Organisms that reproduce relatively early in their lives (e.g.

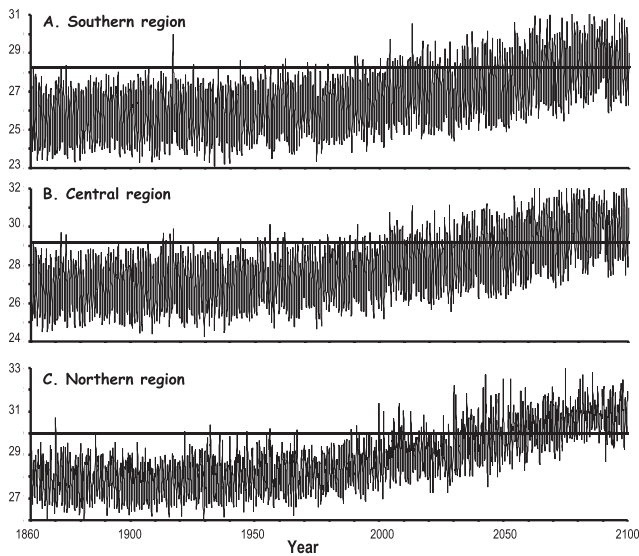


Fig. 10. Sea surface temperature data generated by the global coupled atmosphere–ocean–ice model (ECHAM4/OPYC3, Roeckner *et al.* 1996) and kindly provided by Dr Axel Timmermann of KNMI, Netherlands: (A) southern, 23.5°S, 149.5°E, (B) central (18°S, 147.5°E) and (C) northern (11°S, 143°E) Great Barrier Reef. Temperatures were generated for each month from 1860 to 2100, and were forced by greenhouse warming which conformed to the IPCC scenario IS92a (IPCC 1992). Effect of El Niño–Southern Oscillation (ENSO) events included. Horizontal lines: thermal thresholds of corals at each site.

bacteria, phytoplankton, ephemeral algae) can adapt or evolve in a matter of days to years. Organisms with longer generation times (e.g. fish, corals) are only likely to respond evolutionarily over decades to centuries. This observation is supported by the fossil record of past major extinction events (e.g. at the end of Cretaceous); organisms that appear to have resisted extinction include those with short generation times (e.g. cyanobacteria, calcareous algae, foraminiferans),

whereas organisms with longer generation times such as fish and reef-building corals were severely affected by global crises (Plaziat and Perrin 1992; Copper 1994).

Adaptation

The fact that corals and their zooxanthellae have different thermal optima and maxima suggests that corals have adapted genetically to different thermal regimes (e.g. Table 6). Coles *et al.* (1976) formally presented evidence for the existence of geographical variation in the temperature tolerance of corals and zooxanthellae; corals from Enewetak (average water temperature 28.5°C) could survive a 10 h exposure to 35.6°C whereas most corals from Hawaii (average water temperature 24.5°C) died when water temperatures were raised to 32.4°C. Corals from Malaysia and from Orpheus Island and One Tree Island in Australia show significant shifts in the temperature at which they bleach; corals from cooler regions bleach at lower temperatures (Yang Amri and Hoegh-Guldberg, unpublished).

The observation that corals have adapted to local temperature regimes is not surprising and is a universal feature of all organisms, especially those such as corals that are ectothermic (with no internal temperature control). The observation of heat-sensitive clones (Edmunds 1994; Brown 1997b) among populations of corals suggests that differences in the genetic tolerance of host and zooxanthellae will provide the ground substance of change as habitats move to higher and higher thermal regimes. Recent work by Salih *et al.* (1997b) suggests that intertidal corals with fluorescent pigmentation may be more tolerant to heat stress than those without. These studies suggest that there are genotypes with current populations of corals that may be selected under regimes of increasing temperature. What is clear, however, is that change towards a population dominated by these genotypes may still be a slow process and may depend on the stabilization of sea temperatures.

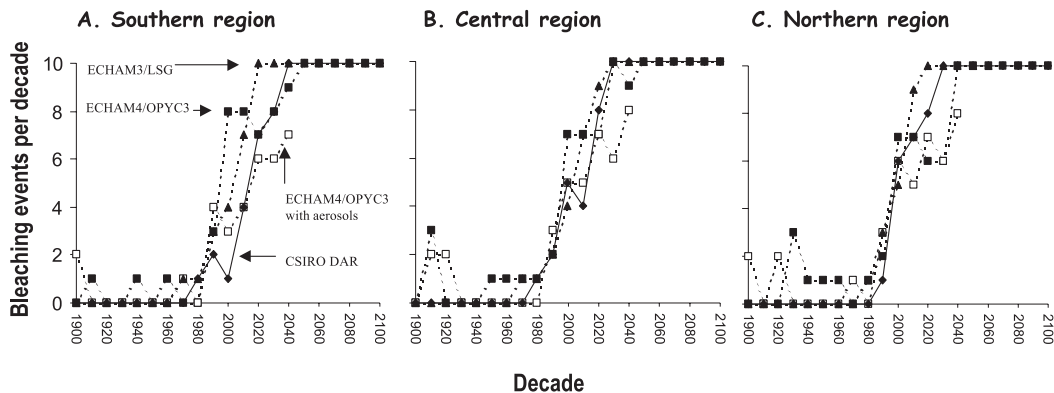


Fig. 11. Number of times per decade that predicted temperatures (see Fig. 10) exceed coral threshold levels (bleaching events) for (A) southern, 23.5°S, 149.5°E, (B) central (18°S, 147.5°E) and (C) northern (11°S, 143°E) localities on the Great Barrier Reef. Models: ■ ECHAM4/OPYC3; □ ECHAM4/OPYC3 with aerosol effect added; ▲ ECHAM3/LSG; and ◆ CSIRO DAR GCM.

In the case of reef-building corals, genes flowing from reefs at warmer latitudes will also influence the rate of change. Currents flowing from latitudes that are warmer may be crucial in the rate of change within a community of corals. These observations do not, however, give us reason to believe that populations of corals and their zooxanthellae will be able to shift rapidly to contain individuals that are better able to stand the increase in temperatures across tropical oceans. Such changes to population structure are likely to take several hundred years. If the close proximity of corals to their thermal maxima is due their inability to respond to the 1°C increase in SST over the past 100 years, then we must conclude that there has been little response from reef-building corals to the changes over those 100 years. The multiple recurrence at the same sites of bleaching events over the past 20 years (some coral reefs have bleached during every major bleaching episode) strongly suggests that populations are not rapidly changing their genetic structure to one dominated by more heat-tolerant individuals.

A second way that corals might increase their survival is to change their zooxanthellae for more heat-tolerant varieties ('Adaptive bleaching hypothesis', Buddemeier and Fautin 1993). Recent evidence suggests that zooxanthellae represent a highly diverse group of organisms (Rowan and Powers 1991; Loh *et al.* 1997). Although this idea has attracted much discussion, it is currently not well supported by critical evidence. The key observation—that corals when heat stressed expel one variety of zooxanthellae and take on another more heat-tolerant variety *while* the heat stress is still present—has never been made. The observation that corals may have a variety of different types of zooxanthellae in the one colony and experience the selective loss of one type during temperature stress (Rowan *et al.* 1997) does not necessarily demonstrate that bleaching is adaptive. Again, if the tips were re-populated by a heat-tolerant form of zooxanthellae during the period in which the stress was present, then the adaptive bleaching hypothesis might have some basis.

Several other features of bleaching that argue against its being adaptive. One of the premises of the Adaptive Bleaching hypothesis is that zooxanthellae of one type are expelled from the host in preparation for being replaced by another variety. Most studies that have measured the concentration of zooxanthellae remaining in bleached corals have found that bleached corals (even the whitest) still have substantial concentrations of the original population of zooxanthellae (10^3 cells cm^{-2} , Hoegh-Guldberg and Smith 1989a; Hoegh-Guldberg and Salvat 1995). This suggests that bleaching has more to do with expulsion of damaged zooxanthellae and their host cell (Gates *et al.* 1992, but see discussion in Brown 1997a) than with the complete removal of one genotype. This does not preclude the possibility that the diversity of different types of zooxanthellae might have a very important role in influencing the rate at which populations of reef-building corals evolve towards greater heat tol-

erance. However, there is no evidence that corals bleach specifically to exchange one genotype of zooxanthellae in their tissues for another.

Acclimation

Corals and their zooxanthellae are able to acclimatize to a wide range of changes in the environment that may vary on a diurnal, weekly or even yearly basis (Gates and Edmunds 1999). Responses to changes in the light environment is a good example. Zooxanthellae acclimatize to higher light intensities during the day by modifying the concentration ratios of quenching xanthophylls (Brown *et al.* 1999), which in turn modify the efficiency of the light reactions (Hoegh-Guldberg and Jones 1999); these changes take a few hours to occur. Over longer periods, zooxanthellae can acclimatize their photosystems to changes in the light environment by regulating the amount of chlorophyll per cell and, hence, the harvesting of light being carried out in a zooxanthella (Falkowski and Dubinsky 1981). Similar modifications are likely to occur with the change in light intensity from summer to winter. As with all physiological systems, there are limits to the extent to which organisms can acclimatize. For example, beyond a certain depth, light intensities are so low that no amount of physiological acclimation by reef-building corals and their zooxanthellae will allow them to live there.

Acclimation to temperature is no different from acclimation to other variables. Reef-building corals live within a thermal range in which they can optimize their physiological performance at set temperatures. If water temperatures are slowly increased, the temperature at which corals bleach can be increased (R. Berkelmans, Great Barrier Reef Park Authority, personal communication; Yang Amri and Hoegh-Guldberg, unpublished). If temperatures are decreased, however, physiological performance will slowly shift back to the original state. These changes include adjustments to the expression of proteins such as heat shock proteins (hsp 70, Sharp *et al.* 1997) and other physiological systems as discussed by Brown 1976b, Gates and Edmunds (1999).

Despite their ability to acclimatize to changing environmental conditions, reef-building corals do not appear to have acclimatized to the rapid increases in sea temperature over the past 20 years. There is no broad pattern suggesting that corals are better at coping when their maximal temperatures are exceeded. During the six major episodes of bleaching, some regions experienced bleaching events every time (Brown 1997a; Berkelmans and Oliver 1999). Corals seem to be just as close to their thermal limits as they were at the beginning of the 1980s, suggesting that acclimation (as well as adaptation) does not seem to have occurred to any great extent. If corals were acclimating (or adapting), then we should see a reduction in the gross extent of bleaching across reefs. The fact that this has not occurred suggests three possibilities: (a) the sporadic and seasonal nature of thermal

stress is such that acclimatory changes do not occur to any extent as thermal stress sets in, (b) the extent to which corals and their zooxanthellae can acclimatize has been exceeded, and/or (c) the rates of change in sea temperature are too fast for adaptation to occur in time.

It can be argued that the complex and sporadic nature of the rise in sea temperature coupled with the variation due to season and El Niño–Southern Oscillation disturbances make acclimation by corals extremely unlikely. Physiological changes during acclimation may also take days and will only remain in place as long as conditions stay the same (Withers 1992). Acclimatory states will change if the environment changes. At present, temperatures exceed the thermal thresholds of corals for part of the year only and are followed by a seasonal decline in temperature; cooler years also usually follow. These two features mean that any thermal acclimation that has occurred during a bleaching year will be lost by the time thermal maxima are exceeded next time. This leads to the second point: although corals and their zooxanthellae may have substantial abilities to acclimatize to changing conditions (Brown 1997b; Gates and Edmunds 1999), there are genetic limits to acclimatization. This may be the reason behind the increase from 1979 onwards in the tendency of reefs to bleach. Increasing sea temperatures have brought corals closer to the limit of their ability to acclimatize over the past 100 years. Any increase above this limit leads to the degeneration of the zooxanthellae and to bleaching.

The rapidity of the changes in the thermal environment may also be a serious challenge to reef-building corals and their zooxanthellae. Much slower temperature changes (e.g. 5–7°C over 5000–7000 years) occurred during the last transition from glacial to post-glacial climates (Schneider 1989; Folland *et al.* 1990) yet were accompanied by dramatic changes in local fauna and flora due to either extinction or migration. Similar changes have been noted for some coral assemblages: Pandolfi (1999) reports the rapid extinction of two species of widespread Caribbean corals (*Pocillopora cf. palmata* and *Montastraea ‘annularis’* species complex), which appears to coincide with the reduction in sea level at the last glacial maximum (18 000 years BP). Pandolfi (1999) proposes that the rapid reduction in habitat at this time for both species may have fallen below a critical threshold size such that coral metapopulation structure may have become critically disrupted.

Broad geological overviews (e.g. Brown 1997b) do not negate the possibility that reefs may decline as environmental conditions change. Coral species have survived greater changes over geological time and are unlikely to be forced into extinction by the projected changes to sea temperatures (Brown 1997b). Hence, the issue is not that corals will become extinct as a result of the projected increases in sea temperature. The projected increases in sea temperature will cause the condition of coral reefs to be severely compromised over the next several hundred years at least. Although short in geological time, this time scale is significant to the

present human use of coral reefs. This is perhaps the key issue associated with the present rates of change in the environment surrounding coral communities.

Consequences of an increased frequency of bleaching

How coral reef ecosystems will change in response to the reduced viability of reef-building corals is a complex question. In theoretical terms, a huge number of endpoints are possible, given the number of interactions that make up an ecosystem as complex and diverse as a coral reef (Hughes and Jackson 1985; Hughes 1989; Tanner *et al.* 1994). Lessons from the past 20 years of mass bleaching, however, have allowed some important insights into the effects to be expected under future changes to tropical sea temperature (Glynn 1993).

Increased coral mortality

One of the most direct effects that coral bleaching has on corals and coral reefs is that affected organisms tend to die at greater rates. Estimates of mortality following mass bleaching range from close to zero in cases of mild bleaching (Harriott 1985) to close to 100% as seen in some shallow-water reefs in Indonesia (Brown and Suharsono 1990) and eastern Pacific reefs following the 1982–83 event (Glynn 1990). Mortalities following mass bleaching in the Central and Western Pacific in 1991 and 1994 have been as high as 30–50% of living corals (Salvat 1991; Gleason 1993). Mortality appears to increase with the intensity of the bleaching event, which is determined by how much and how long temperatures remain above the maximum mean summer temperatures.

Although scientific reports are still in the process of being published, the 1998 bleaching event has been followed by high and perhaps unprecedented mortality. Mortalities on the Great Barrier Reef have been recorded at 80–90% in some sites such as reef crest sites at One Tree Island at the southern end of the reef (Yang Amri, unpublished). Corals of some genera (e.g. *Pocillopora*) have become hard to find (S. Ward, R. Jones and G. Beretta, personal communication). There have been substantial mortalities among corals in the central Great Barrier Reef (Baird and Marshall 1998; Marshall and Baird 1999). Mortality was family specific (similar to that noted by Glynn 1993 and Hoegh-Guldberg and Salvat 1995) with staghorn corals (Acroporidae) being the worst affected. Bleaching affected all colonies of *Acropora hyacinthus* and *A. gemmifera* and 70–80% were dead 5 weeks after the onset of bleaching. An indication of the severity of the 1998 bleaching event on the Great Barrier Reef is the fact that corals as old as 700 years died. Given that these corals can grow to >1000 years old, it has been suggested that 1998 was one of the most severe events in the past several hundred years (ISRS 1998b).

Data from other localities (mainly personal communications) suggest similar patterns of mortality: French Polynesia (J. Jaubert), Maldives (W. Allison), Indian Ocean (D. Obura,

pers. comm., Wilkinson *et al.* 1999), Indonesia (M. Erdmann), north-western Australia (L. Smith and A. Heyward). Bleaching has been followed by mortalities of 20–100% of corals. Acroporids are consistently the worst affected, with the long-lived *Porites* being the least affected (CHAMP Network 1999; Hendee 1998).

The mortality of corals following a bleaching event is proportional to the length and extent to which temperatures rise above summer maxima for any locality. There is little doubt that present rates of warming in tropical seas will lead to longer and more intense bleaching events. Given the behaviour of reefs over the past 20 years, most indicators point to the fact that mortality rates are likely to rise within the next few decades to levels that may approach almost complete mortalities. In 1998, the greatest mortalities coincided with the warmest sea temperatures. The increasing frequency of bleaching events also has implications. The abundance of corals will be severely affected if bleaching events kill the adults before they are able to mature and reproduce (Hoegh-Guldberg and Salvat 1995). For example, acroporid corals take ~4–5 years to mature (Harrison and Wallace 1990). Bleaching events at present occur on average every 4 years. If the frequency continues to increase, the logical prediction is that most acroporids will fail to reach maturity and hence reproduce. The problem is exacerbated for corals that take longer to mature, and this may eventually select for those corals that are able to reproduce earlier in their life histories (r-strategists) as opposed to those that need to survive longer before they reproduce (k-strategists). This type of selection is balanced against the relative toughness of some long-lived species (e.g. *Porites* spp.), and makes the shift in community structure of corals relatively unpredictable.

Decreased coral reproduction

In addition to killing corals, increased temperature affects coral populations by reducing reproductive capacity (Szmant and Gassman 1990). In a comparison of the fecundity of 200 bleached and unbleached colonies of reef-flat corals at Heron Island after the 1998 bleaching event, bleaching reduced reproductive activity in most reef-flat corals examined; bleached colonies of many important reef-flat species (*Symphyllia* sp., *Montipora* sp., *Acropora humilis*, *Favia* sp., *Goniastrea* sp. and *Platygyra daedalea*) contained no eggs at all (Ward *et al.* 1998). These bleached corals, even though having recovered their zooxanthellae, did not spawn during the normal spawning period in November. In other prolific reef-flat species (*A. aspera*, *A. palifera*, *A. pulchra* and *M. digitata*) there were significantly fewer eggs in bleached than in unbleached corals (Ward *et al.* 1998). These results are particularly important because they point to a number of insidious effects of bleaching events on corals that may not be immediately evident yet may play a very important role in how coral ecosystems recover. Lower numbers of reproductive propagules after bleaching events may lead to even lower rates at

which coral populations will re-establish themselves. Persistent bleaching events such as those predicted for 20–40 years' time may mean that corals that are not killed will fail to reproduce—with obvious consequences.

Hoegh-Guldberg, Harrison and co-workers have shown experimentally that the temperatures at which corals bleach also slow the development of gonads within corals and interrupt a number of other key processes (e.g. fertilization, Harrison and Ward, unpublished). The significance of these results is considerable. Although established corals may recover from some bleaching events, the number of recruits may be affected. Already, there is field evidence that recruitment may completely fail after severe bleaching events such as that experienced in the Indian Ocean. A. Heyward, L. Smith (personal communication) and co-workers at the Australian Institute of Marine Science noted very low recruitment during the exceptionally warm periods off the west coast of Australia at Karatha in 1998.

Changes in reproductive condition are likely to affect the distribution and abundance of reef-building corals, which is important for determining how reefs might recover following disturbances. Differences in the connectivity of reef systems and the life histories of corals are crucial for determining patterns of recovery or decline in Caribbean reef systems (Hughes and Tanner 2000). Recent evidence that coral populations may be largely self-seeding despite relatively high levels of genetic connectivity (Ayre and Hughes 2000) also challenges the idea that reef systems may rapidly be repopulated after the removal of adult corals; for a wide range of reefs across the Great Barrier Reef, larval dispersal is surprisingly limited (Ayre and Hughes 2000). This is especially exacerbated for corals that brood or have short-lived larval stages. Other insights are changing the view that the supply of new recruits to a reef may be independent of the health or abundance of the parent generation on a particular reef. A large-scale study (Hughes *et al.* 1999) has shown a close correlation between the fecundity of adult corals and the establishment of larval recruits to a particular site: e.g. variation in space and time of the fecundity of three common *Acropora* species explained most of the variation (72%) in acroporid recruitment. The dependence of recruitment on the size and health of the adult population suggests that the direct effects of temperature (or any anthropogenic factor) on the fecundity of corals will have direct effects on the abundance of new recruits and hence of adult reef-building corals. These influences of thermal stress on the reproductive and population biology of corals are likely to be important in understanding the abilities of reefs to recover from thermal events like those seen in 1998. However, despite their importance, these effects are only partly understood and should be a priority of future studies.

Reduced reef productivity and growth

Although mortality might not always eventuate, reef-building corals that undergo bleaching have reduced growth, calcifi-

cation and repair capabilities following bleaching (Goreau and Macfarlane 1990; Glynn 1993; Meesters and Bak 1993; Yang Amri and Hoegh-Guldberg, unpublished). The primary effect of increased temperature is the loss of zooxanthellae from reef-building corals and other symbiotic invertebrates. As zooxanthellae are the principal engine of primary production in these organisms, the rate of photosynthetic productivity of bleached reef-building corals and other symbiotic organisms decreases dramatically (Coles and Jokiel 1977). This has a quite substantial influence on overall reef productivity because reef-building corals contribute a substantial proportion of the total productivity of coral reef ecosystems (Muscatine 1980, 1990).

The photosynthetic activity of zooxanthellae is also the chief source of energy for the energetically expensive process of calcification (Muscatine 1980, 1990). The reduced ability to grow and calcify may also translate into a reduced ability to compete for space with other organisms such as macroalgae, which may eventually eliminate reef-building corals from particular reefs. Changes in community structure have occurred in coral reefs in the Caribbean and eastern Pacific (Glynn 1993; Hughes 1994; Shulman and Robertson 1996). In each case, community structure has moved away from communities dominated by reef-building corals to communities dominated by macroalgae.

Additional complications: changes in the aragonite saturation state of sea water

Pittock (1999) points to a range of factors associated with climate change that are likely to influence the development of coral reefs. Principally, two other factors are identified as important in addition to increased sea temperature: decreased alkalinity and increased sea level rise. The addition of CO₂ above a solution will lead to changes in the concentration of chemical species such as protons (increasing acidity) and carbonate ions. It has been predicted that increases in the CO₂ concentration in the atmosphere will decrease the aragonite saturation state of sea water in the tropics by 30% (Gattuso *et al.* 1998; Kleypas *et al.* 1999b). This would be expected to decrease the calcification rate of corals and other organisms by 14–30% by 2050. The ability of organisms to acclimate to these changes, however, is unknown. Coral reefs represent a balance between calcification and erosion. Normal rates of deposition are high (up to 20 cm year⁻¹) compared with rates of reef growth (1 cm year⁻¹, Done 1999). This suggests that the rate of physical and biological erosion is huge and that a decrease in the rate of calcification of as little as 5% will lead to a net loss of calcium carbonate.

The implications of a net loss of deposited calcium carbonate from the reef systems that protect coastlines are enormous. A reduction in coastal protection due to weakened or rapidly eroding coral reefs could adversely affect millions of human dwellings and substantial proportions of coastal habitats such as mangroves and seagrass beds that support fisheries and provide crucial nursery areas for up to 90% of all

commercial species.

Coral growth and productivity also interact with changes in sea level, another consequence of global climate change. Best estimates suggest that sea level has risen by as much as 25 cm over the past century, with estimates of sea level rise in the next 100 years approaching 95 cm (Pittock 1999). The requirements of reef-building corals and their zooxanthellae for light confine corals to the upper layers of tropical oceans. Changes in sea level will cause reef ecosystems at the depth limit of coral growth to experience light conditions that will no longer sustain coral growth. Consequently, coral communities at these depths would be expected to disappear. As sea levels rise, however, new spaces for coral growth will become available at the upper regions of coral growth.

Predictions that coral reefs will drown as a result of sea level change are not without debate. Fast growing coral species such as members of the genus *Acropora* add up to 20 cm per year (Done 1999) to their branch tips and hence will have no trouble keeping pace with sea level change. The problem becomes considerable for slower growing species; rates of the rise in sea level (0.95 cm per year) begin to match upward growth rates in *Porites* (~1 cm per year, Barnes 1973; Barnes and Lough 1989). If growth rates are reduced by thermal and other stresses, then the sea level change expected under even moderate global climate change will present additional challenges for coral reefs in the future. However, coral calcification rates do not translate directly as reef accretion, which is about 100 times slower; rising sea level may lead to faster and hence less-consolidated reef accretion. This in turn may reduce structural strength of coral reefs and hence make them more vulnerable to storms and other erosional forces.

Interaction between sea temperature rise and other anthropogenic effects

The loss of vitality of reef-building corals is also likely to influence how coral reef ecosystems respond in the face of other anthropogenic influences. Factors such as eutrophication, increased sedimentation, tourism and destructive fishing practices may interact with global climate change to produce new and potent synergistic effects (Wilkinson and Buddemeier 1994; Wilkinson 1999, this volume). Changes in sea temperature can combine with other factors to completely destroy reefs (e.g. Goreau 1992) including those in the Caribbean (e.g. Hughes 1994). Increased rates of coral disease such as Black Band disease (Edmunds 1991), the mass mortality of diademid sea urchins (Hughes *et al.* 1987) and outbreaks of predators such as crown-of-thorns starfish (*Acanthaster planci*; Moran 1986) may also be linked to reef disturbances related to increased sea temperatures. Influences of increased temperature may be subtle and involve such things as the temperature-related death of coral 'crustacean guards' (normally protecting corals from predation by starfish, Glynn 1983) or more rapid development of larval crown-of-thorns starfish which is temperature-dependent (Hoegh-Guldberg and Pearse 1995).

Although hard to prove, these possible connections suggest that there are a myriad ways that reefs may or may not change in the face of warmer conditions in tropical seas in the future.

Changing community structure

Reef-building corals are not all equally susceptible to the influence of increased temperature. For example, some species such as the massive corals *Porites* spp. are relatively resistant to temperature stress, and if they do bleach they tend to recover with little or no increase in overall mortality (Salvat 1991; Gleason 1993). In contrast, the staghorn corals (*Acropora* spp.) show a greater sensitivity to slight increases in water temperature (but see Glynn 1993), and up to 95% of colonies may bleach (Salvat 1991; Gleason 1993; Hoegh-Guldberg and Salvat 1995) and die in the 3–6 months following the period of temperature stress (Salvat 1991; Gleason 1993).

Interspecific differences in resistance of corals may relate to type of zooxanthellae and the light environment within the tissues of the coral (see Table 1, point 1b). Mass bleaching episodes have the potential to dramatically alter the species richness of coral reef communities (Gleason 1993; Glynn 1993). Local extinction of coral species (e.g. Glynn 1988, 1990) and one near-global extinction of a hydrocoral species (Glynn and de Weerd 1991, de Weerd and Glynn 1991) have been reported. How changes in species composition of reefs will affect long-term stability of coral reefs is unclear but has been reviewed by Done (1999).

Done (1999) outlines four possible scenarios for coral reef systems under the growing stresses of the addition of CO₂ and other greenhouse gases to the earth's atmosphere. These scenarios are:

(a) *Tolerance*: it is assumed that corals and other symbiotic organisms can acclimatize to the changes in aragonite saturation state and in SST, and hence that nothing changes within reef communities. While probably involved in the early stages of environmental change, two aspects need to be added to the discussion of this point. Firstly, current projections suggest that tropical sea-temperatures will keep rising over the next century at least. Secondly, there are genetic limits to acclimation and hence tolerance.

(b) *Faster turn-over*: it is assumed that coral reefs experience increases in mortality that reduce life expectancy; the same species are there but communities shift to a younger age structure.

(c) *Strategy Shift*: it is assumed that hardier species (e.g. *Porites* spp.) replace less hardy species (e.g. *Acropora* spp.). This is probably already starting to operate, with differential mortality in many reefs over the past 20 years (e.g. Hoegh-Guldberg and Salvat 1995) and increasing rarity of some species (e.g. Glynn and de Weerd 1991; de Weerd and Glynn 1991).

(d) *Phase shift*: it is assumed that corals are replaced altogether by another group of organisms (e.g. macroalgae). This has been reported for some areas of the Caribbean by Hughes (1994), Shulman and Robertson (1996), Aronson *et al.*

(1999) and Precht and Aronson (1999). Ultimately, if sea temperatures are not constrained, and corals are unable to acclimatize or adapt, coral communities in all parts of the tropics will almost certainly undergo phase shifts in the short term (i.e. next few decades or centuries). Once these communities have shifted, they would be expected to require a long time to return to their original states.

Consequences for organisms other than reef-building corals

Reef-building corals provide much of the primary productivity of coral reef ecosystems. Solar energy captured by the zooxanthellae of corals is released directly to the water column as mucus or is consumed directly by invertebrate and fish corallivores. In addition to providing much of the primary energy, the activities of reef-building corals also provide the primary shelter for the majority of organisms associated with coral reefs (Muscatine 1980; Crossland *et al.* 1991). Consequently, reductions in the abundance and diversity of reef-building corals are likely to influence the majority of other coral reef organisms. Fishing yields will be vastly reduced as reef viability decreases (Carte 1996; Munro 1996), leading to much-reduced yields of protein for dependent human populations. Tropical fishery yields are already on the decline worldwide in response to many other anthropogenic factors, and present problems may be exacerbated by the projected increase in tropical sea temperature.

The effects of reducing the productivity of reef systems on birds and marine mammals are expected to be substantial. There are, however, few if any studies that have measured the impact although there are accounts of sea bird mortalities and reduced sea turtle conditions associated with severe El Niño events. On Heron and One Tree islands at the southern end of the Great Barrier Reef, for example, nesting by the black noddy tern (*Anous minutus*) failed in 1998 and this was coupled with high adult mortality. The reduced productivity of coral reefs during the earlier part of the year may have been responsible for reduced populations of fish prey and hence increased starvation of these island dwelling birds (Hoegh-Guldberg, personal observation). Although unsupported by rigorous study at this point, these observations suggest that considerable 'downstream' effects may be felt by organisms high in the food chain as reef productivity is reduced.

The fate of the Great Barrier Reef over the next 50 years

The Great Barrier Reef, the world's largest continuous coral reef, consists of 2100 km of interconnected coral reef and was proclaimed as a World Heritage Area in 1975. The Great Barrier Reef Marine Park Authority (GBRMPA) was established to manage the largest marine park system in the world.

As elsewhere in the tropics, land and sea temperatures have been increasing within the Great Barrier Reef Marine Park. Jones *et al.* (1997) noted a significant increase in annual summer and winter air temperatures around Magnetic Island

(an inshore reef of the central section of the Great Barrier Reef) since 1950 and postulated that unusually high air temperatures drove temperatures upward in shallow waters of the reef. Aerial surveys across the reef during March and April 1998 revealed that inshore reefs were the worst affected by bleaching (Berkelmans and Oliver 1999), reflecting the differences in physical factors between inshore and offshore reefs. Using *in situ* measurements supplied by GBRMPA, and data from the Global Ocean Surface Temperature Atlas (IGOSTA; 'ships of opportunity') plus other data sets from 1903–94, Lough (1999) showed that SSTs within the reef park have steadily increased over the past 100 years and that SSTs in early 1998 were the warmest in 95 years of instrumental data. The extent of warming over the past century is $\sim 1^\circ\text{C}$ and hence is similar to that being reported for other tropical localities worldwide (Table 2). The greatest rate of warming on the Great Barrier Reef has occurred at the southernmost localities; it has increased over the past 30 years and is now well over 1°C per century (Table 3, Lough 1999).

SSTs are predicted to exceed the thermal threshold for corals in IPCC scenario A (IS92a) and bleaching to surpass the 1998 event within the next 20 years (Fig. 10); from 2020 onwards, the average bleaching event is likely to be similar or greater than the 1998 event.

The early events during the development of the Great Barrier Reef are described above. As a result of the occurrence of the highest thermal anomalies ever seen (A. E. Strong, 10 February 1998), 67% of inshore reefs on the Great Barrier Reef had high levels of coral bleaching ($>10\%$), 25% of inshore reefs had extreme levels of bleaching ($>60\%$). A large proportion ($>14\%$) of offshore reefs also showed high levels of bleaching (Berkelmans and Oliver 1999). Australian coral reefs other than the Great Barrier Reef were similarly affected; on Scott Reef off the north-west coast of Australia, hard and soft corals decreased in abundance from 30–60% cover to $<10\%$ at most sites (Smith and Heyward, personal communication).

Work is in progress to ascertain how these sites will recover from impaired reproduction and mortalities of up to 90–100% of all affected corals in some places. Estimates of the length of time needed for recovery range from 10 to 30 years (Hughes 1994; Connell *et al.* 1997; Done 1999) and depend heavily on the frequency and intensity of bleaching events. There is probably also a strong latitudinal effect; reefs at higher latitudes and hence lower sea temperatures are likely to take longer to recover. The frequency of bleaching events in the Great Barrier Reef region is predicted to increase by as much as 1.6–1.7 more events per decade (slope of events per decade *v.* time in Fig. 11) until it reaches 10 per decade by the year 2030. On this basis, the reefs are likely to be maintained in an early successional state or to experience the more serious Phase Shift outlined by Done (1999), with a shift to communities dominated by organisms other than reef-building corals (e.g. macroalgae). Given the patterns reported by Berkelmans and Oliver (1999) for the susceptibility of reefs

on the Great Barrier Reef to local warming effects, the inshore reef systems would be expected to show the first signs of a move away from being dominated by reef-building corals.

Conclusions

Even under moderate greenhouse scenarios (IS92a—a doubling of current greenhouse gas concentrations by 2100), present and future increases in sea temperature are likely to have severe effects on the world's coral reefs within 20–30 years. Most coral reef systems are predicted to experiencing near-annual bleaching events that will exceed the extent of the 1998 bleaching event by the year 2040. Some coral reefs (e.g. Caribbean, South-east Asian) will reach this point by 2020. Cooling by anthropogenic aerosols will have little effect on the time that the endpoint is likely to be reached. On the Great Barrier Reef, expected changes lie between the rapid rates expected in the Caribbean and South-East Asian reefs and the somewhat slower changes of the Central Pacific. A better understanding of the capacity for corals and zooxanthellae to adapt to these rapid and on-going changes is required. Present evidence, however, suggests that corals and their zooxanthellae are unable to acclimate or adapt fast enough to keep pace with the present rapid rate of warming of tropical oceans. If the mortality of reef-building corals continues to increase, changes in the distribution of corals will almost certainly occur. Given the central role of corals and zooxanthellae in the structure and function of coral reefs, these changes are likely to have severe and negative effects on the health of coral reefs world-wide by the middle to end of next century. The ecological and economic effects of these changes have not been properly assessed and should be a priority of future research. If, however, the scenario presented in this paper continues to be supported, then a rapid reduction of greenhouse gas emissions (60–80%, Pittock 1999) over the next decade must be put into effect immediately.

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